REPRODUCTIVE TIMING OF PASSERINES IN URBANIZING LANDSCAPES

DISSERTATION

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By

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ABSTRACT

We live on an urbanizing planet where development profoundly impacts ecological communities, including those within protected natural areas. Within this context, effective conservation of biodiversity ultimately requires that ecologists understand both the patterns and mechanisms of urban-associated influences on native plant and animal communities. While a growing body of literature probes the effects of development on community structure and composition, more subtle behavioral and demographic consequences of urbanization remain generally overlooked. One key example of a neglected consequence of urbanization is seasonal timing of life cycle events, particularly the tendency of many urban birds to breed earlier in the spring than their rural-breeding counterparts. The overall objectives of this dissertation were to (1) describe the phenological and biological differences in avian reproduction in urban and rural forests, (2) identify the underlying ecological mechanisms responsible for observed patterns, and (3) identify the demographic consequences of phenological shifts in reproduction. To do this, I studied common plants and two focal bird species, Northern Cardinals (*Cardinalis cardinalis*) and Acadian Flycatchers (*Empidonax virescens*), in riparian forests embedded within landscapes along a rural-to-urban gradient in central Ohio, USA between 2001-2007.

As a first step to understanding avian reproductive phenology, I examined vegetation phenology and, specifically, evaluated two hypotheses that could account for advanced green-up in forests along an urban to rural gradient: advanced phenology within individual species or differences in woody plant community. I was particularly interested in spring leafing phenology of *Aesculus glabra* Willd. (Ohio buckeye), *Lonicera maackii* (Rupr.) Herder (Amur honeysuckle), and *Acer negundo* L. (box elder) in eleven forests spanning an urban to rural gradient in central Ohio, USA. These three species are well represented in all study sites, are relatively early leafing species, and are used as nesting substrates by the focal bird species. From February-April 2006, I monitored these species, recorded woody plant composition, and documented daily minimum and maximum temperatures at each site. There was an overall pattern of advanced phenology (e.g., bud break, leaf elongation) within species in more urban landscapes which might be associated with temperatures. More importantly, there was evidence for shifts in woody plant communities along the urbanization gradient, mainly driven by the abundance of *L. maackii,* an invasive exotic species, in the more urban forests. Both because leaves of *L. maackii* emerge weeks earlier than native woody species and the shrub is very abundant in urban forests, the earlier green-up of urban forests may be partly a consequence of invasion by this species.

Despite several published accounts describing patterns of advanced reproductive phenology in urban versus rural populations of birds, the causes and consequences of altered reproductive phenology associated with urbanization are not well understood. Studying Northern Cardinals in urban and rural forests in central Ohio, USA between 2004-2007, I found that the earliest dates of both nesting activity and clutch initiation

were about seven to ten days earlier in urban versus rural sites. Temperature accumulations in March best predicted the timing of breeding, whereas vegetation phenology, site-level survival, and the availability of nest sites failed to explain variation in breeding phenology of cardinals. There was no apparent benefit in terms of number of fledglings produced over the breeding season based on initiation of the first nesting attempt. On a per nest basis, the expected number of fledglings produced per successful nest remained constant over the course of the season at ~1.7 fledglings per successful nest. The absence of a benefit to early breeding may be the consequence of the tendency for nest survival to increase over the breeding season.

Because late winter temperatures appeared to contribute to the advanced breeding of the resident cardinal, I asked if Neotropical migratory birds would exhibit the same phenological shifts given that they do not return to breeding grounds until much later in the spring. From 2001-2007, Acadian flycatchers were studied in 35 different forests spanning an urban to rural gradient in central Ohio, USA. The general pattern of breeding phenology was opposite that described for most resident and short-distance migrant birds. At higher levels of urbanization, dates of arrival and clutch initiation were later and cessation of breeding was earlier than in forests within more rural landscapes. The underlying causes of the phenological differences are less clear but may be related to disproportionate settlement of urban forests by small 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.

In light of the delayed breeding of urban flycatchers compared to rural individuals, I examined the possibility that phenological shifts were driven by habitat selection and, specifically underutilization, of urban landscapes. Urban forests provide a potential situation where such underutilization of habitats might occur because (1) urban forests often support lower densities of Neotropical migratory birds than rural forests and (2) anthropogenic disturbance and habitat alterations are likely to result in mismatches between cues typically used in habitat selection and actual habitat quality. I developed a habitat selection model to predict fitness and settlement patterns one would expect to observe if flycatchers underutilized urban forests. Based on model predictions and empirical field data, I suggest that urban forests are not underutilized and may even be overused. This finding strongly suggests that the pattern of reproductive phenology in the Acadian flycatcher resulted from behavioral processes driven by the low quality habitat offered by urban forests.

Although my research showed that urbanization can dramatically affect the reproductive phenology of native bird species, it also highlighted several key research needs. First, additional study is needed in order to understand why urban habitats represent low quality habitat for Neotropical migratory birds. Second, research is needed to understand the causes and implications of seasonal variation in nest survival. Seasonal variation was present in both focal species but affected them differently. Third, seasonal patterns in food availability should be evaluated to determine if birds attempt to time reproduction to match food resources and if urbanization alters the timing of food availability. Finally, assessment of the survival and recruitment patterns based on

landscape context and timing of fledging will be important for understanding population dynamics and predicting population level effects of variation in timing of breeding.

This research provides important refinements on our understanding of avian ecology in urbanizating landscapes. In particular, the breeding phenology of both focal species were influenced by urbanization but with different mechanisms, trends, and fitness effects. Earlier breeding by the Northern Cardinal was not associated with production of more fledglings, and was best explained by March temperatures. In contrast the Neotropical migratory Acadian Flycatcter initiated breeding earlier in more rural forests and earlier breeders produced more fledglings. This research demonstrated that urban forests provide low-quality habitat for Acadian flycatchers which in turn influences territory settlement patterns and reproductive timing. Conservation of native bird species in the face of urbanization will need to consider that different species respond differently to urbanization.

DEDICATION

To Beth:
You could not have been more supportive.
Thank you.

I greatly appreciate Aaron Boone who taught me how to hold Northern Cardinals to prevent their biting me. This surely saved me many reddened fingers and knuckles.

I thank my parents who cultivated my interest in the natural world and raised me in a place where I could spend countless hours wandering through the woods.

Finally, I thank my parents, parents-in-law, my sisters, sister-in-law, Aunt Linda and Aunt Joyce for all their support- both material and immaterial- through this process. I am especially grateful for their love and support of Beth, Savannah, J and Lydia. I am sure I will never fully comprehend how invaluable you all were through this process.

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FIELDS OF STUDY

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CHAPTER 1

INTRODUCTION

Urban development is a pressing conservation issue. More so than other land

conversions (e.g., agriculture or agroforestry), the loss of natural areas and intensification

of human activity associated with urbanization are generally permanent on the landscape

given that urban development is typically a terminal land use state (Houghton 1994,

Dobson et al. 1997). While currently about half of the world's population live in urban

areas, by 2050 this proportion is expected to increase to two-thirds of the world's

population (United Nations 2007a). Although the amount of urban land on Earth sounds

deceptively small at ~3% (United Nations 2008b), the amount of the land areas needed to

support urban areas is large. Consequently, the impacts of an urbanizing planet will

increasingly impact the abiotic and biotic processes of our world and ultimately will

constrain our ability to conserve biodiversity (Grimm et al. 2008). In this chapter, I

briefly review how urbanization affects abiotic and biotic attributes of ecosystems and,

ultimately, how this affects the reproductive phenology of birds.

Urban development is associated with tremendous changes in the abiotic

environment. Among the most obvious ways that urban landscapes differ from rural ones

are the creation of structures, transportation and utility corridors, which profoundly

impact biogeochemical cycles including the water cycle, greenhouses gases, etc (Grimm et al. 2008). Urban areas also have altered acoustic (Landsberg 1981, Pheasant et al. 2008) and light (Longcore and Rich 2004) environments both through introduction of novel features (e.g., automobile and industrial noises and street and structure lighting) and manipulation due to the urban structures. For example, tall structures can reduce solar radiation in some places as well as influence sound propagation (Picault et al. 2005). Less obvious are the impacts that urbanization has on climatic patterns, which include the well known phenomenon, the "urban heat island effect," that results in cities with higher average temperatures than surrounding rural areas (Schmidlin 1989, Taha 1997). Further, urban areas also tend to have higher amounts of thunderstorms, less snow and frost cover, and altered wind patterns (Landsberg 1981).

Changes in the abiotic environment are associated with dramatic changes in the biotic environment as well. Most obvious, urban development requires the removal of vegetation and the covering of soil with impervious surfaces thus preventing vegetation growth. Thus, remnant vegetation in urban areas is typically highly fragmented and patchy (Grimm et al. 2008). Further the vegetation communities in developed areas and remnant patches within urban areas are typically highly altered due to direct plantings by humans (Whitney 1980) and increased proliferation of exotic species into remnant patches of vegetation (Borgmann and Rodewald 2005, Vidra and Shearer 2008). The changes associated with the vegetation and the built environment lead to one of the ubiquitous patterns associated with urbanization, namely the decrease in biodiversity (Grimm et al. 2008) and the increasing biotic homogenization of urban areas (McKinney

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2006). In bird communities these changes usually include increased abundances of granivores, exotic species, and non-migratory species with concomitant reductions in insectivores and Neotropical migrants (Marzluff et al. 2001). Besides more obvious changes in community composition, finer-level biotic effects also accompany urbanization. For instance, trophic interactions may be altered through introductions of novel predators (Flux 2007) or elimination of predators (Crooks and Soule 1999). Further, population dynamics also may be altered through changes in mortality or fecundity (Marzluff et al. 2001, Prange et al. 2003, Rodewald and Shustack 2008b). Even behavioral shifts may be prompted by urbanization; for example a historically ground-nesting bird that recently shifted to using elevated nests sites in an urban environment (Yeh et al. 2007).

Another change observed in plant and animal communities associated with urbanization is advancement of spring phenology, which relates to the seasonal timing of life cycle events of plants and animals (Erz 1966, White et al. 2002, Zhang et al. 2004). In plants, advanced spring phenology manifests in earlier spring flowering and leafing dates (Roetzer et al. 2000, Defila and Clot 2003, Lu et al. 2006). In birds, earlier nesting is commonly observed in urban versus rural populations (Erz 1966, Eden 1985, Antonov and Atanasova 2003, Luniak 1988, 2004, Rollinson and Jones 2002). Many of the abiotic and biotic changes associated with urbanization have been implicated in advanced reproductive phenology in urban areas. Potential causes include elevated temperatures, advanced vegetation phenology, altered vegetation composition, increased food availability, anthropogenic light pollution, and greater conspecific or heterospecific

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densities (Erz 1966, Eden 1985, Bowman and Woolfenden 2001, Rollinson and Jones 2002, Antonov and Atanasova 2003, Schoech and Bowman 2003). However to my knowledge, these factors have not been measured at the actual study site concurrent with the documentation of avian reproductive phenology.

The annual timing of reproduction can have important consequences in terms of avian fitness. Birds that breed earlier are generally thought to have an advantage over individuals who breed later. The benefits of initiating nesting early in the spring can arise in several ways including increased clutch size, renesting, adult and fledgling survival, and fledgling recruitment.

Earlier nests tend to have larger clutches (Klomp 1970, Perrins 1970) and fledging rates and egg masses (Arnold et al. 2006 but see Schwagmeyer and Mock 2008). Indeed, decreasing clutch size over the breeding season is a common pattern in single brooded species (Perrins 1970). If birds are able to produce larger clutches by breeding earlier, then this may confer an advantage to reproducing earlier in terms of potential number of young fledged. However, this possibility depends on the reason that clutch size declines over the season. Perrins (1970) suggested that the decline was due to declining food resources as the breeding season progressed. However, other explanations include reduced bird condition for females to produce eggs for replacement clutches. Females may reduce their investment in eggs because of declining probability of nest survival as the season progresses. Another possibility is that later breeding birds may be inherently less able to produce eggs, as more of these low-clutch-producing females are nesting, the overall mean clutch size will decline. Barba et al. (1995) found that Great Tit

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clutch sizes were smaller in nests that were initiated later, though competion with House

Sparrows for nest sites may have contributed to this pattern. See also references in Barba

et al. (1995) for other examples of decreasing clutch size over the season.

In multi-brooded species, the trends in clutch size over the breeding season

generally do not follow the monotonically decreasing pattern observed in single brooded

species. Multi-brooded species often begin nesting very early with clutch sizes

increasing to a peak and then declining throughout the rest of the season, a pattern that

may be driven by food availability for females to produce eggs (Perrins 1970).

Additionally, birds that initiate earlier in the year have more time for renesting

(Barba et al. 1995, Ortega et al. 2006, Murray and Nolan 2007). Renesting allows for

production of more fledglings over the course of the season either by replacing

depredated nests (Faivre et al 2001), fledging multiple broods (Wolfenbarger 1999,

McGraw et al. 2001) or having larger broods (Dow 1982 as cited in Greenwood and

Harvey 1982, Smith and Moore 2005).

Earlier nesting allows juveniles more time to gain experience, improve body

condition, and prepare for migration in the following autumn compared to young from

later nests. Thus juveniles from earlier nests may experience elevated survival (Perrins

1970, Norris 1993, Barba et al. 1995, Møller et al 2006, Vitz 2008). Post-fledgling

survival and recruitment might be the most relevant fitness component related to earlier

seasonal reproduction because the ultimate measure of the fitness of an individual is its

genetic contribution to successive generations. Various proximate measures of this

contribution have included survival of the nest, number of fledglings produced, and

survival of the fledglings, and recruitment of juveniles into the breeding population. Recruitment, though perhaps the best estimate for fitness, is extremely difficult to measure. Fledgling survival is also difficult to quantify and the literature provides few measurements of fledgling survival and recruitment, but Perrins (1970) describes several early attempts to measure fledgling survival and recruitment. For example, Great Tit (*Parus major*), Gannet (*Sula bassana*), and Blackbird (*Turdus merula*) survival to three months post-fledging decreased with increasing nest dates (Perrins 1970). Yet the pattern of higher fledgling recruitment from earlier nests is not ubiquitous and may not remain constant within a population. Møller et. al (2006) found that Artic Tern fledglings recaptured as adults were more likely to be from late nests early in their study (1930s) and from earlier nests late in their study (1990s) suggesting that increased juvenile survival from earlier nests may not be consistently higher than fledgling survival from later nests. Barba et al. (1995) found that fledglings produced by earlier nesting Great Tit (*Parus major*) were more likely (11% of fledglings) to be recruited into the breeding population than fledglings (2%) from later nesting Great Tits. However, in many cases dispersal and survival and recruitment can not be separated.

Adults also could benefit from early completion of nesting by devoting more energy to molting (Morales et al. 2007, Gardner et al. 2008) and preparing for winter or migration (Nilsson and Svensson 1996), which may ultimately promote higher over-winter survival (Wiggins et al. 1998).

Objectives and Chapter Overview

The overall objectives of this dissertation were to (1) describe the phenological and biological differences in the reproductive timing and seasonal productivity of birds in urban and rural forests, (2) identify the underlying ecological mechanisms responsible for the patterns, and (3) identify the demographic consequences of phenological shifts. To do this, I studied common plants and two focal bird species, Northern Cardinals (*Cardinalis cardinalis*) and Acadian Flycatchers (*Empidonax virescens*), in riparian forests embedded within landscapes along a rural-to-urban gradient in central Ohio, USA between 2001-2007.

In chapter 2 (formatted for *Biological Invasions*), I evalutate alternative explanations for why urban forests green-up sooner than rural forests. I demonstrated that there was a pattern for individual species to display advanced leafing phenology associated with urbanization. However, the major driver of earlier green-up appears to be the abundance of invasive, exotic honeysuckle (*Lonicera maackii*). This was an important study to complete first, as both temperature and vegetation phenology were subsequently used as variables for predicting when Northern Cardinals (*Cardinalis cardinalis*) initiate breeding.

In chapter 3 (formatted for *Condor*), I address the question of why Northern Cardinals breed earlier in urban forests and assess the reproductive benefits of their earlier breeding. To do this, I first documented the tendency of birds to breed earlier in urban versus rural forests, and then evaluated several possible mechanisms generating this pattern. While Northern Cardinal breeding was best explained by temperatures, even

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more so than urbanization per se, the benefits to early breeding were not apparent, likely due to increasing nest survival over the season.

In chapter 4 (formatted for *Ecological Applications*) I ask the question, "are urban forests underutilized by Acadian flycatchers?" This is an important question to address for several reasons. While Neotropical migratory birds are typically underrepresented in urban forests, the causes of this pattern are unknown. Recent attention in the literature to mismatches between the cues for habitat selection and habitat quality (e.g., ecological traps and underutilized resources, Gilroy and Sutherland 2007) have emphasized that the ecological literature often fails to sufficiently acknowledge that density within a habitat is not an adequate indication of habitat quality (van Horne 1982). Indeed, lower densities in urban forests could be a result of either low habitat quality or avoidance of high quality habitat. Using a combination of modeling and field data, I found strong evidence that urban forests are not underutilized and are lower quality habitat for Acadian Flycatchers.

Chapter 5 (formatted for *Auk*) represents a similar study as chapter 3 but with a Neotropical migratory species, the Acadian Flycatcher. Thus, I analyzed the pattern of breeding phenology, assessed impacts on related fitness metrics, and determined why these patterns occurred. In many ways the Acadian flycatcher displays opposite responses to urbanization as the Northern Cardinal. I found that the delayed reproduction of the urban flycatchers contrasted sharply with that of the Northern Cardinal. This is an important finding, as delayed reproductive phenology as a result of urbanization has not been previously documented in Neotropical migratory birds.

Study Region and Study Sites

Thirty-five riparian forest stands were studied within the urbanizing landscapes of the Scioto River Watershed in central Ohio (ca. 40N 00' 83W 00') (see Rodewald and Bakermans 2006 for site selection procedure; see Appendices A and B for names of location of sites). Not all 35 sites were used in each study or in each year, however, the woody vegetation communities across all 35 sites appeared similar (Rodewald and Bakermans 2006). Sites were located in mature riparian forest of approximately 70 to 450 meters in width and ≥ 250 m length and along rivers in approximately 20 to 40 m in width. Common overstory trees included sycamore (*Plantanus occidentalis*), boxelder (*Acer negundo*), silver maple (*Acer saccharinum*), sugar maple (*Acer saccharum*), black walnut (*Juglans nigra*), white ash (*Fraxinus americana*), Eastern cottonwood (*Populus deltoides*), American hackberry (*Celtis occidentalis*), and honey locust (*Gleditsia tricanthos*). Common woody understory plants include honeysuckle (*Lonicera* spp.), common spicebush (*Lindera benzoin*), multiflora rose (*Rosa multiflora*), tall pawpaw (*Asimina triloba*), Ohio buckeye (*Aesculus glabra*), and saplings of canopy trees (Leston and Rodewald 2006, Rodewald and Bakermans 2006, chapter 2).

Avian species richness was similar across sites, but community structure showed some associations with urbanization, primarily with Neotropical migratory birds being negatively related to urbanization and resident species being positively correlated with urbanization (Rodewald and Bakermans 2006). Common Neotropical migratory birds included Acadian Flycatcher (*Empidonax virescens*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Red-eyed Vireo (*Vireo olivaceus*), Indigo Bunting (*Passerina cyanea*),

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Baltimore oriole (*Icterus galbula*), and House Wren (*Troglodytes aedon*). Short distance

and resident species include American Robin (*Turdus migratorius*), Cedar Waxwing

(*Bombycilla cedrorum*), Brown-headed Cowbird (Molothrus ater), Common Grackle

(*Quiscalus quiscula*), American Goldfinch (*Carduelis tristis*), Downy Woodpecker

(*Picoides pubescens*), Eastern Tufted Titmouse (*Baeolophus bicolor*), Carolina

Chickadee (*Poecile carolinensis*), White-breasted Nuthatch (*Sitta carolinensis*), and

Northern Cardinal (*Cardinalis cardinalis*) (Rodewald and Bakermans 2006).

Although previous studies in this system have discovered and described many

important aspects of the ecology of riparian forests in an urbanizing landscape, my

dissertation builds upon several key findings. First, we know that abundance of invasive

bush honeysuckle is positively associated with urbanization (Borgmann and Rodewald

2005). My dissertation expands upon this observation to demonstrate that the abundance

of honeysuckle appears to drive a more general vegetation phenological shift associated

with urbanization. Second, elevated temperatures are not only related to Northern

Cardinal abundance (Leston and Rodewald 2006) but also seem to be responsible for

slight advances in leafing phenology (chapter 2) and advances in Northern Cardinal

breeding phenology (chapter 3). Third, previous research has shown that Acadian

Flycatcher density is negatively related to urbanization (Bakermans and Rodewald 2006,

Rodewald and Bakermans 2006), and this relationship seems to reflect the low habitat

quality provided by forests in urbanizing landscapes rather than an incorrect assessment

of habitat quality by the birds (chapter 4). The low quality habitat provided by urban

forests seems to be the main factor leading to abbreviated nesting seasons by Acadian

Flycatchers, primarily through differential habitat selection by individuals of varying quality (chapter 5).

As the planet continues to become more urban, native species will continue to be relegated to progressively smaller areas. Maintaining native biodiversity within cities is likely to become increasingly important and desirable. The results of this dissertation suggest that the impacts of urbanization on birds as mediated through breeding phenology may be relatively minor. Breeding phenology apparently did not influence fitness of Northern Cardinals, rather heavy nest predation may be the main factor affecting this species. While variation in breeding phenology was related to Acadian Flycatcher fitness, it was not directly related to urban-meditated breeding phenology, rather it appeared to be generated by the overall lower habitat quality of urban forests. This suggests that identifying the causes of the reduction in habitat quality in urban areas for Neotropical migratory birds will be a critical step if urban forests are to provide valuable habitat for Neotropical migratory birds.

CHAPTER 2

INVASIVE *LONICERA MAACKII* (RUPR.) HERDER PROMOTES EARLIER GREEN-UP OF URBAN FORESTS

2.1 Abstract

Despite the widespread recognition that urban areas are frequently dominated by exotic

and invasive plants, the consequences of these changes in community structure have not

been explicitly considered as an explanation for the pattern of advanced leaf phenology,

or early green-up, reported in many urban areas. We evaluated two hypotheses that could

account for advanced green-up in forests along an urban to rural gradient: advanced

phenology within individual species or differences in woody plant community. We

monitored the spring leafing phenology of *Aesculus glabra* Willd. (Ohio buckeye),

Lonicera maackii (Rupr.) Herder (Amur honeysuckle), and *Acer negundo* L. (box elder)

in 11 forests spanning an urban to rural gradient in central Ohio, USA. From February-

April 2006, we monitored these species, recorded woody plant composition, and

documented daily minimum and maximum temperatures at each site. We found an

overall pattern of advanced phenology within species in more urban landscapes. Monthly

average minimum temperatures increased with increasing urbanization whereas monthly average maximum temperatures were similar across the urban to rural gradient. We also found evidence for shifts in woody plant communities along the urbanization gradient, mainly driven by the abundance of *L. maackii,* an invasive exotic species, in the more urban forests. Because *L. maackii* leafs out weeks earlier than native woody species and is very abundant in urban forests in our study area, we suggest that the invasion of forests by this species contributes to the earlier green-up of urban forests.

2.2 Introduction

Evidence of spring seems to arrive earlier in cities than the surrounding countryside. Spring flowering and flushes of new green leaves give an overall greener appearance to the city in advance of the surrounding countryside (Defila and Clot 2003, Fisher et al. 2006). In fact, satellite data have shown that green-up may occur in cities as much as 7-10 days earlier and the effects can extend beyond the concentration of developed land area (White et al. 2002, Zhang et al. 2004). Elevated urban temperatures, also called the urban heat-island effect, have often been invoked to explain this pattern. The association between temperature accumulations, a measure of the amount of warming a site experiences, and spring phenology is well established in plants and insects. Phenological models based on temperature can explain much of the variation in phenology from year to year (Mussey and Potter 1997, Chuine et al 2000, Menzel 2002, Schwartz 2003).

When considering differences in green-up across large areas, plant composition, particularly the contribution of invasive plants, is typically not considered. Yet, because each plant species has a specific spring phenology (Augspurger and Bartlett 2003, Schwartz 2003, Pellis et al. 2004), plant composition might strongly contribute to differences in spring green-up among locations. For example, two adjacent areas, one comprised of early leafing species and another of late leafing species would exhibit an overall difference in spring development despite experiencing similar temperatures (Chen 2003). Because urban and rural areas often differ in plant composition (Whitney and Adams 1980, Gaston et al. 2005, McKinney 2006, Godefroid and Koedam 2007), floristics should be considered when examining variation in spring phenology over large areas. Thus, the fact that urban areas tend to be well represented by exotic species (McKinney 2002) may exaggerate phenological differences between urban and rural areas.

Understanding the patterns and causes of advanced green-up is important for understanding ecological implications for altered phenology in urban forests, which are conserved, in part, for their ecological values. For example, phenology of plants is related to that of insects, an important food source for both migrating and breeding birds (Visser et al 1998, 2006). Additionally, because leaf cover may affect the extent to which a bird perceives a potential nest site as suitable, nest site availability for breeding birds may be influenced by plant phenology (Hansell 2000, Leston and Rodewald 2006). Unfortunately, phenological differences among forests in urban and rural landscapes are poorly understood, despite the commonly observed pattern of advanced green-up in urban

compared to rural forests (Fisher et al. 2006). This limited understanding partly derives from the fact that most phenology studies in urban landscapes have been conducted in gardens or the developed matrix (Mussey and Potter 1997, Roetzer et al. 2000, Schwartz 2003, Lu et al 2006). However, advanced green-up in urban forests may be expected to differ from that reported from non-forested situations due to structural differences that may buffer some of the temperature differences normally detected in urban and rural non-forested land (Gomez et al. 1998) as well as differences in species composition.

To understand what may cause earlier spring green-up in urban forests, we evaluated the evidence for two hypotheses.

Advanced phenology hypothesis: Earlier greening of urban compared to rural landscapes is the consequence of advanced phenology of plant species. Therefore, we predict that individual plant species in urban areas exhibit earlier bud-break, leaf emergence, and/or faster shoot development than do the same species in more rural landscapes.

Floristic composition hypothesis: Earlier greening of urban compared to rural landscapes is a product of differences in floristic composition among landscapes, such that urban areas tend to be more extensively represented by species that display earlier spring leafing phenology. Therefore, we predict that the woody plant community in urban forests contains a greater proportion of species and individuals that normally exhibit early leaf flush than do rural sites.

Because of the strong link between spring leafing phenology and temperature and the trend for elevated temperatures in urban areas (i.e., an urban heat island effect), we also examined temperature trends along an urban to rural gradient in order to help inform our interpretation of phenological patterns.

2.3 Methods

Site selection

We selected 11 mature-forest remnants located along rivers in central Ohio, USA. All forested sites were >100 m wide and were selected to represent an urban to rural gradient subject to several logistical constraints (e.g., winter access, permission from landowner). These 11 sites represent a subset of 35 sites that we have used since 2001 to evaluate the response of avian communities to urbanization (Rodewald and Bakermans 2006, Rodewald and Shustack 2008).

Landscape quantification

To quantify the landscape context of each site, we first obtained aerial photos from the county auditors of Delaware, Franklin, and Madison counties, Ohio, USA. All photos were taken between 2002 and 2004. Next, we generated a buffer with a 1-km radius from the center of each site, and digitized the areas of forest, agriculture (including hayfields), mowed (e.g., manicured lawns, golf course, playing fields, etc), and paved areas using ArcGIS 9.1 (ESRI, Inc). Then, we determined the proportion of each cover

type and counted the number of buildings within the 1-km buffer. We used a principal components analysis based on the correlation matrix to reduce these six landscape variables to a single variable that explained ~78% of the variation in landscape composition among sites (eigenvalues for components 1 through 6: 4.691, 0.726, 0.414, 0.097, 0.042, 0.030). Each of the six landscape metrics was highly and significantly correlated with this first component (correlation coefficients: forest = -0.86; agriculture = -0.79; mowed = 0.77; paved = 0.92; roads = 0.97, number of buildings =0.95; all ps<0.005). We used this first component as an index of urbanization and we refer to it as our "urban index." Sites within more urban landscapes have larger urban index values (Table 2.1).

Species composition

We made use of previously established study grids that were either 2 ha (on 7 sites) or 4 ha (on 4 sites) in size. Each grid was situated to maximize the area included between the river's edge and the forest's edge and so the 2-ha area was as compact as possible while maintaining straight-edged grids. Each grid was further divided into 0.25-ha blocks that were as close to square as possible. From a random starting 0.25-ha block, we systematically selected every other block (for the 2-ha grids) or every fourth block (for the 4-ha grids). From the center of each selected 0.25 ha grid, we identified and measured the diameter at breast height (dbh) of every woody stem greater than 3 cm dbh within 11.3-m radius of the center of the plot. We sampled the four sites with 4-ha grids in July of 2006. We sampled the remaining seven sites in July 2007. Time and logistical

constraints prevented us from sampling all 11 sites in 2006. Because our analysis is

focused on counts of woody stems greater than 3 cm dbh we do not believe that sampling

the sites in two consecutive years affected results. We grouped several similar species

together, primarily based on difficulty in identification and similarity of forms. We

combined *Acer saccarhum* and *Acer nigrum*, all *Fraxinus* (ashes), all *Crataegus*

(hawthorns), and all *Quercus* (oaks). For analysis, we divided all woody stems into 2

size classes: <8 cm dbh (small) or ≥8 cm dbh (large). We chose these two size classes

because smaller individuals of the same species often leaf out earlier than larger

individuals (Seiwa 1999, Augspurger and Bartlett 2003, but see Tomita and Seiwa 2004)

and we reasoned that smaller individuals of the same species might contribute more to

earlier leaf-out than larger individuals of the same species. We collapsed the tree species

into a site-by-species matrix with two columns for each species (small and large) and

with each cell representing the counts of stems for that site-and-species combination

(Table 2.2).

Phenology monitoring

In 2006, we attempted to monitor 10 individual honeysuckle (*Lonicera maackii*),

7 individual box elder (*Acer negundo*) and 7 individual Ohio buckeye (*Aesculus glabra*)

at each site. However, some individual plants were excluded from analysis because

several of the marked shoots were eaten or had otherwise died. Plants sampled were

those nearest to randomly located points within grids. A plant was sampled if it had at

least four apparently living branches that could be easily reached (between ~1.0-2.5 m

high). We did not discriminate based on plant height, although most plants that met this criterion tended to be shorter individuals and their crowns were not in the canopy. We avoided branches that were adventitious shoots unless there were no suitable alternative plants. For *A. negundo* and *A. glabra*, we selected the terminal bud from a branch that was closest to each of the four cardinal directions; we marked each stem by tying a small piece of flagging on the stem. For *L. maackii*, we similarly selected four branches, one that was closest to each of the cardinal directions and nearest to 1.5 m in height. We marked the most distal bud on the *L. maackii* by making a black dot with a Sharpie pen on the stem at the base of the bud. The second-most distal bud was marked with two black dots on the stem. *L. maackii* has an opposite bud pattern, so for each shoot we randomly selected either the left or right side bud and then alternated sides for each subsequently sampled shoot.

We created a qualitative coding scale ranging from 0-8 for each species ranging from no growth to completion of leaf elongation (coding modeled after Pellis et al. 2004). Plants were monitored weekly by one of four observers and a code was assigned to each bud. Each observer was provided with photographs and text descriptions of codes, and we periodically reviewed coding by individuals to maximize inter-observer and intra-observer reliability, although we did not quantify reliability. Phenology monitoring ceased when buds completed leaf expansion, i.e. leaf full sized, flattened and in normal growing orientation). In 2006 monitoring began in early February for *L. maackii* and in mid-March for *A. negundo* and *A. glabra*.

Phenological timepoints

We considered bud break for each individual plant to be the first date when at least 75% of the buds displayed some green growing tissue between the bud scales. Leaf elongation was reached when 75% of the leaves on one individual plant were flat and had reached their final growing orientation. For *A. negundo* and *A. glabra*, leaf elongation was defined as when the first full-sized set of leaves from the bud reached this description. For *L. maackii*, leaf elongation was defined as the date by which the first and second set of full-sized leaves had separated from the growing axis. This arbitrary check point for *L. maackii* was selected to allow more time for growth between bud break and leaf elongation, because *L. maackii* grows rapidly and has relatively small leaves. We estimated bud break and leaf elongation dates for each site as the median date when individuals at that site had reached the respective phenophase. We used the site median bud break and site median leaf elongation dates for all analyses. As an additional measure of spring growth, we attempted to take an "instantaneous" measurement of how much growth had occurred between bud break through mid-April. We were unable to measure every plant in the same day in 2006; between 17-19 April we measured the length of shoot growth from each marked bud. We ordered site visits to avoid a bias in site visitation relative to location on the urban index (Spearman's correlation $P = 0.101$).

Temperatures

Three to five digital thermometers (Taylor digital min/max, Taylor USA) were deployed at each of the 11 sites. We selected random locations within each site and

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found the nearest place where we could hide the thermometer from potential vandals as most of the 11 sites were open to the public. Each thermometer sampled air temperatures via a small probe that we tacked to a branch or trunk about 1-1.5m above ground. We attempted to place each probe so that it was out of direct sunlight and had overhead cover (to avoid precipitation accumulation); however, the amount of overhead cover varied and some probes likely received direct sunlight at some times of the day. After we calibrated thermometers to a standard glass thermometer over a 12-h period, thermometers were deployed prior to 31 December 2005.

The digital thermometers store maximum and minimum temperatures for six 24-h periods as well as an ongoing 24-h period. After seven 24-h periods, the oldest period is erased and the ongoing temperatures for the current period are stored. To collect seven days of maximum and minimum temperatures by visiting each site once per week, we recorded the temperatures on the seventh day shortly before the end of the seventh 24-h period. This ensured that we had six complete 24-h periods and one nearly complete (~22-24) 24-h period for the seventh day. To maximize the length of time that temperatures were recorded for the seventh day, we staggered each thermometer's start and end time between ~11:00 and ~12:30 EST (+1 hour later after the start of daylight saving time). This methodology would only be an issue if the minimum or maximum temperature for the current 24-h period had not yet occurred. However, we expected that minimum temperatures would typically occur in the early morning and the maximum temperatures would typically occur in the late afternoon of the previous day. An examination of our data confirms that this pattern held. For various reasons, there were

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occasional days for which the minimum and maximum temperatures were not collected. We filled in these missing days with the average of all the minima or maxima for that same day.

Using the minimum and maximum temperatures from each thermometer for each day, we calculated the daily degree-day accumulation. Degree-days reflect the amount of warming a site experiences and can be calculated with different lower and upper thresholds. Bascially, temperature accumulations are calculated based on daily minimum and maximum temperatures (e.g., (min +max)/2). We calculated the daily degree-day accumulations in two different ways: no lower threshold and 0° C lower threshold, which is commonly used as a lower threshold in phenological studies (Chuine et al. 1999). For a lower threshold of 0° C we replaced the daily minimum temperatures with 0° C whenever the measured minimum fell below 0° C. To calculate the daily degree-days we took the average of the minimum (or 0° C) and maximum daily values. We summed the degree-days over each month to calculate the monthly temperature accumulation. We then calculated the site average monthly minimum and maximum, and temperature accumulations based on the averages and sums from each thermometer for which we had measurements for >93% of days in each month.

Community phenology

Because we collected phenological data on only three species, we characterized the relative phenology of other species based on the literature. For 22 of the 23 most common species (or genera as discussed above), in our samples we located studies or

reports that presented spring leafing (i.e. no flowering references were used) phenology information (Trelease 1884, Lamb 1915, Smith 1915 [based on Lechowicz 1984 figure 4], Ahlgren 1954, Altman and Dittmer 1962, Lechowicz 1984 [figure 1], McGee 1986, Augspurger and Bartlett 2003). Because the studies were performed in different years, and/or locations, and with different phenophases, we were unable to use dates directly from these sources. Instead, we calculated the weighted average ranking based on spring phenology. We weighted the ranking for each species based on the number of sources available for that species. Because each source contained different numbers of species (minimum of 8) relevant to our study, we scaled each ranking from 0 to 1 before calculating the weighted average ranking. Because we were interested in relative patterns of phenology, we consider this approach to meet our current objectives. Further, because there were unequal numbers of species in the rankings from different studies, we assumed that each study contained both early- and late-leafing species to capture the range of phenologies in our samples. We recognize that the order of species would vary based on which phenophase is considered, but the general pattern of early and late species generally holds regardless of which leafing phenophase was used (Figure 1 in Lechowicz 1984). For one species (*L. maackii*) we could not find published data which compared multiple species that were also included in our study, therefore, we used the data from the present study to incorporate this species into the final ranking. Our final ranking ordered the 23 most common species in our samples from earliest to latest in spring leafing phenology.

Statistical Analysis

In order to evaluate if the three species displayed different phenologies compared with each other irrespective of degree of urbanization, we used Kruskall-Wallis tests for species differences in bud break, leaf expansion and shoot length. We assessed support for the advanced phenology hypothesis using Spearman's correlations between median bud break, leaf expansion, and shoot lengths for each species on the urban index. We used nonparametric correlations because four of the nine phenology response variables were non-normal (Shapiro-Wilk's normality test, Ps < 0.05) and no single transformation could make all the variables normal. Because our prediction for advanced phenology was directional, we used one-tailed t-tests for the correlation coefficients. A positive relationship with the urban index would support the advanced phenology hypothesis.

We assessed support for the floristic composition hypothesis by using detrended correspondence analysis (DCA) to examine patterns within the woody plant community, specifically, if sites ordered consistently with the rural-to-urban gradient generated from the landscape data. We did not downweight rare species because they always occurred in samples (sites) with other common species (ter Braak and Smilauer 2002). We did not transform our species data because we suspected a linear trend between species and urbanization rather than a multiplicative relationship (Leps and Smilauer 2003). Next, we examined how the DCA ordered plant species and their phenological characteristics (i.e., early, average, or late leaf-out) relative to the ordering of the sites.

We examined patterns in temperature across the urban to rural gradient by using least-squares regression, where we regressed the monthly site-level temperature

accumulations, average minimum, and average maximum on the urban index. While 1 (average minimum for May) of the 24 temperature variables was non-normal (Shapiro-Wilk's, $P = 0.01$), for simplicity of interpretation we did not transform those data. A negative association between temperature accumulations and the urban index would indicate an urban heat island effect is experienced in these forests.

Based on our initial results, we performed several follow-up analyses to further explore the relationships detected in our data. We assessed the overall relationships of the phenology correlations with Fisher's combined probability tests on the p-values for the phenology correlations. Then, we examined the influence of each species on the ordination of sites by removing one species and repeating the DCA for each species in the samples. We then conducted Spearman rank correlations between all resulting site ordinations.

We further divided the sites into urban (>0 based on urban index) and rural (<0 based on urban index) and used a multi-response permutation test (MRPP with Euclidean distances and n/sum(n) weighting of groups) to examine if there were differences in woody plant community based on an urban and rural dichotomy. Because we found a significant result of this test, we conducted an indicator species analysis (Dufrene and Legendre 1997) based on the same urban/rural dichotomy to determine which species were better represented in urban and rural sites.

Statistical significance was set to $P = 0.05$. We report nominal *P*-values throughout, while acknowledging that some inferences would be weakened by correction for the multiplicity of tests performed. We tested the significance of Spearman

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correlations and the slopes of the regressions with one-tailed t-tests because of the directional predictions of our hypotheses. We assessed normality of all our temperature and phenology response variables with Shapiro-Wilks tests. For the temperature variables we assessed linearity by fitting a regression with slope = 0 to the residuals, and we examined plots of predicted values and residuals to inspect for constancy of variance. Kruskall-Wallis tests (Proc NPAR1WAY), Regressions (Proc GLM), and correlations (Proc CORR) were performed with SAS 9.1 (SAS Institute, Cary, NC USA). We conducted ordinations, indicator species analysis, and MRPP using PC-ORD 5.0 (McCune and Mefford 1999)   Ordination diagrams were generated with CANODRAW 4.12 for Windows (Biometrics- Plant Research International, Wageningen, The Netherlands).

2.4 Results

L. maackii was the earliest leafing of the three species we monitored. Median budbreak over all sites differed by species ($F_{2,30}$ = 238.96, $P < 0.0001$); L. maackii (10 February) was ~ 6 weeks earlier than bud break for A. glabra (31 March) and A. negundo (7 April). Median date of leaf expansion also differed by species ($F_{2,30}$ = 36.67, $P < 0.0001$); L. maackii (7 Apr) was earlier than for A. glabra (19 April) and A. negundo (20 April). Median shoot lengths differed by species ($F_{2,30}$ = 8.469, $P = 0.0012$) and were shortest in A. negundo (25.0 mm; range 16.4-40.0) and similar for L. maackii (43.7 mm; range 39.5-57.1) and A. glabra (41.6 mm; 33.7-119.3) (Appendix C, Appendix D.1).

Advanced phenology hypothesis

We found an overall pattern of advanced phenology with increasing urbanization but the strength of the relationships varied by species and phenophase (Table 2.3, Appendix C). There were two nominally significant correlations: bud break for *L. maackii* and shoot length in *A. glabra*. All but one of the trends were in the direction predicted by advanced phenology in more urban forests (one-tailed binomial test, *P* = 0.0195). An overall test of the p-values of the nine phenology correlations also supports a relationship between phenology and urbanization (Fisher's combined probability test, $\chi^2_{0.05,18} = 44.5$, *P* = <0.001).

Floristic composition hypothesis

We found differences in the woody plant community related to urbanization. The first axis of the DCA captured 25.9% of the variance of the species data; this axis loosely grouped sites into urban and rural sites, closely approximating the urban index with >0 on the index reflecting more urban sites and <0 reflecting more rural sites. Thus, the first axis seemed to reflect how plant community composition was related to urbanization. The second axis captured 8.5% of the variance of the species data, but we could not clearly discern how it related to either urbanization or other environmental gradients (Figure 2.1). There was not a clear pattern to the placement of early and late leafing species along the first ordination axis (Figure 2.2).

Temperatures

There was an overall pattern toward higher temperatures with increasing urbanization. The trends were strongest for average monthly minimum temperatures, which were nominally significant for the months January through May. Although in the direction predicted by the urban heat island, the slope estimates for average monthly maximum temperatures were essentially zero. Trends in temperature accumulations reflected the patterns in maximum and maximum temperatures; degree-day accumulations with no lower threshold had a stronger relationship with urbanization than accumulations with a 0°C lower threshold (Table 2.4, Appendix D.2).

Our follow-up DCAs assessing the influence of each species confirm that *L. maackii* was responsible for the ordination of sites based on plant community. Without small *L. maackii* stems in the DCA there was no apparent urbanization gradient in the DCA. Further confirming the effect of *L. maackii* on the ordination, the DCA performed without the small *L. maackii* stems was the only ordination that resulted in a non-significant correlation with the original DCA that included all species (Table 2.2). Urban versus rural differences in plant community were also confirmed with MRPP (T = -2.92, *P* = 0.019). Indicator species analysis based on the urban and rural groupings produced two species that were characteristic of urban sites (small *L. maackii*, *P* = 0.022, large *J. nigra P* = 0.030) and one species that was characteristic of rural sites (large *P. deltoides*, *P* = 0.026); Two other species with *P* < 0.10 were identified; large *A. saccharinum* with rural sites (*P* = 0.054) and small *Vitis* spp. with urban sites (*P* = 0.060). Of the three

nominally significant species, *L. maackii* is a very early leafing species, *J. nigra* is a very late leafing species and *P. deltoides* is a middle-to-late leafing species.

2.5 Discussion

We found evidence for both the advanced phenology and floristic composition hypotheses to explain earlier green-up in urban forests; however, their relative importance to community green-up is likely to be very different. Our results demonstrate that one species, the invasive exotic *L. maackii*, is primarily responsible for phenological shifts in the woody plant community in urban forests. Because *L. maackii* is the earliest species to leaf-out in our forests, exhibits earlier bud break in more urban landscapes, and dominates the shrub layer in many urban forests in this system (Borgmann and Rodewald 2005, this study), we suggest that this one species generates an overall earlier green-up in these forests while the remainder of the woody plant community appears to be largely similar between urban and rural forests. Although we found no statistical difference in *L. maacki* leaf expansion or shoot length related to urbanization, we expect there to be more green leaves and shoots earlier in the spring simply due to the high abundance of *L. maackii* in the urban forests. We also think it is reasonable that one species can drive the perception of overall earlier phenology based on our anecdotal observations of localized, dense patches of *A. glabra*, another early leafing species. These dense patches of A. *glabra* become noticeably green before the surrounding forest does (D.S. pers. obs.). Similar to our study, Remes (2003) found that one early-leafing dominant shrub generated earlier leafing phenology compared to a forest comprised of a diversity of

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understory species, although this pattern was not related to landscape context as in the present study. Our study demonstrates another way in which an invasive exotic species can have profound effects on native communities. The abundance of *L. maackii* in urban areas is likely driven by the fact that it was once widely promoted as a wildlife and ornamental species (Luken and Thieret 1996) and its fruits are readily consumed and dispersed by birds (Bartuszevige and Gorchev 2006).

While numerous studies have documented advanced phenology in non-forested matrices, as far as we know, only one previous study (Fisher et al. 2006) has specifically considered such phenology in forest remnants in urban and rural areas. Our study goes beyond a binary classification of urban and rural because we quantified urbanization through landcover measurements. However, there did appear to be a threshold in the abundance of *L. maackii* between urban and rural forests even though we intentionally selected sites to represent an urban to rural gradient. We also demonstrated that the urban heat island effect is experienced within forest fragments even though forests may have some capacity to buffer temperature variations within the forest (Gomez 1998, Augspurger and Bartlett 2003, Lamptey et al 2005). Because temperature accumulations are related to spring phenology, it is therefore not surprising that we also found a tendency toward earlier phenology within a species for our three focal species. Yet, patterns in temperature accumulations were driven mostly by variation in the minimum temperatures which may be less important than maximum temperatures for leaf development (Schwatz 2003).

We only considered woody tree species greater than 3 cm dbh. The effect of herbaceous species, and woody stems smaller than 3 cm dbh on the pattern of spring green-up was not considered. Because temperatures were elevated in urban forests, we would predict a similar pattern of advanced phenology in these other species as well (Houle 2007). However, there could be large differences in these components of the plant community (Drayton and Primack 1996, Moffat and McLachlan 2004, Duguay et al 2007) in part mediated by *L. maackii* (Collier et al. 2002, Gorchov and Trisel 2003, Dorning and Cipollini 2006, Meiners 2007) that could lead to different patterns of green-up on the forest floor because short-stature and short-lived species may demonstrate greater variability in leaf phenology (Uemura 1994). In addition, we did not concurrently quantify whether our urban forests green-up earlier than rural forests. Rather, we inferred that earlier green-up in the urban forests in our study system is likely based on satellite observations of Columbus, OH (Zhang et al. 2004) and observations of earlier green-up in other urban versus rural forests (Fisher et al. 2006). Further research is needed to more precisely quantify the differences in green-up between urban and rural forests, to quantify the contributions of *L. maackii* to green-up, as well as the degree to which plant growth forms other then trees and shrubs promote spring green-up in urban forests.

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site	site number	forest	agriculture	mowed	paved	road	no. buildings	urban index
Pubhunt	7	0.499	0.322	0.080	0.008	0.008	210	-2.990
Prairie	6	0.285	0.469	0.124	0.026	0.022	58	-2.386
Creeks	2	0.533	0.095	0.104	0.041	0.021	92	-2.170
Sgalena	9	0.434	0.143	0.297	0.017	0.012	185	-1.640
Galena	3	0.352	0.155	0.223	0.040	0.024	360	-1.269
Woodside	11	0.250	0.113	0.398	0.067	0.045	1227	0.525
Rushrun	8	0.316	0.000	0.409	0.090	0.060	1611	1.173
Kenny	4	0.295	0.000	0.341	0.167	0.061	1733	1.434
Cherry	1	0.222	0.020	0.364	0.155	0.075	997	1.453
Lou	5	0.113	0.000	0.277	0.234	0.079	2272	2.599
Tuttle	10	0.093	0.000	0.339	0.305	0.086	2285	3.271

Table 2. 1: Quantification of the landscape within 1 km of each study site in central Ohio, USA. The values for forest, agriculture, mowed, paved and road reflect the proportion of the 1km landscape in that cover type. No. buildings is a count of the number of buildings in that same area. The urban index is the first component of a principal components analysis of the six cover types (see text).

Table 2. 2 Names for woody plants measured in eleven forest fragments in central Ohio,
USA. The record for each species consists of two lines with counts of large stems (>8cm
dbh) and small stems (3-7.9 cm dbh). Final rank refers to order of leafing phenology (see
text) based on phenological estimates from one to eight different sources (references: 1:
Trelease 1884, 2: Lechowicz 1984 (Fig. 2.4), 3: Lamb 1915, 4: Altman and Dittmer 1962,
5: Lechowicz 1984 (Fig 2.1), 6: McGee 1986, 7: Augspurger and Bartlett 2003, 8: this
study). Site numbers refer to sites named in Table 2. Species for which no rank is
reported were only found in very small numbers and not included in the rankings. r_S is
the spearman rank correlation coefficient between the site orderings from DCA with all
species included and the site orderings from a DCA without that species. See text for
details.

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Table 2.2

species	site (number)	cherry (1)	creeks (2)	galena (3)	kenny (4)	lou (5)	prairie (6)	pubhunt (7)	rushrun (8)	sgalena (9)	tuttle (10)	woodside (11)	rank	r_S	P	references
Fraxinus spp. (ash)																
large stems		3	2	2	1	0	6	1	1	16	0	4	16	1.00	<0.001	1,2,4,5,6,7
small stems		0	0	0	1	0	2	2	2	4	10	1		1.00	<0.001	
Prunus serotina Ehrh.(black cherry)																
large stems		0	0	12	0	0	1	0	5	0	1	0	5	1.00	<0.001	3,4,5,6,
small stems		0	0	2	0	0	0	0	3	1	2	0		1.00	<0.001	
Robinia pseudoacacia L.(black locust)																
large stems		0	0	2	5	1	0	0	0	0	8	0	17	0.99	<0.001	1,3,4,6
small stems		0	0	0	1	0	0	0	0	0	2	0		1.00	<0.001	
Juglans nigra L.(black walnut)																
large stems		3	0	0	3	6	2	1	13	4	5	2	20	0.99	<0.001	2,3,4
small stems		0	0	0	3	0	0	0	6	0	7	0		1.00	<0.001	
Acer negundo L.(box elder)																
large stems		28	18	6	16	20	23	24	10	25	13	19	3	0.99	<0.001	1,2,3,4
small stems		6	10	1	2	24	24	5	37	33	50	11		0.96	<0.001	

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Table 2.2. continued

Aesculus glabra Willd.(buckeye)

large stems	2	2	0	3	0	19	13	2	0	0	23	4	0.98	<0.001	2,3,4,7
small stems	1	0	1	0	0	15	7	4	0	0	22		0.98	<0.001	

Euonymus alatus (Thunb.) Sieb.(burningbush)

large stems	0	0	0	0	0	0	0	0	0	0	0		1.00	<0.001	
small stems	0	0	0	0	0	0	0	5	0	0	0		1.00	<0.001	

Cephalanthus occidentalis L.(buttonbush)

large stems	0	0	0	0	0	0	0	0	0	0	0		1.00	<0.001	
small stems	0	0	0	0	0	0	0	0	3	0	0		1.00	<0.001	

Populus deltoides Bartr. ex Marsh.(cottonwood)

large stems	0	3	3	1	2	0	0	1	0	9	0	7	1.00	<0.001	1,2,3,4,5
small stems	0	0	0	0	0	0	0	0	0	0	0		1.00	<0.001	

Sambucus spp. (elderberry)

large stems	0	0	0	0	0	0	0	0	0	0	0		1.00	<0.001	
small stems	0	0	0	1	0	0	0	0	0	0	0		1.00	<0.001	

Ulmus spp. (elm)

large stems	0	6	19	1	3	15	0	12	5	2	0	10	0.99	<0.001	1,2,3,4,5,6,7
small stems	0	0	29	0	0	5	1	13	4	11	0		0.99	<0.001	

Table 2.2. continued

Vitis spp. (grapevine)

large stems	2	0	0	0	0	0	1	0	0	0	0	23	0.88	<0.001	1
small stems	17	2	0	20	1	0	1	9	0	0	4		0.97	<0.001	

Celtis occidentalis L.(hackberry)

large stems	0	1	0	1	10	6	1	6	4	0	2	21	1.00	<0.001	3,4,7
small stems	0	0	0	1	3	4	8	4	4	6	0		1.00	<0.001	

Craetagus spp. (hawthorn)

large stems	4	0	0	0	0	0	0	0	3	0	0	6	1.00	<0.001	2
small stems	1	0	0	0	1	0	0	2	3	0	0		1.00	<0.001	

Carya spp. (hickory)

large stems	1	0	0	0	0	0	1	0	0	0	0	19	1.00	<0.001	2,3,4,5,6,7
small stems	0	0	0	0	0	0	0	0	0	0	0		1.00	<0.001	

Gleditsia triacanthos L.(honeylocust)

large stems	0	0	0	0	0	1	1	13	1	0	0	24	1.00	<0.001	3,4
small stems	0	0	0	0	0	0	0	4	0	0	0		1.00	<0.001	

Lonicera maackii (Rupr.) Herder (Amur honeysuckle)

large stems	3	0	0	12	0	0	0	2	0	0	0	1	0.99	<0.001	8
small stems	9	0	0	297	80	0	0	108	1	63	0		-0.35	0.298	

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Table 2.2. continued

Morus spp. (mulberry)

large stems	0	0	1	0	24	0	0	0	0	6	0	15	1.00	<0.001	3,4,
small stems	0	0	2	0	1	0	0	0	0	13	0		1.00	<0.001	

Quercus spp. (oak)

large stems	1	0	0	0	0	0	0	0	3	0	0	13	1.00	<0.001	1,2,3,4,5,6,7
small stems	2	0	0	0	0	0	0	0	0	0	0		1.00	<0.001	

Maclura pomifera (Raf.) Schneid.(osageorange)

large stems	0	0	0	0	2	0	0	28	0	0	0	22	1.00	<0.001	2
small stems	0	0	0	0	0	0	0	4	0	0	0		1.00	<0.001	

Asimina triloba (L.) Dunal(pawpaw)

large stems	10	0	0	0	0	0	0	0	0	0	4	8	1.00	<0.001	3
small stems	28	0	0	8	0	0	7	0	0	0	17		0.99	<0.001	

Prunus spp., *Malus* spp., *Pyrus* spp. (prunus)

large stems	0	0	0	0	0	0	0	0	0	0	0	12	1.00	<0.001	1
small stems	0	0	0	0	0	0	1	0	0	5	0		1.00	<0.001	

Acer rubrum L.(red maple)

large stems	0	0	0	0	0	0	0	0	1	0	0	9	1.00	<0.001	1,3,4,5,6
small stems	0	0	0	0	0	0	0	0	0	0	0		0.99	<0.001	

Table 2.2 continued

Acer saccharinum L.(silver maple)															
large stems	0	17	23	0	0	1	1	0	0	1	0	2	0.89	<0.001	1,2,3,4
small stems	0	2	3	0	0	0	0	0	0	0	0		1.00	<0.001	
Lindera benzoin (L.) Blume(spicebush)															
large stems	0	0	0	0	0	0	0	0	0	0	0		1.00	<0.001	
small stems	2	0	0	0	0	0	0	0	0	0	0		1.00	<0.001	
Acer saccharum L.(sugar maple)															
large stems	12	0	0	0	0	0	3	14	0	0	0	11	0.99	<0.001	1,2,3,4,5,6,7
small stems	4	0	1	0	0	0	0	35	0	0	0		1.00	<0.001	
Liquidambar styraciflua L.(sweetgum)															
large stems	0	0	0	0	0	0	0	0	0	0	0		1.00	<0.001	
small stems	0	0	0	0	0	0	0	2	0	0	0		1.00	<0.001	
Platanus occidentalis L.(sycamore)															
large stems	0	17	2	0	0	5	6	0	0	0	1	14	0.98	<0.001	2,3,4
small stems	0	0	0	0	0	1	0	0	0	0	0		1.00	<0.001	
unknown															
large stems	0	0	0	0	0	0	0	0	0	0	0		1.00	<0.001	
small stems	0	0	0	0	0	1	0	0	0	0	0		1.00	<0.001	

species	bud break		leaf expansion		shoot length	
	r_S	p	r_S	p	r_S	p
A. negundo	-0.51	0.053	-0.48	0.066	0.42	0.100
A. glabra	-0.34	0.151	-0.47	0.074	0.53	0.048
L. maackii	-0.60	0.026	-0.43	0.091	-0.02	0.479

Table 2. 3: Spearman rank correlation coefficients and *P*-values for one-tailed *t*-tailed between the urban index and site median bud break, leaf elongation, and shoot length across eleven forest in central Ohio, USA.

	temp accumulations				temp accumulation(0)				Average max temp				Average min temp			
month	m	R^2	t	*P*	m	R^2	t	*P*	m	R^2	t	*P*	m	R^2	t	*P*
Jan	3.08	0.18	1.426	0.187	1.79	0.09	0.946	0.369	0.01	0.00	0.089	0.931	0.19	0.41	2.477	0.035
Feb	3.63	0.27	1.828	0.101	1.28	0.08	0.911	0.386	0.06	0.03	0.527	0.611	0.20	0.48	2.873	0.018
Mar	3.65	0.26	1.781	0.109	1.94	0.15	1.248	0.243	0.06	0.05	0.667	0.521	0.18	0.40	2.429	0.038
Apr	4.64	0.32	2.036	0.072	4.39	0.30	1.974	0.080	0.09	0.11	1.032	0.329	0.22	0.38	2.365	0.042
May	3.02	0.17	1.341	0.213	3.02	0.17	1.341	0.213	0.00	0.00	-0.030	0.977	0.20	0.33	2.114	0.064
Jun	2.51	0.12	1.087	0.305	2.51	0.12	1.087	0.305	0.01	0.00	0.142	0.890	0.15	0.23	1.660	0.131

Table 2. 4: Slope estimates (m), coefficients of determination (R2), t-statistics, and nominal one-tailed p-values based on simple linear regression with temperature variables as independent variables and urban as the dependent variable (temp accumulations=degree day accumulations with no minimum; temp accumulation(0)= degree day accumulations with 0°C as minimum; Average max temp =average maximum temperatures, Average min temp =average minimum temperatures).
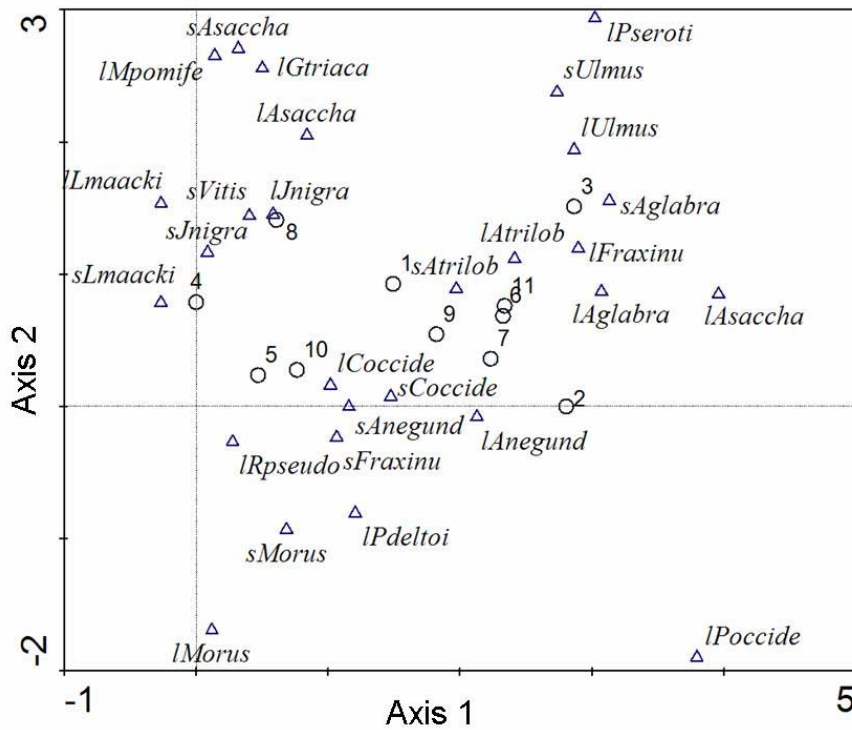
Figure 2. 1: Detrended correspondence analysis with eleven sites and woody tree and shrub species in central Ohio, USA. Prefixes "l" and "s" refer to large (>8 cm dbh) and small (3-7.9 cm dbh) trees and shrubs. Species that were represented by at least ten stems are shown in the figure and indicated by the first letter of the genus name and the beginning of the species name. Each species is indicated by triangles. Sites are denoted by circles and labeled with numbers that correspond to site numbers from Table 2.2. Axis 1 captured 25.9% of the variance in the species data and loosely grouped sites into urban (six most negative sites) and rural (five most positive) sites. Axis 2 captured 8.5% of the variance of the species data but lacked an obvious interpretation. Notice that the most urban sites are grouped together towards the left on axis 1.

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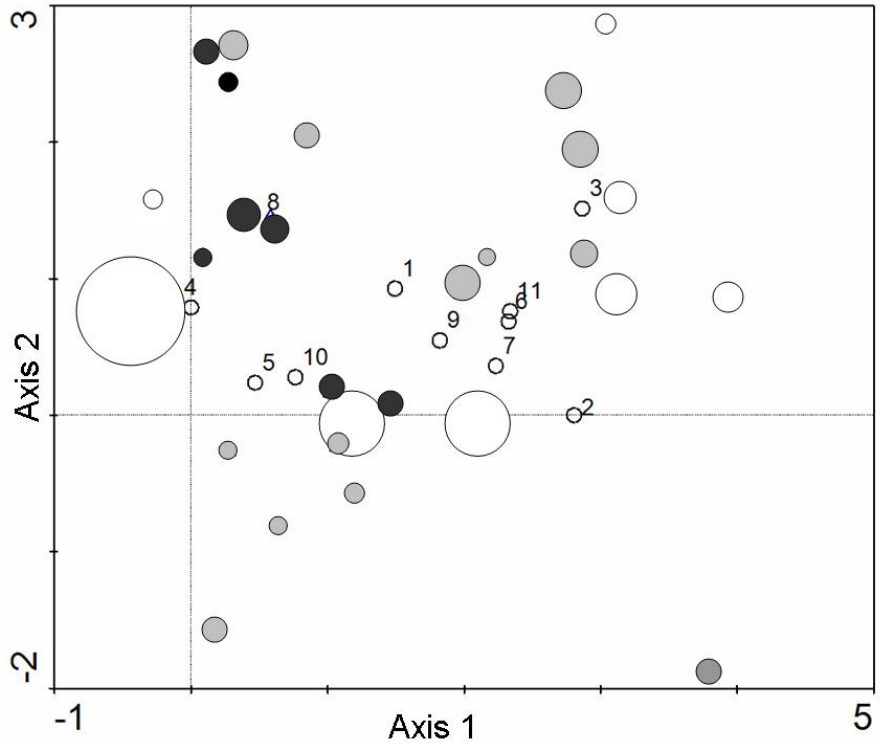
Figure 2. 2: Detrended correspondence analysis of woody tree and shrub species at eleven sites in central Ohio, USA. This is the same DCA as Fig. 2.1 but the species are represented with circles whose area reflects the relative abundance of stems. The shading of circles represents timing of spring leaf phenology for a each species shown in Fig. 2.1. White circles are the earliest leafing species, black circles the latest leafing species, and gray circles are species between the early and late species. Sites are denoted by the small bold, white circles that are labeled with numbers corresponding to site numbers shown in Table 2.2**.** Axis 1 captured 25.9% of the variance in the species data and loosely grouped sites into urban (six most negative sites) and rural (five most positive) sites. Axis 2 captured 8.5% of the variance of the species data but lacked an obvious interpretation. The largest white circle to the far left represented *L. maackii* stems between 3-7.9 dbh.

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CHAPTER 3

NEST PREDATION NEGATES BENEFITS OF EARLY-SEASON BREEDING IN THE URBANIZING MIDWEST

3.1 Abstract

While the patterns of advanced reproductive phenology in urban versus rural populations
of birds are generally well described, the causes and consequences of altered reproductive
phenology associated with urbanization remain poorly understood. We studied the
patterns, causes, and consequences of altered reproductive timing of Northern Cardinals
(*Cardinalis cardinalis*) nesting in urban and rural forests in central Ohio, USA between
2004-2007. The earliest dates for both nesting activity and clutch initiation were seven to
ten days earlier in urban versus rural forests. However, after accounting for differences
in Northern Cardinal density across sites, the timing of nest initiation was not
significantly related to urbanization. Using an information-theoretic approach we
evaluated several potential mechanisms explaining variation in nesting phenology.
Temperature accumulations in March were the best predictor variables explaining

breeding phenology, though January temperatures, amount of urbanization within the surrounding landscape, and conspecific density also received some support. In contrast, vegetation phenology (i.e., bud break, leaf elongation), site-level survival rates of adults, and the availability of nest sites failed to explain variation in breeding phenology of Northern Cardinals. Contrary to findings from other studies, breeding earlier in the season was not significantly related to the number of fledglings produced over the season. Rather, the expected number of fledglings produced per successful nest remained constant over the course of the season at ~1.7 fledglings per successful nest. The absence of a benefit to early breeding may be the consequence of high rates of nest predation early in the breeding season.

3.2 Introduction

Biologists have noted for decades that urban birds tend to reproduce earlier than their rural conspecifics (Erz 1966). Since then, numerous studies have demonstrated that birds in urban areas begin to lay eggs earlier than their rural counterparts (Cramp 1972, Eden 1985, Morneau et al. 1995, Rollinson and Jones 2002, Antonov and Atanasova 2003, Schoech and Bowman 2003). Although inferences that can be drawn from some early studies focusing on urban-associated shifts in breeding phenology are limited due to confounding variables related to sites or years (Cramp 1972, Eden 1985, Morneau et al. 1995), several more robust evaluations of differences between urban and rural populations have provided strong evidence of advanced urban phenology (Rollinson and Jones 2002, Antonov and Atanasova 2003, but see Sodhi et al. 1992). Temporally

advanced reproduction has ranged from five days in Magpies (*Pica pica,* Eden 1985,

Antonov and Atanasova 2003) to one to four weeks in Blackbirds (*Turdus merula,*

Luniak 1988, 2004).

Advanced breeding phenology in cities may stem from differences between rural

and urban areas in terms of (1) lighting or effective photpheriod, (2) local climate, (3)

vegetation, (4) food resources, (5) individual quality of birds, and (6) density of

conspecifics. First, for most temperate bird species, photoperiod is thought to be the

main factor determining when birds reproduce (Hahn et al.1997). The natural

photoperiod can be modified by artificial light sources and this has been shown to

promote reproductive readiness (Bartholomew 1949). In an urban environment the

natural photoperiod is supplemented by anthropogenic lighting which may advance

physiological readiness for reproduction. Second, temperature is also considered to be an

important factor influencing reproductive timing (Meijer and Drent 1999, Saino et al

2004). Warmer temperatures may advance the physiological readiness of a bird and

serve as an ecological cue to the potential of food resources. Thus, the temperatures in

the months leading up to breeding may promote or retard reproductive readiness (Storey

and Nicholls 1982) while warmer temperatures in the days and weeks prior to breeding

may induce a bird to reproduce (Meijer et al. 1999). Comparatively warmer temperatures

than in rural areas may be one attribute of cities (i.e., the urban heat island effect) that

promotes earlier reproduction. Third, vegetation development or phenology may create

nest sites and/or provide nesting material, a potential stimulus for reproduction (Whitman

1919, Lehrman et al 1961 as cited in Collias 1964). Indeed, urban areas often display

advanced plant phenology relative to rural areas (Defila et al. 2003) and this advanced vegetation phenology might lead to earlier avian breeding in urban areas (but see Schoesh and Bowman 2003). A fourth factor that influences avian reproductive timing is availability of food. Abundant food resources during the winter and spring may allow birds to be in better condition earlier in the spring and to gain resources faster in order to initiate reproduction sooner (Schoech and Bowman 2003, Meijer and Drent 1999). Urban habitats often provide abundant amounts of food via bird feeders and fruiting ornamental shrubs (Chace and Walsh 2006) making this a likely mechanism to promote timing of avian breeding. Fifth, individual variation can lead to differences in reproductive timing. For instance, older, more experienced individuals may reproduce earlier than younger birds (Nol and Smith 1987). If birds in urban areas have greater rates of survival (Luniak 1994) then urban areas may be overrepresented by older, more experienced individuals who are more likely to breed earlier than younger birds. Sixth, density of the local population, which is often affected by urbanization, may also mediate reproductive timing through behavioral interactions with other conspecifics (Jerzak 1995, Silverin and Westin 1995) leading to advanced breeding.

Although earlier seasonal initiation of breeding is often positively associated with reproductive success, this generalization does not appear to extend to all populations experiencing urban-mediated advanced reproduction. For example, equivalent numbers of fledglings might be produced in urban and rural populations despite earlier reproduction by urban populations (e.g., Australian Magpies (*Gymnorhina tibicen*), Rollinson and Jones 2002). In contrast, urban populations might experience higher

hatching success or even produce more total fledglings, but this might not be due to date of nest initiations (e.g., Magpies, (*Pica pica*), Antonov and Atanasova 2003). Further, differences in temporal patterns of nest survival between urban and rural populations might leads to similar levels of nest success despite differences in timing of nest initiations (e.g., Florida Scrub-Jays (*Aphelocoma coerulescens*), Bowman and Woolfenden 2001).

Environmental changes associated with urbanization are generally implicated in altered breeding phenology, but they are seldom directly measured concurrently with breeding phenology (Rollinson and Jones 2002, Antonov and Atanasova 2003). In fact, among the many environmental factors that potentially influence breeding, only temperature is routinely evaluated and even then it is often collected in a location different than the actual study area (Eden 1985, Rollinson and Jones 2002). Moreover, because most studies documenting advanced urban phenology have occurred in the urban matrix (Cramp 1972, Eden 1985, Morneau et al. 1995, Rollinson and Jones 2002, Antonov and Atansova 2003, Schoech and Bowman 2003), we do no know if the same patterns occur in patches of undeveloped native (and nonnative) vegetation. Indeed, Perrins (1970) noted that birds often initiated breeding earlier in suburban gardens than adjacent woodlands, suggesting that bird breeding phenology in undeveloped habitats in urban and rural landscapes might not vary. In addition, studies demonstrating advanced urban phenology rarely consider implications for season-long reproductive success; instead they focus on first nesting attempts (Eden 1985, Antonov and Atanosova 2003).

As urbanization consumes more and more land area, it will become increasingly important to understand how subtle consequences of development might ultimately influence population demography. Understanding demographic patterns and processes remains a critical need in the area of urban avian ecology (Marzluff et al. 2001).

In this study, we sought to understand the patterns, causes and consequences of altered reproductive phenology associated with urbanization. Using Northern Cardinals (*Cardinalis cardinalis*) breeding in forest fragments in urbanizing landscapes as our focal species, we specifically addressed three questions. One, how does the timing of nest initiation differ between forests in urban and rural landscapes? Two, which local factors (vegetation phenology, adult experience, nest site availability, social factors, temperatures, and other features of urbanization) best explain variation in reproductive phenology? Because our previous research (Rodewald and Shustack 2008a) demonstrated that there were no differences in adult survival or per capita number of fledglings between urban and rural sites, we asked, three, what are the consequences of variation in the timing of initiation on an individual level?

3.3 Methods

STUDY SITES AND LANDSCAPE

We studied Northern Cardinals in 14 mature riparian forests within and around Columbus, Ohio, USA. Northern Cardinals were used for a study species because they are a native, resident species that occurs in our study sites year round and thus are

susceptible to environmental changes associated with urbanization throughout their annual cycle. Northern Cardinals initiate nesting early in the spring (starting in late March and early April), and make multiple nesting attempts throughout the season. Northern Cardinals often place their nests in the understory or midstory, which facilitates finding their nests (Halkin and Linville 1999). Further, Northern Cardinals are present in sufficient numbers (although at varying densities) at all 14 sites to allow for their study (Rodewald and Shustack 2008a).

Study sites were located in mature forest corridors (>250 m long and 100 m wide) along rivers, and were separated from each other by >2 km. Forests tended to be narrow and linear but connected to other forests in the landscape. Our field efforts were focused on these forests, although Northern Cardinal territories regularly contained adjacent areas (such as neighborhoods and parkland) as well. We attempted to monitor Northern Cardinals that defended territories that encompassed portions of our designated forest and neighboring habitats. We did not monitor territories that were exclusively in the surrounding nonforested habitats. The surrounding landscapes were dominated by agricultural (e.g., row crop, hayfields, pasture) and urban (e.g., roads, parking lots, buildings) land cover. Twelve sites were used in 2004-2007 and two additional sites (Tuttle and Kenny) were added in 2005.

The landscape (314 ha) surrounding each site was quantified within 1 km of the approximate center of each site. We used digital orthophotos (i.e., similar to aerial photos, taken 2002-2004) and existing data (road, building, etc., shapefiles) from county auditors to calculate the proportion of each landscape in roads, pavement, lawn,

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agriculture as well as the number of buildings. Using landscape data from the 14 sites

used in this study and an additional 21 sites used in another study (Table 1 in Rodewald

and Shustack 2008b) we collapsed these five variables into an "urban index" using a

principal components analysis. The 'urban index" was the first component of the PCA

and explained ~80% of the variation among sites. Further, all five variables loaded

strongly in the urban index and had high correlations with the urban index ($r>|0.80|$). We

used the urban index as a continuous variable in our model rankings in order to capture

variation associated with urbanization that we did not specifically measure (see below).

We also separated sites categorically into urban and rural sites in order to compare

breeding phenology variables (see below). Sites were considered "urban" if the urban

index was >0; conversely, rural sites had an urban index <0. One site (Elk Run Park) was

classified as "urban" despite an urban index value <0 (e.g., -0.16) because it was

surrounded by high number of buildings and residential development (Table 1 in

Rodewald and Shustack 2008a).

NEST AND TERRITORY MONITORING

In 2004-2007 we intensively monitored each site for Northern Cardinal activity. Males

and females were captured in mist nets using both passive and target banding with aid of

song recording and decoy. Upon capture Northern Cardinals were individually marked

with a U.S. Geological Survey aluminum band and a unique combination of three color

bands. For each captured bird, sex, wing chord length (mm), tarsus length (mm), and

mass (g) and age (adults or hatch year) was recorded.

Breeding pairs were monitored in efforts to locate as many nests of each focal

territory as possible. Nests were located by systematically searching potential nest

substrates as well as by observing adult behavior. Once found, nests were monitored at

2-5 day intervals to determine the nest fate (failure or success and number of young

fledged). After completion of a nest, territories were monitored for subsequent nesting

attempts. Locating nests late in the season was more difficult due to vegetation structure

and higher nest placement, but we continued to search for new nests and monitor adult

activity through August each year (although some nesting activity continued later, D

Shustack pers. obs). Therefore the number of nesting attempts reflects a minimum of the

number of attempts made (Wolfenbarger 1999). Over the course of the season,

invariably some birds produced fledglings from nests that were not found. When we

found fledglings from unmonitored nests we deduced the parents on the band

combinations of the adults tending the fledglings. If neither adult were banded, we used

used locations of fledglings, nesting history of the territorial birds, and stage of nesting

and presence of banded individuals of neighboring territories to deduce nesting history

for each pair.

While we attempted to band one or both adults on each focal territory sometimes

neither adult was banded. Observations of banded birds showed that nearly all birds

retained the same mate across all nesting attempts in the same season and therefore, we

assumed that unbanded individuals remained on the same territories and with the same

mates throughout the breeding season. If we failed to either find nests or to observe

adults for several weeks, we assumed that adults could have produced fledglings that

went undetected and, therefore, we did not include these pairs in analyses of seasonal productivity. Further, in our analysis of the relationship between the numbers of fledglings produced based on dates of nest initiations, we only used territories that were adequately monitored. While it is possible that this data set includes several few territories from which we missed the first nesting attempts, we think it is unlikely that any undetected fledglings were produced from these territories.

NEST SITE AVAILABILITY

In most years the earliest Northern Cardinal nests were initiated before green vegetation provided concealment. These earliest nests were located in nest sites that provided some concealment from woody cover such as honey locust spines or grape tangles. We reasoned that sites rich in these "pre-leafout" nest sites might allow earlier nesting at those sites. Accordingly, we quantified abundance of pre-leafout nest sites from early to mid April 2006 and 2007 by sampling potential nest sites along transects (50 m wide) through each of the eleven sites. The first transect was located a random distance along the river and oriented in a random direction until reaching the forest edge, resulting in variable transect lengths at each site. Additional transects were located at 50 m intervals until 30 observations of potential nest sites were made or until no more transects would fit at a site. Transect lengths were estimated using a GIS with digital orthophotos of the study sites. We considered pre-leafout nests sites as those cardinals have been observed to use in the past: dense grape tangle, dense shrub branches, dead branches/brush pile,

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honey locust thorns, evergreen shrubs or trees, and a few others. The perpendicular distance from the nest site to the transect line was estimated by pacing. Further, we estimated the number of potential nest sites when the nest sites occurred in a cluster (e.g., in a large grapevine tangle). All potential nest site sampling was performed by one observer (DPS).

Using program DISTANCE 5.0 (Thomas et al. 2006), we estimated the density of potential nest sites at each site. We assumed that detection probability was similar for each site so only one detection function was estimated for all transects together. Using that function, we estimated the number of potential nest sites for each site. Most sites were sampled in 2006 and 2007 although a few were sampled in only one year. Estimates from each year were averaged into one estimate of the density of pre-leafout nest sites for each site (Appendix D.3).

VEGETATION PHENOLOGY

At eleven sites in 2006 we monitored the leafing phenology for three common species (Amur honeysuckle (*Lonicera maackii)*, Box elder (*Acer negundo*), and Ohio Buckeye (*Aesculus glabra*)) which are regularly used as nesting substrates. We determined the site median dates for bud break, leaf expansion, and the average shoot length in mid-April (see chapter 2 and Shustack et al. *in review* for detailed methodology). Median dates of bud break (i.e., green leafy material visible between bud scales) for each species as well as the leaf-out date (leaf fully elongated and in normal growing orientation) and shoot length of honeysuckle were used as predictor variables in the models for cardinal

breeding phenology given their influence on nest sites and foraging substrates for
breeding birds.

TEMPERATURES

Because temperatures can constrain the timing of reproduction in birds, we measured
daily minimum and maximum temperatures at 11 sites between 1 January - 30 June 2006
and from all 14 sites in 2007. In 2006 our instrumentation (Digital min/max
thermometer, Model 1441, Taylor Precision Products, Las Cruces, New Mexico, USA)
permitted collection of only daily minimum and maximum temperatures (see chapter 2
for more details). Using different instrumentation (ibutton thermochron, model
DS1922L, Maxim Integrated Products, Sunnyvale California, USA) in 2007 temperatures
were recorded every 15 minutes at $\geq$four sampling points per site and, from these data,
we calculated average daily minimum daily maximum temperature for each site.
Minimum and maximum temperatures were used to calculate the daily temperature
accumulations ((min +max)/2).   For each month at each site we calculated the average
daily minimum and maximum temperatures for January and March. We also determined
the monthly temperature accumulations for January and March by summing the daily
temperature accumulations over the month. January temperatures were used as a metric
for the harshness of winter, whereas March temperatures were included because prior
research indicated that the temperatures immediately leading up to breeding influence the
initiation of breeding (Meijer et al. 1999). Temperatures values from 2006 and 2007 were

averaged for inclusion as predictor variables in our models (Appendix D.2, Appendix D.4).

BIRD AGE AND EXPERIENCE

Because older and more experienced birds may breed earlier (Nol and Smith 1987), greater survival in urban compared to more rural areas (Luniak 2004) might promote earlier breeding for city birds due to the prevalence of older individuals. Although we found no evidence that survival rates were related to urbanization as a whole (Rodewald and Shustack 2008a), we still examined the possibility that variation in survival rates among sites (program MARK, White 2006) might be related to breeding phenology. We reasoned that sites with higher adult survival would contain older and more experienced birds (Appendix D.5).

INDIVIDUAL CONDITION

Evaluating the relationship between individual condition and breeding phenology is important because larger individuals or those in better condition may be able to initiate breeding earlier if size or condition affects resource acquisition and/or pairing success. To do this, we first tested for a relationship between individual morphology and timing of reproduction using least square regression. Because our exploratory analyses failed to show a significant relationship between morphology (i.e., wing length, tarsus length of mass for either male or females) and initiation of nesting activity, these variables were not ultimately included in our models.

CONSPECIFIC DENSITY

The number or density of conspecifics may either promote earlier reproduction (e.g.,

birds try to get competitive advantage for mate acquisition, Silverin 1995) or potentially

retard breeding initiation (e.g., in environments where food is limited). Through intense

monitoring and spot-mapping at each site in each year, we annually estimated the number

of Northern Cardinal territories within a 2-ha grid at each site (4-ha grid at four sites-

Kenny, Lou, Rush Run, and Tuttle). We used the mean number of Northern Cardinal

territories (2004-2006) on our 2-ha as an estimate for breeding density (Rodewald and

Shustack 2008a).

3.4 Statistical Analyses

We compared urban and rural site in terms of day of year of the first clutch

initiation, detection of first nesting activity and density-adjusted first nesting activity

using t-tests (PROC TTEST, SAS 9.1). Each year was treated separately because annual

differences are common due to warmer or cooler springs.

To assess the relative support for each potential mechanism on reproductive

timing, we used an information theoretic approach (Burnham and Anderson 2002). First,

likelihood values generated for each model were used to calculate AIC_c scores.

Subsequently, each model was ranked based on its difference from the model with the

smallest AIC_c value (i.e., $\Delta AIC_c = 0$ indicated the highest ranked model). Models with

$\Delta AIC_c < 2$ were considered to be equally plausible given the data. Akaike's weight (*w)*

showed the weight of evidence for a particular model. We used the same model set for each breeding phenology variable but ranked the model sets separately.

We determined the dates for three breeding phenology metrics for each site and year separately. First, we determined the date of the first detection of nesting activity (i.e., typically initiation of nest building). Second, we determined the date of the first clutch initiation at each site. Third, we determined the date when the nth individual initiated nesting at a site (hereafter termed "density-adjusted first nesting activity date"), where n is the (rounded) density of the site (Table 1 in Rodewald and Shustack 2008a) given that (a) sites with more individuals would be expected by chance to have earlier breeders and (b) Northern Cardinal density was positively related to urbanization (Leston and Rodewald 2006, Rodewald and Shustack 2008a). All n individuals at a site were not necessarily the n pairs using the gridded area as our search area extended somewhat beyond these 2-ha grids. We used this density-adjusted metric instead of median clutch initiations dates because of difficultly in determining when all females at a site had initiated their first nesting attempts. Not all females were banded and thus undetected movements in and out of the site were possible. We also were unable to search some areas with territories extending outside the study sites because these areas included private property and dense residential areas. Finally, we reasoned that we might be more likely to miss some first nesting attempts in the high density urban sites because high abundance of Northern Cardinals which might lead to estimating a relatively later median date of breeding in urban areas. We believe the density-adjusted metric both accommodates the concern that earlier clutch initiations would be expected by chance in

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higher densities sites, and solves the problem of finding all first nesting attempts from every nesting pair on a site.

We then used multiple regression (PROC GENMOD) to relate each predictor variable to the breeding phenology variables. In each model set we also included a null model which was simply a year effect. Each model also contained additive year effects. While we suspected that annual differences might affect absolute dates of breeding (i.e., early versus late years), we expected that the general order of sites would be comparable among years. The final model set was the same for each response variable and included the urban index, temperatures (January minimum, January maximum, January temperature accumulations, March minimum, March maximum, and March temperature accumulations), nest site density, adult survival, vegetation phenology (bud break and leaf-out for box elder, honeysuckle, and Ohio buckeye, as well as shoot length for honeysuckle) and conspecific density.

We examined consequences of variation in individual reproductive timing in several ways. First, we compared the timing of fledging in urban versus rural forests with a Kolmorgov-Smirnov test (PROC NPAR1WAY). Second, we looked for a relationship between first clutch initiation date of each female and her associated season-long productivity, and the number of detected attempts she made with PROC GENMOD. Third, we examined the pattern of the number of fledglings produced per successful nest over the course of the season (PROC GENMOD). Fourth, we used a modified form of logistic regression called logistic exposure (Shaffer 2004) to estimate nest survival over the course of the season. Fifth, we tested for effects of number of nesting attempts,

seasonal productivity and the date of clutch initiation on the probability of resighting an individual in a subsequent year (PROC LOGISTIC). All analyses were conducted in SAS 9.1 (2006). We report means +/- one standard error and parameter estimates from relevant models.

Based on our initial analyses (see RESULTS) showing (1) no relationship between seasonal productivity and initiation of nesting and (2) increasing nest survival probability over the season, we examined the relationship between nest survival and seasonal productivity by constructing a simulation in SAS 9.1. In the simulation we imposed our observed seasonal nest survival pattern (Fig. 3.1) on a bird's breeding season. We defined the date of her initiation of nesting and assumed that she would continue breeding until the end of the breeding season. We compared the probability of nest survival for a given day to a random number to determine if the female was successful in nesting on that day. After determining whether the nest survived for every day of the breeding season, we counted the number of times a female experienced a series of 35 consecutive days of nest survival (i.e., the approximate number of days to successfully fledge young beginning at nest building [nest building = four days, laying = two days, incubation = 12 days, nestling period = 10 days, post-fledgling care = seven days] before renesting). We further assumed that a female renests immediately after 35 days. We simulated a nesting history for 1000 females which initiated nesting on every day of the breeding season (31 March to 11 September). Then for each day we determined median and upper and lower 95% confidence intervals for the number of fledglings produced by females which initiated on that day.

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3.5 Results

The earliest Northern Cardinal nesting activity was consistently detected in urban

forests, though the pattern was significant only in 2005 and 2006 (Fig. 3.2A). Similarly,

the earliest clutches were initiated in urban forests, but the patterns were significant in

only 2004 and 2005 (Fig. 3.2B). Interestingly, once we adjusted for density of

conspecifics, nesting activity was initiated at comparable times in urban and rural forests

(Fig. 3.2C), suggesting that either density *per se* or density-related detection probability

was an important contributing factor (Appendix D.6). Despite variation in model

rankings, there was generally consistent evidence that warmer temperatures in March

promoted earlier breeding. Indeed, March temperature (temperature accumulations

through March) were ranked < 2 ΔAIC_c for all three model sets and was the only variable

ranked < 2 ΔAIC_c for the first clutch initiations. A second pattern among the three

nesting phenology variables was that models reflecting the timing of leaf emergence

and/or development, availability of nest sites, and Northern Cardinal survival rates

received very little support (ΔAIC_c < 6 in all model set ;Tables 3.1-3.3). In addition to

March temperatures, the models for the urban index and Northern Cardinal density were

also ranked < 2 ΔAIC_c for the first nesting activity, and the average March minimum

temperatures and January minimum temperatures were <2 ΔAIC_c for the density adjusted

nesting initiation model set.

Neither the timing of successful nests (N = 158 rural successful nests, N = 347

urban successful nests; D = 0.084, *P* = 0.43) nor the timing of fledging (N = 274 rural

fledglings, N = 619 urban fledglings; D = 0.072, *P* = 0.28, Fig. 3) differed between urban

and rural sites. We failed to find evidence of a relationship between when a bird initiated

its first clutch and the number of fledglings produced over the season (N = 302 female

nesting histories; β = -0.0005, χ^2 = 14.7, P = 0.78; Fig. 3.4). Nevertheless, we found that

females initiating earlier nests completed a greater number of nesting attempts over the

season, with females initiating in mid-June making about two nesting attempts (N = 302

female nesting histories; β = -0.0106, χ^2 = 38.3, P < 0.001). The number of fledglings

per successful nest remained approximately constant over the season at approximately 1.7

Northern Cardinal fledglings (β_0 = -0.523, χ^2 = 22.1, P < 0.001) per successful nest (N =

505 fledging events; β = -0.0003, χ^2 = 0.2, P = 0.69). Nest survival (survival over the

entire nest cycle) increased over the season from ~18% on April 1 to ~46% on August 1

(β_0 = -2.018, β = 0.007, χ^2 = 37.5, P < 0.001; N = 1227 nests, $N_{effective}$ = 16,044 [see

Rotella et al. 2004] Fig 3.1). The probability of resighting marked birds in subsequent

years was not related to number of nesting attempts (males: β_0 = -0.016, β = -0.293, χ^2 =

2.34, P = 0.12, N = 112 male histories; females: β_0 = -0.174, β = -0.2221, χ^2 = 1.1, P =

0.29, N = 91 female histories), seasonal productivity (males: β_0 = -1.22, β = 0.175, χ^2 =

2.2, P = 0.14, N = 112 male histories; females: β_0 = -1.038, β = 0.094, χ^2 = 0.5 P=0.50, N

= 91 female histories) or clutch initiation date (males: β_0 = -0.828, β = 0.000, χ^2 =

0.0012, P = 0.97, N = 112 male histories; females: β_0 = -0.832, β = 0.000, χ^2 < 0.001, P =

0.99, N = 91 female histories) in the previous year.

The results of the simulation showed that the total number of expected successful

nests would decrease over the season as a female initiated later in the season but the

confidence interval around the expected values are wide (Fig 3.5).

3.6 Discussion

Consistent with previous studies on the breeding phenology of urban birds, we found evidence for advanced reproduction associated with urbanization. Earliest dates of both nesting activity and clutch initiations averaged seven to ten days earlier in urban versus rural sites. However, the pattern of advanced breeding did not persist after adjusting for differences in possible detection of cardinals among sites (i.e., we are more likely to detect an earlier nesting attempt at sites with greater densities of breeding cardinals). Rather than implicating that resources provided by urbanization advance breeding phenology, our study provides strong evidence that temperature is the key factor explaining variation in timing of reproduction across sites. Contrary to our initial expectations, vegetation phenology, nest site availability, and survival probability were comparatively unimportant factors affecting breeding phenology. Perhaps even more interesting, though, we found no apparent benefits or costs to when birds initiated breeding despite variation in dates that individuals initiated nesting.

For decades, the ornithological literature has emphasized the benefits of earlier reproduction within a breeding season (reviewed in Perrins 1970 and Drent 2006), particularlys in terms of increased number of fledglings produced over the course of a breeding season (Norris 1993, Verlhurst et al. 1995). This benefit can arise in several different ways. First, early clutches tend to be larger (Klomp 1970, Perrins and McCleery 1989), which allows the possibility of producing more fledglings. Second, food availability often peaks earlier in the season and thereby renders early broods less food-limited than later ones (Van Noordwijk et al. 1995, Marshall et al. 2002, Drent

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2006). Third, early reproduction permits a longer breeding season, thereby increasing the opportunity for additional nesting attempts and the production of a greater number of fledglings (Barba et al. 1995, Ortega et al. 2006, Grzybowski and Pease 2005, Murray and Nolan 2007). Fourth, in systems where nest survival declines over the season, earlier nests would have the best chance for success (Roos 2002, Schieg et al. 2007, Small et al. 2007). Nevertheless, despite the various ways in which early reproduction can allow for greater seasonal productivity, our data provided no evidence of benefits to early versus later breeding. We did not detect any relationship between the number of fledglings produced over the season and when a female initiated nesting for the season. Further, the number of fledglings produced from successful nests did not vary appreciably over the course of the breeding season, but stayed approximately constant at about 1.7 fledglings per successful nest.

Why did we not find evidence for benefits of advanced reproductive timing? We suggest that the strong seasonal pattern in nest survival might be responsible. Interestingly, this pattern is opposite to that which would contribute to higher seasonal productivity; nest survival increased over the season. Thus, high nest failure rates early in the season may constrain any potential for increased seasonal productivity due to early breeding. Our simulation supports the notion that the nest survival pattern observed in our system can effectively negate any potential to detect a benefit to early breeding in terms of the number of successful nests or fledglings.

While our results suggest that low nest survival might reduce benefits of early breeding, we were unable to adequately evaluate other potential mechanisms including

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trade-offs in clutch size, food availability, and duration of nesting season length. Of

these we have anecdotal evidence that food availability did not play an important role as

we found no pattern in the number of fledglings produced per successful nest over the

course of the season. The absence of this pattern suggests that peaks in food availability

and/or increased clutch size of earlier nests may not be as important in this system as in

others (Van Noordwijk et al. 1995, Visser et al. 2006) both because Northern Cardinals

have long nesting seasons (>120 days) and small clutch sizes (~3 eggs, Scott et al. 1987).

Given that nest survival was low early in the season and early nesting was

unrelated to the number of fledglings produced, why then do early birds not postpone

breeding until their chances of nest success improve? In other words, why should a bird

breed early when its chances of being successful are terribly low? One important caveat

is that although our simulation demonstrated that a high predation rate prevented the

detection of a numeric benefit to early reproduction, this is not equivalent to showing the

absence of any benefit for individuals initiating early clutches. For example, while there

is only a small probability that an early nest will fledge any young, this probability is still

greater than zero (i.e., the probability associated with not nesting at all). Because

cardinals can renest quickly (Scott et al. 1987) and lay small clutches (1-4 eggs, Scott et

al. 1987, Halkin and Linville 1999), the main cost to early nesting might be the

opportunity cost of only a few days of nest-building which is likely to be low (Stanley

2002) and the time and energy required to lay a new clutch (Williams 2005). In addition,

a potential benefit to high nest failure rates might include energy saved tending fledglings

which might lead to increased longevity of the adult (McCleery et al. 1996), thus

allowing for more nesting attempts over a bird's lifetime. Though we could not directly evaluate lifetime reproductive effort and success, our data do not suggest the presence of a relationship among the number of confirmed nesting attempts, seasonal productivity, first clutch initiation date, and the probability of resighting a bird in a subsequent year, which collectively suggest that cardinals survival does not decline with increased reproductive effort.

Another potential benefit to early reproduction in spite of high nest failure is that the value of success may be greater than success later in the season. Specifically, fledglings produced early in the season are expected to have higher survival rates and, therefore are more likely to be recruited to the population (Perrins 1970, Norris 1993, Barba et al. 1995, Verboven and Visser 1998, Drent 2006, Møller et al 2006, Vitz 2008). Thus, in terms of recruitment, a fledgling produced in May might be much more valuable than a fledgling in August (reviewed in Nilsson 1994, Fig. 6). If this is true, then breeders should take a greater risk (face higher nest failure) to produce fledglings early in the season rather than later.

An extended breeding season might be advantageous even if more fledglings are not produced. For instance advanced first annual reproduction may promote extended breeding seasons and birds that are successful in early nest attempts may not use this "insurance policy" whereas birds with failed early attempts might nest later into the summer. Completing nesting activity earlier in the summer gives individuals more time and energy to invest in molting and preparing for winter (Morales et al. 2007, Nilsson and Svensson 1996, Gardner et al. 2008).

The pattern of advanced reproductive phenology in urban landscapes has traditionally been associated with the modified environment and resources available in cities. We show that to the extent that urbanization modifies local climates (i.e., temperatures), urban development may indeed promote earlier breeding. Despite variation in the timing in the initiation of breeding, we demonstrated that there is no apparent benefit associated with advanced breeding – a situation that is the consequence of higher nest predation rates earlier in the breeding season. While we were unable to detect any benefits or costs associated with early, life-history theory suggests that a number of trade-offs are associated with the timing of reproduction. However, the costs and benefits may be different in a top-down regulated population (i.e., a system with heavy nest predation rate like ours) compared to bottom-up (food supply) regulated population. Further research is needed in order to evaluate potential other costs and benefits to early reproduction in urban areas.

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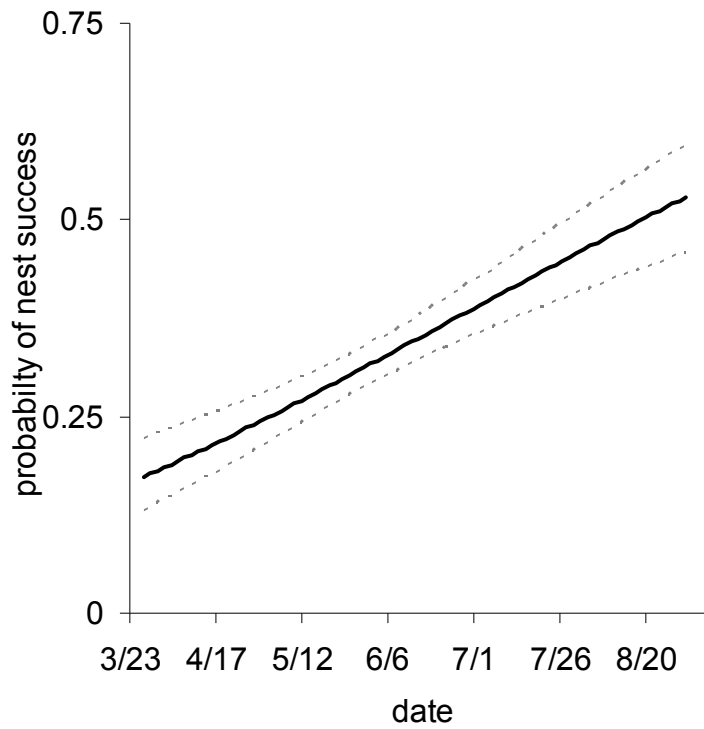
Figure 3. 1: Relationship between date and and nest success for 1227 Northern Cardinal nests monitored in central Ohio, USA between 2004-2007. Nest success is calculated based on daily survival estimates derived from logistic exposure regression analysis.

Figure 3. 2 : A-C. Mean (and +/- 1 SE) julian day of detection of first nesting activity (A), mean first clutch initiation day of year (B), and density-adjusted nesting activity (C) of Northern Cardinals on urban and rural sites in central Ohio, USA between 2004-2007. Numbers above bars indicate *P* values for t-test between urban and rural means.

continued

Figure 3.2 continued

B — first clutch initiation

Bar chart showing day of year (y-axis, 90–125) for rural (grey) and urban (white) groups across years 2004–2007 (x-axis).

- 2004: 0.03
- 2005: 0.03
- 2006: 0.10
- 2007: 0.08
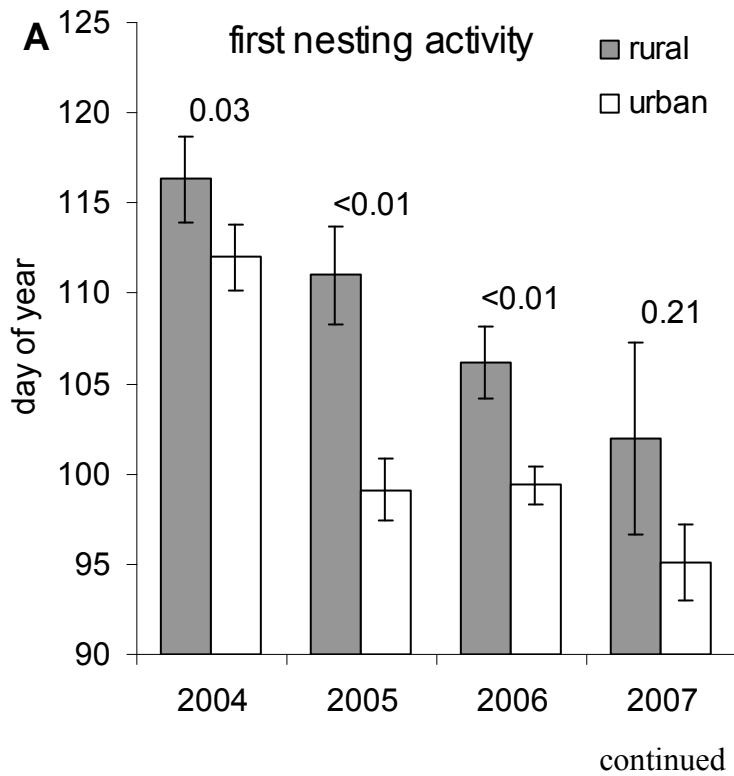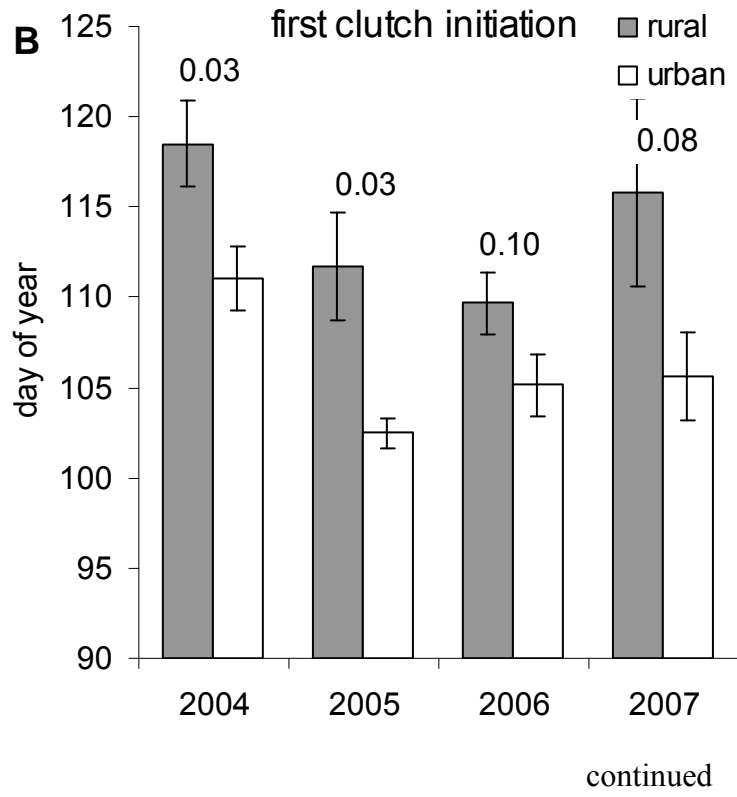
Table 3.2 continued
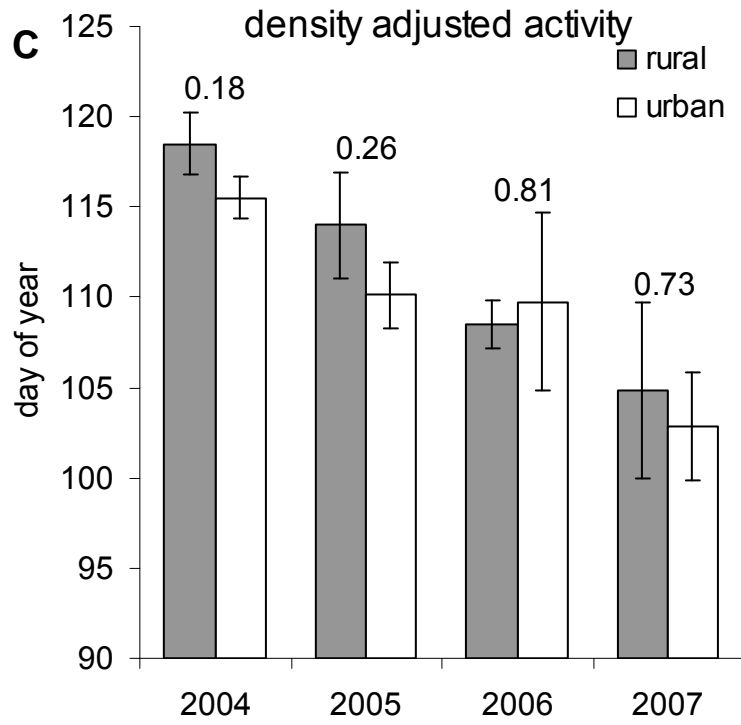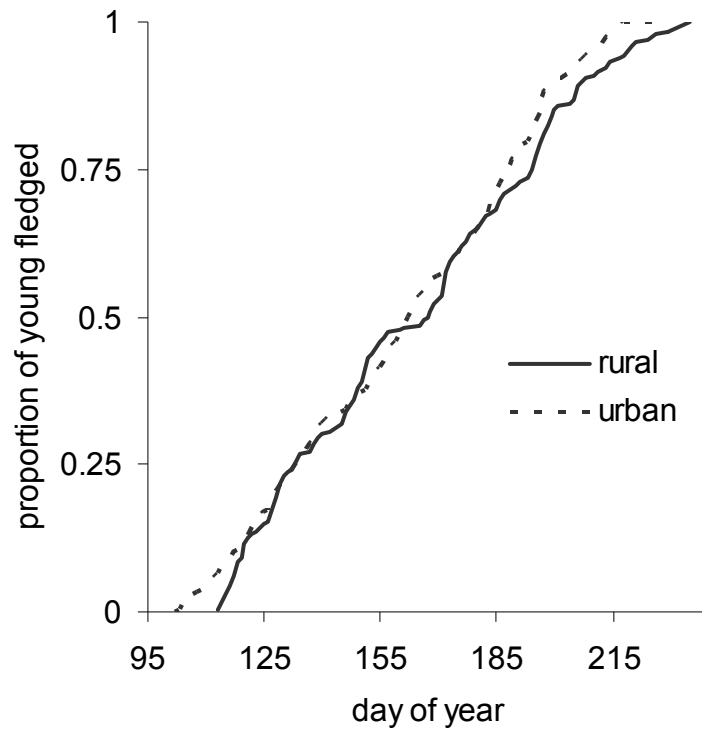
Figure 3. 3: Julian day of Northern Cardinal fledglings from urban and rural sites in central Ohio, USA from 2004-2007. Differences in patterns of timing of fledglings between urban and rural sites are not significant (D = 0.072 , P = 0.28).
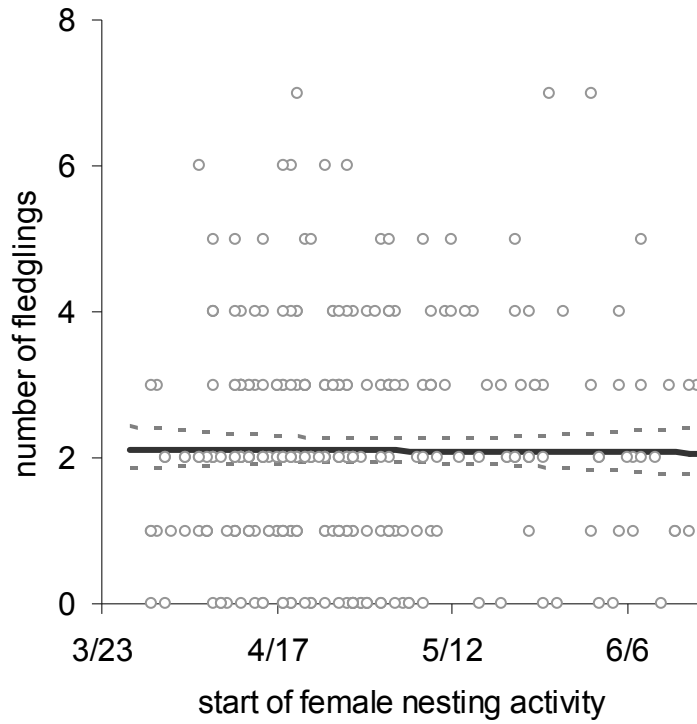
Figure 3. 4: Number of fledglings produced per Northern Cardinal female per breeding

season (N = 302 female nesting histories) based on when nesting was initiated in central

Ohio, USA between 2004-2007.
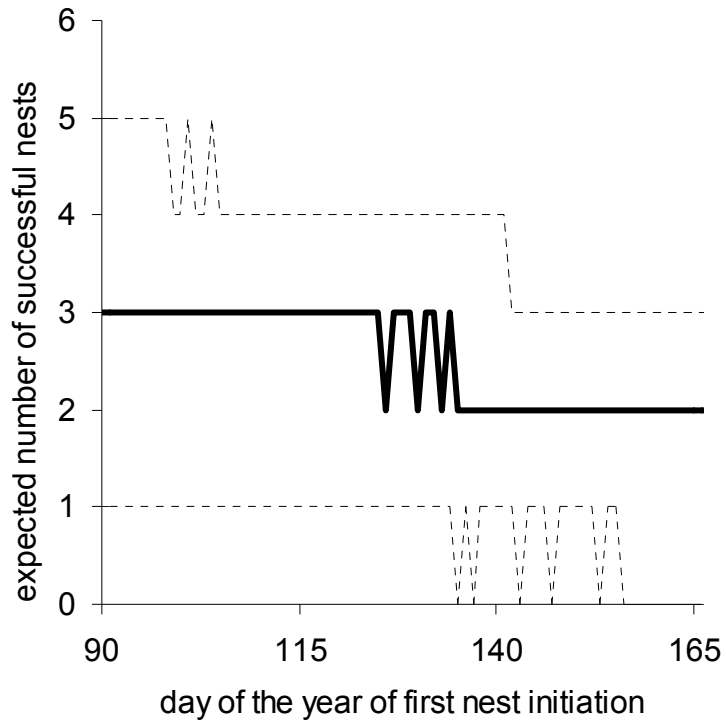
Figure 3. 5: Expected number of successful nests produced over the course of the season based on when a bird initiated nesting for the season and subject to the nest survival probability pattern we observed (e.g., Fig. 3.1). Bold line is the expected number of successful nests based on simulation of 1000 females on each day of the year. The dashed lines show upper and lower 95% confidence intervals. The day of year spans 31 March (day 90) and 15 June (day 166). Notice the wide confidence intervals that include two successful nesting attempts throughout the interval (see text for details).

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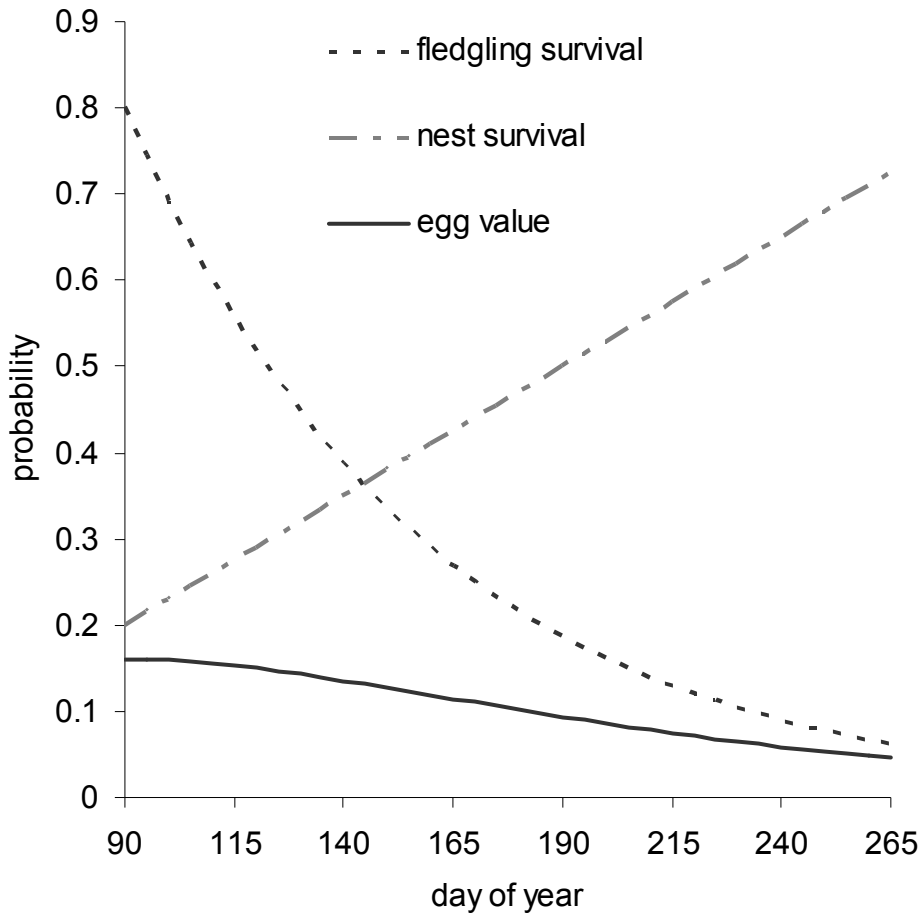
Figure 3. 6: Nest success over the breeding season (dashed and dotted line, i.e., empirical estimates from this study) and hypothetical relationship between fledgling survival to the next breeding season (dotted line), and value per egg (bold line) based on nest survival x fledgling survival. Value of one egg represents probability that an egg laid on a given day of year will result in a recruit to the population the next year. Notice that nest survival is lowest in the beginning of the season but hypothetical probability of recruitment from an egg is highest earliest in the season if fledgling recruitment declines based on when fledging occurred. We show one possible relationship between fledgling survival to the next breeding season but many relationships are possible.

model[a]	K	deviance	ΔAIC_c	w_i
urban index	5	1294.78	0.000	0.297
March temperature	5	1308.48	0.442	0.238
cardinal density	5	1322.01	0.874	0.192
March min temperature	5	1372.88	2.460	0.087
Jan min temperature	5	1405.59	3.449	0.053
Jan temperature	5	1406.49	3.476	0.052
March max temperature	5	1444.36	4.592	0.030
Jan max temperature	5	1516.79	6.647	0.011
null	4	1637.27	7.271	0.008
honeysuckle bud break	5	1541.68	7.330	0.008
buckeye bud break	5	1550.98	7.583	0.007
adult survival	5	1563.31	7.915	0.006
honeysuckle leaf elongation	5	1594.18	8.737	0.004
honeysuckle shoot length	5	1616.87	9.330	0.003
box elder bud break	5	1618.93	9.384	0.003
nest site availability	5	1636.91	9.848	0.002

[a]AIC_c of the top model was 274.85

Table 3. 1 Model rankings based on AIC_c for models explaining day of year of detection of first nesting activity by Northern Cardinals on 14 sites in central Ohio, USA between 2004-2007. All models include additive year effects and the null model contains only year effects.

model[a]	K	deviance	ΔAIC$_c$	w$_i$
March temperature	5	1077.92	0.000	0.662
March max temperature	5	1180.13	3.805	0.099
Jan temperature	5	1200.90	4.538	0.069
March min temperature	5	1208.61	4.806	0.060
urban index	5	1223.53	5.322	0.046
Jan min temperature	5	1270.75	6.912	0.021
Jan max temperature	5	1286.39	7.426	0.016
cardinal density	5	1309.23	8.165	0.011
honeysuckle leaf elongation	5	1314.16	8.323	0.010
honeysuckle shoot length	5	1449.00	12.425	0.001
adult survival	5	1451.87	12.508	0.001
null	4	1548.22	12.621	0.001
honeysuckle bud break	5	1503.98	13.989	0.001
buckeye bud break	5	1505.73	14.038	0.001
box elder bud break	5	1540.87	15.007	0.000
nest site availability	5	1548.15	15.205	0.000

[a]AIC$_c$ of the top model was 267.15

Table 3. 2 Model rankings based on AIC$_c$ for models explaining day of year of first clutch initiations by Northern Cardinals on 14 sites in central Ohio, USA between 2004-2007. All models include additive year effects and the null model contains only year effects.

model[a]	K	deviance	ΔAIC_c	w_i
March temperature	5	1064.40	0.000	0.325
March min temperature	5	1069.16	0.187	0.296
Jan min temperature	5	1080.48	0.630	0.237
Jan temperature	5	1134.17	2.666	0.086
nest site availability	5	1230.22	6.081	0.016
March max temperature	5	1289.72	8.065	0.006
Jan max temperature	5	1289.77	8.066	0.006
null	4	1380.40	8.333	0.005
box elder bud break	5	1299.34	8.377	0.005
urban index	5	1301.81	8.456	0.005
buckeye bud break	5	1309.48	8.703	0.004
honeysuckle leaf elongation	5	1339.32	9.649	0.003
honeysuckle bud break	5	1355.32	10.148	0.002
adult survival	5	1366.02	10.478	0.002
honeysuckle shoot length	5	1372.73	10.684	0.002
cardinal density	5	1380.38	10.918	0.001

[a] AIC_c of the top model was 266.62

Table 3. 3 Model rankings based on AIC_c for models explaining day of year of density-adjusted first nesting activity by Northern Cardinals on 14 sites in central Ohio, USA between 2004-2007. All models include additive year effects and the null model contains only year effects.

CHAPTER 4

ARE URBAN FORESTS UNDERUTILIZED BY

NEOTROPICAL MIGRATORY BIRDS?

4.1 Abstract

Incorrect assessment of habitat quality by birds can results in relatively high quality

habitats supporting fewer individuals than would be most adaptive. Urban forests

provide a potential situation where such underutilization of habitats might occur because

(1) urban forests often support lower densities of Neotropical migratory birds than rural

forests and (2) anthropogenic disturbance and habitat alterations are likely to result in

mismatches between cues typically used in habitat selection and actual habitat quality.

We developed a model to predict expected patterns in patch-level density, fitness, and

individual quality derived from either accurate assessment of urban forests as poor

quality habitats or the undervaluing of urban forests (i.e., quality is not correctly

assessed). A key component in our model that is lacking from previous habitat selection

models is the explicit and simultaneous incorporation of variation in intrinsic individual

quality and habitat quality into realized fitness. Our model predicts that if urban forests

are underutilized then individuals of identical quality (e.g., body condition) will occupy

relatively higher quality habitats in more urban landscapes and have higher fitness than

similar quality birds in rural habitats, even though lower patch average density, fitness

and individual quality might be lower in the urban patch. We then tested the degree to

which urban forests are underutilized using our seven year data set of a Neotropical

migratory bird species breeding in urbanizing Midwestern landscapes. Field data suggest

that urban forests are not underutilized and may even be overused given their apparently

lower habitat quality. This study describes another way to detect underutilization of

habitats and emphasizes the importance of determining the factors that contribute to low

quality habitat in urban forests.

4.2 Introduction

A common pattern associated with urbanization is a decrease in Neotropical

migratory birds (Lancaster and Rees 1979, Beissinger and Osborne 1982, Blair 1996,

Germaine et al. 1998, Allen and O'Connor 2000, Dunford and Freemark 2004, Palomino

and Carrascal 2006). Even in patches of remnant vegetation (e.g., forests) diversity and

densities of Neotropical migratory birds are usually lower in urban patches compared to

those in rural landscapes (Rotterborn 1999, Rodewald and Bakermans 2006), a pattern

generally attributed to differences in habitat quality. Indeed, a number of plausible

conditions might diminish quality of urban habitats. For example, changes in diversity or

structure of vegetation that accompany urban development (Lancaster and Rees 1979,

Tilghman et al. 1987, Borgmann and Rodewald 2005, Chace and Walsh 2006) may

reduce habitat quality as experienced by a bird. In addition, internal fragmentation of

urban forests due to human recreation (Boyle and Samson 1985, Miller et al. 2001,

Mullner et al. 2004, but see Miller and Hobbs 2000, Lindsay et al. 2008) and dog walking

(Miller et al.. 2001, Banks and Bryant 2007) may negatively affect certain Neotropical

migratory birds. Urbanizing landscapes may sustain larger populations of nest, juvenile,

and adult predators including cats (Beckerman et al. 2007, Sims et al. 2008), squirrels

(Friesen et al. 1995, Glennon and Porter 2007), corvids (Marzluff et al. 2001),

mesopredators like raccoons (Prange and Gehrt 2004), as well as the brood parasite,

brown-headed cowbird (*Molothrus ater*, Askins 1995, Burhans and Thompson 2006).

Although labeling urban habitats with these conditions as low quality given these

conditions is conceptually attractive, a more thoughtful approach would be to consider

how alternative scenarios predicted by habitat selection theory could result in similar

avian distributional patterns.

The most frequently invoked habitat selection models assume that individual

organisms can accurately perceive, assess, and respond to habitat quality. In the case of

ideal free habitat selection (sensu Fretwell and Lucas 1970), lower densities in urban

forests are the consequence of lower habitat quality. However, due to density-dependent

mechanisms (e.g., crowding effect), patches of varying quality ultimately achieve

equivalent levels of patch-average fitness. Under the ideal-despotic habitat selection,

lower habitat quality in urban areas also leads to lower densities in urban forests but with

one important qualification – because birds defend territories for exclusive use, density-

dependent feedbacks are dampened. Thus, the ideal-despotic model results in low quality

patches achieving lower patch-average fitness than high quality patches. In this paper we

collectively refer to both ideal free and ideal despotic (or dominance) models as our "low

quality urban forest hypothesis", where birds correctly perceive urban forests as lower

quality habitat than rural forests.

A failure to correctly perceive habitat quality also could generate lower densities and occurrences of Neotropical migratory birds in urban versus rural forests. This process is similar to mechanisms producing ecological traps, where cues for habitat selection are disassociated from the underlying habitat quality (Ward and Schlossberg 2004, Ahlering and Faaborg 2006, Campomizzi et al. 2008). As described by Gilroy and Sutherland (2007), lower densities could result from a selection bias against urban forests even if inherent quality were comparable to rural forests. For example, if a cue for high quality habitat is manipulated or removed, this could prompt individuals to avoid even high quality habitats and eventually lead to lower densities in the less-preferred but high quality habitat. Failure to select high quality habitat would lead to missed opportunities for fitness gains, lower population levels, and underutilization of the avoided high quality habitat (Gilroy and Sutherland 2007). Because urbanization is associated with dramatic changes to the landscape, alteration of habitat cues may result in urban forests being underutilized by Neotropical migratory birds. We call this process that would generate lower densities in urban forests the "underutilized urban forest hypothesis."

Lower patch-level fitness is typically interpreted as representing lower quality habitat (Johnson 2007) and would tend to support the "low quality urban habitat hypothesis" over the "underutilized urban forest hypothesis." Few studies have examined fitness effects on birds in remnant habitats in urban landscapes; even fewer have explicitly considered Neotropical migratory birds. Birds in urban habitats have been shown to have lower nest survival (Bakermans and Rodewald 2006, Grandmaison and Niemi 2007 but see Danielson et al 1997, Morrison and Bolger 2002, Newell and

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Kostalos 2007), produce fewer fledglings per capita (Bakermans and Rodewald 2006, Rodewald and Shustack 2008), have smaller clutch sizes (Horak 1993) and elevated rates of brown-headed cowbird parasitism (Burnhans and Thompson 2006, Rodewald and Shustack 2008). Although relationships between urbanization and fitness components are not always consistent among studies, ecologists generally assume that the paucity of Neotropical migratory birds in urban areas is a consequence of lower habitat quality than rural areas.

While few would dispute that habitat quality can profoundly affect fitness, research also demonstrates that variation in individual intrinsic quality contributes to fitness as well. For example, female Eastern Kingbirds (*Tyrannus tyrannus*) with smaller tarsi produce larger clutches, and experience less nest predation, and have greater lifetime reproductive success (Murphy 2007) and older eagles (*Aquila chrysaetos* and *Hieraaetus fasciatus*) had greater reproductive success than younger eagles, even after accounting for habitat heterogeneity (Carrete et al. 2006). Thus, if the "underutilized urban forest hypothesis" applies then higher quality individuals would be expected to preferentially occupy the preferred, though equal quality habitat. If the preferred high-quality habitat is limiting, then low quality individuals would be overrepresented in the urban habitat and this could result in lower patch-average fitness in urban areas despite similar underlying habitat quality in urban and rural areas.

In this study we evaluated the extent to which distribution and fitness of birds across a rural-to-urban landscape gradient comply with either the low-quality or underutilization hypotheses. To do this we modified the Pulliam and Danielson (1991)

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ideal-preemptive model of habitat selection to include variation of individual quality and errors in perception of habitat quality. This model was then used to predict patch-level densities, patch-level fitness, and the fitness of individuals of similar quality that should be observed under both the "low quality urban forest hypothesis" and the "underutilized urban forest hypothesis." We then applied seven years of field data from an Acadian Flycatcher population breeding in central Ohio, USA to evaluate the extend to which urban habitats represent lower quality habitat or are underutilized by Acadian flycatchers.

4.3 Model development

We began with the ideal-preemptive model of habitat selection proposed by Pulliam and Danielson (1991). This model is similar to the ideal-free model proposed by Fretwell and Lucas (1970) in that individuals are ideal and have complete knowledge of the quality of the habitats. In both models, individuals are free of any costs associated with selecting habitats. However, the ideal-preemptive model differs from the ideal-free model in one key respect – it incorporates within-patch habitat heterogeneity so that each successively colonizing individual occupies a successively lower quality territory without reducing the fitness prospects of the previous colonizers. There is no density-dependent reduction in habitat quality (e.g., through crowding) only a site-dependent reduction in the quality of habitat used (i.e., Rodenhouse et al. 1997). Thus an individual selecting a territory will select the best of the unoccupied territories because previously selected breeding sites have been "preempted." A key prediction of the ideal-preemptive model is that the individuals occupying the worst territory in each patch will have equal fitness,

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but the patch-level average fitness will be lower in the lower quality patch. This contrasts with the ideal-free distribution, where the patch-average fitness is expected to be equal across patches. Further, the ideal-preemptive model does not assume any resistance to subsequent settlers, as the ideal despotic (dominance) model does (Fretwell and Lucas 1970).

We defined $\beta_{in}(n_i)$ as the habitat quality experienced by the individual who utilizes the nth best territory in habitat i when there are n_i individuals already breeding in habitat i. However, in contrast to the ideal-preemptive model, individuals do not make their habitat selection decision based on $\beta_{in}(n_i)$. In order to incorporate the possibility of errors in the perception of habitat quality, as suggested by Gilroy and Sutherland (2007) where high quality habitat is undervalued, we incorporated an additional term P_i reflecting a modification to the perceived quality of habitat i. Thus, in our model, birds have ideal information about the *perceived* quality of each territory $P_i\beta_{in}(n_i)$ and choose an available territory that has the highest *perceived* quality. While various relationships between perceived and actual habitat quality are possible (e.g. Kristan 2003) we use this simple relationship to reflect the idea that all territories in a patch are not perceived at their actual quality because of a lack of some cue. Yet, the fitness of the individuals is related to the actual habitat quality, $\beta_{in}(n_i)$.

A key assumption of previous habitat selection models (Fretwell and Lucas 1970, Pulliam and Danielson 1991, Rodenhouse et al. 1997, Donovan and Thompson 2001, Kokko and Sutherland 2001, Kristan 2003) is that all individuals are equal. Our model incorporates variation in individual quality that affects the fitness outcome of that

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individual. We assume that individuals of equal quality will have equal fitness if they occupy habitats of equal quality. However, if individuals of differing quality occupy territories of the same quality, the lower quality individual will have lower fitness because of its lower individual quality. We define Q_i as the individual quality of individual i and generate a Q_i from a normal distribution with mean=0 and a defined standard deviation (*sd*).

In the model each individual selects a breeding territory from the available breeding territories that has the maximum perceived quality, $P_i \beta_{in}(n_i)$. Individuals select territories in descending sequence of individual quality, Q_i, of each individual. Thus the highest quality individual selects the territory with the highest perceived quality and so on until all individuals have selected the highest available perceived territory at the time of their selection. Each individual will then experience a fitness that is related to its territory quality (e.g. $\beta_{in}(n_i)$) and its individual quality (e.g. Q_i). We do not know the empirical relationship between the contribution of habitat quality and individual quality to fitness of an individual. Therefore we assume that the fitness realized by an individual is the sum of the individual quality (Q_i) and the habitat quality ($\beta_{in}(n_i)$), with an additional term (*q*) to define the relative contribution of individual quality as compared to habitat quality. Hence, the fitness of individual i in territory n in patch i is represented as $F_i = qQi + \beta_{in}(n_i)$. In this way, an average individual (e.g. Q_i=0) would have a fitness (F_i) based solely on the habitat quality and above average individuals (e.g. Q_i>0) do better than average individuals and so on.

4.4 Simulation

We used this model to simulate two hypotheses that could produce lower densities and fitness in urban versus rural forests. We used a simple two patch case but expect the results to be more widely applicable. Each patch (denoted with subscripts R and U reflecting our interests in rural and urban and patches) had 100 territories which were assigned integer habitat quality values based on the exponential function $f(x)= \theta e^{-\theta x}$ (Pulliam and Danielson 1991, Kristan 2003), with $x = 0$ to 10 by integers. This generates a habitat distribution where low quality habitats are more abundant and higher quality habitats are fewer.

We generated a population (N) of 100 individuals from a normal distribution of mean=0 and standard deviation of five (sd=5). We used a standard deviation of five so that approximately 95% of the individuals would have a Q_i between -10 and +10. We assumed that the individual quality contribution (q) to fitness was half of the contribution of the habitat quality, reflecting the greater importance of habitat quality over individual quality to fitness. Further, we bounded the fitness (F_i) of each individual between 0 and 10 in order to reflect maximum and minimum thresholds on fitness. For example, an individual with Q_i=10 will have a F_i=5 when $\beta_{in}(n_i)$=0, but will have F_i=10 when $\beta_{in}(n_i)>/=5$. We do not specifically define "fitness," but in this case it could be thought of as the number of offspring produced by the individual in that territory.

Each simulation consisted of placing individuals onto territories based on the decision rules of the model (i.e. selecting the perceived best available territory) and subsequently calculating the fitness of each individual based on the territory quality and

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the individual quality. The output of each simulation consisted of 1) the number of individuals in each patch, 2) the patch-average quality of the individuals and the patch-average fitness of each patch, 3) the average quality and fitness of the average individuals within each patch. For this calculation, we defined individuals of "average" quality as individuals with $Q_i < |0.25sd|$. We performed each simulation 100 times. We report the mean values from the 100 runs and the standard deviations of those values.

We simulated the two hypotheses by altering parameters θ and P. First we simulated the "low quality urban forest hypothesis" which assumes that habitat quality is lower in urban areas and assessment of habitat quality is accurate (Fig. 1A). We made $\theta_R=0.1$, $\theta_U=0.4$, $P_R=1$, and $P_U=1$. We simulated the "underutilized urban forest hypothesis" which states that habitat quality is similar in urban and rural forests but that individuals perceive urban habitat as a lower quality than it actually is (Fig. 1B). For this hypothesis we made $\theta_R=0.1$, $\theta_U=0.1$, $P_R=1$, and $P_U=0.5$ (Table 1). We used one set of parameters for each hypothesis to illustrate the key similarities and difference of these two mechanisms.

4.5 Field Methods

In previous studies we reported that densities and seasonal productivity of Acadian flycatchers were negatively related to urbanization whereas clutch initiations were positively related to urbanization (Bakermans and Rodewald 2006, Rodewald and Bakermans 2006, Rodewald and Shustack 2008). Thus, this population of Acadian flycatchers in an urban to rural landscape displays the patterns produced by both of our

hypotheses, specifically lower densities and lower fitness components (fewer fledglings and delayed clutch initiation) in forests of more urbanized landscapes. In the current study we expand on our previous studies with an additional year of data. In the current analysis we also analyzed data from individual birds for which we have both individual morphometric data (i.e. we captured and banded the individual) and data on fitness components.

The methods we used to quantify the landscape around each site and collecting field data are described in detail in a previous study (Rodewald and Shustack 2008). Briefly, the landscape was quantified based on proportions of different land cover surrounding each of 35 forest sites in central Ohio, USA. Using a principle components analysis these land cover variables were collapsed into a single variable explaining 80% of the variation. We called this new variable the urban index; higher values reflected sites in more urbanized landscapes. Acadian flycatchers were studied between 2001-2007. As possible, individual Acadian flycatchers were measured, banded, and monitored through their breeding cycle in each year. We recorded tarsus length, unflattened wing chord, and mass on individual birds. Based on intensive field methods (see Rodewald and Shustack 2008) we located nests and determined when clutches were initiated. We standardized the clutch initiation dates across years to the median clutch initiation date in 2006 (e.g., in 2005 the median clutch initiation date was two days later than in 2006, therefore we subtracted two days from each clutch initiation date from 2005). We determined the number of fledglings produced by each individual over the course of the breeding season and the number of nesting attempts by each individual. In

each year we intensively searched the study sites to determine if previously banded

individuals returned to the study site.

Analysis

Based on the simulation results (see Results) we found that the major difference

between the "low quality urban habitat hypothesis" and "underutilized urban forest

hypothesis" was when individuals of equal quality (i.e., $Q_i < |0.25sd|$) from each habitat

were compared. When simulated under the "low quality urban forest hypothesis"

individuals of equal quality had similar fitness values in either habitat patch. In contrast

under the "underutilized urban forest hypothesis," equal quality individuals achieved

higher fitness in the urban patch due to settlement patterns. Under this hypothesis the

highest quality individuals occupied territories in the preferred rural patch until

$P_U \beta_{U1}(n_{i0}) = P_R \beta_{Rn}(n_i)$. After best available perceived territories between patches was

equal, an individual which selected the urban territory would actually select a territory

with an actual quality $1/P_U$ times the actual quality of the best available rural territory.

This critical difference led us to look for relationships between individual

variation and fitness components in our population of Acadian flycatchers. We reasoned

that if we found evidence for individuals of equal quality (i.e., as detetermined by similar

morphological features) performing better (higher values for fitness components) in

urban compared to rural areas than this would support the "underutilized urban forest

hypothesis" whereas if individuals of equal quality performed equally well regardless of

position on the urban index, we would fail to support the "underutilized urban forest hypothesis" in favor of the "low quality urban forest hypothesis."

To determine the effect of individual quality on fitness after accounting for the effects of habitat quality, we included both habitat quality (i.e. urban index) and individual quality (i.e. morphology variables) in regression models. We specifically lexamined slopes of parameter estimates for the individual variables. Based on the "low quality urban forest hypothesis" we would predict nonsignificant parameter estimates equal to zero. Parameter estimates that were statistically significant and in the direction suggestive of lower quality individuals having higher fitness component values would support the "underutilized urban forest hypothesis."

Specifically, for both males and females, we looked for relationships between individual characteristics (wing length, tarsus length, body size, body mass, and condition) with fitness components (clutch initiation date, nest survival, number of fledglings, probability of renesting, and probability of being resighted in a subsequent year). We do not know what specifically contributes to individual quality in the Acadian flycatcher, but morphological features are likely candidates (Murphy 2007). For some individuals we had more than one year of fitness-related data (i.e. they were confirmed breeders in >1 year), but typically individuals were only captured once. Consequently, we used morphological data from original capture date and fitness data from all years. Fitness information from each female or male from each year was treated as an independent observation in the analyses. Age may be related to individual quality either through greater survival of higher quality individuals or through experience gained by

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older individuals (Nol et al. 1987, Preault et al. 2005), though we do not have age information.

In our previous research we reported relationships between some individual morphology variables and the urban index (Rodewald and Shustack 2008). High levels of multicollinearity could obscure the independent effects of the urban index and the individual morphological metrics (Gotelli and Ellison 2004). We assessed multicollinearity between the urban index and all morphological measurements (one per individual bird and each sex separately) by using Spearman's correlations. All correlations were low ($r < |0.21|$) so we did not consider multicollinearity to be a concern in our analyses. In order to assess if individuals of similar size performed better in urban forests, we examined each individual characteristic along with the urban index in regression models. A significant and positive slope (except for clutch initiation) for the urban index would indicate that at a given level of individual morphological characteristic, individuals in more urban areas have higher fitness components, the critical prediction separating our two hypotheses.

We used least squares regression to examine relationships between the natural logarithm of the clutch initiation date. We used the natural log of the clutch initiation date to improve the normality of residuals. Although residuals from one regression were still non-normal, for simplicity we used this transformation for all of these regressions. (Non-normality should not affect the direction of the slope parameter, the object of our main interest). We report the P value for Shapiro-Wilks tests for normality for these regressions (PROC UNIVARIATE; SAS 9.1). We used logistic exposure models (PROC

GENMOD; Shaffer 2004) to examine the relationship between nest survival and individual morphological variables and the urban index. In the nest survival regressions we included the day of the year as a variable because our previous results have indicated an important seasonal effect to nest survival (D. Shustack unpublished data). We used logistic regression (PROC LOGISTIC, SAS 9.1) to assess the probability of renesting and resighting an individual in a future year based on individual morphology and the urban index. We assessed the goodness-of-fit of the logistic regression and logistic exposure models with Hosmer-Lemeshow tests. Because negative binomial regressions did not converge properly for the number of fledglings, we used Poisson regression (PROC GENMOD) to examine the relationship between the number of fledglings and individual morphological variables and the urban index. The Pearson chi-square goodness-of-fit value divided by the degrees of freedom yielded values ~0.3 suggesting that underdispersion was an issue. Therefore we adjusted the standard error and significance estimates from these Poisson regressions by the square root of the Pearson chi-square divided by the degrees of freedom (Allison 1999). We report this value as the scale parameter in the results and the Pearson chi-square goodness-of-fit value divided by the degrees of freedom as C in the results. We acknowledge that we performed numerous significance tests for the slopes of the parameters in our models but we do not make multiplicity corrections and report nominal *P*-values throughout.

4.6 Results

Both of our simulations were able to generate the common patterns reported in
urbanizing landscapes. Both hypotheses produced lower densities, lower patch average
fitness, and lower patch average bird quality in the urban patch compared to the rural
patch. However, comparison of average individuals (i.e. $Q_i < |0.25sd|$) among sites
revealed a key difference. Average individuals under the "low quality urban habitat
hypothesis" had similar fitness to the average individuals in the rural patch. However,
under the "underutilized urban forest hypothesis", at a given level of individual quality,
individuals in the urban patch had higher fitness than the individuals in the rural patch
(Table 1, Figs. 2). Considering two birds (e.g., A and B) of similar quality (e.g. $Q_A \approx Q_B$)
reveals why this pattern emerged. Because birds A and B are of similar quality, the term
qQi contributes equally to F_i for both birds. Therefore only habitat quality, β_A and β_B,
leads to variation in their fitness. Under either hypothesis, if both individuals went to the
same patch, they would occupy territories of approximately equal quality and thus fitness
of each would be similar. If bird A and B settled different patches, they would still both
select territories with similar *perceived* habitat quality. Under the "low quality urban
forest hypothesis" the perceived habitat quality is synonymous with the actual habitat
quality ($P_R=P_U$) and therefore birds A and B would occupy territories so that $\beta_A \approx \beta_B$,
thus birds A and B would have similar fitness (horizontal dotted line in Fig. 1A). Under
the "underutilized urban forest hypothesis" the bird which selected the urban patch,
selected a territory where $P_U\beta_U \approx \beta_R$. Therefore, the individual in the urban habitat
actually selected a territory (e.g., horizontal dashed line in Fig. 1B) that is better than the

territory available to a bird settled in the preferred rural patch, where the best territories are already occupied. In the case of our simulations where P_U=0.5, the bird selecting the urban territory selected a territory that was equal to B_R/0.5 or 2x better than the rural territory.

Individual morphometric measurements were weakly correlated ($r<|0.21|$) with the urban index and only correlations with male wing chord and male weight had $P<0.05$ (Table 2). Only two (female condition and weight) of the ten negative binomial regression coefficients were in the direction (positive) predicted by the underutilization hypothesis. Three coefficients (male tarsus, condition and weight) had P-values <0.10 and none below P=0.05 (Table 3).   One least squares regression coefficient (female wing chord) for the natural log of clutch initiation dates were in the direction predicted by the underutilization hypothesis but the coefficient had a $P>0.6$. All male regression coefficients had $P<0.06$; but none were in the direction predicted by the underutilization hypothesis (Table 3). The urban index was not a significant regression coefficient for any nest survival or probability of renesting regressions ($P>0.10$) but all parameter estimates were in the direction predicted (positive) by the underutilization hypothesis (Table 4). No parameter estimates for the urban index were significant for the probability of resighting males or females and the direction of the parameters were mixed (Table 5). The coefficients for the urban index based on the Poisson regression for the number of nesting attempts had four Ps less than 0.06 for males but none of the parameter estimates for males or females were in the direction predicted (positive) by the underutilization hypothesis (Table 5).

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4.7 Discussion

Modeling. The output from our models demonstrates that lower density of individuals and lower patch-average fitness outputs do not necessarily indicate that habitats are of lower quality than those with higher densities and higher patch-average fitness. In fact, the disconnect between habitat quality and fitness/density measures can arise when individuals fail to select high quality habitats and there is variation in individual quality that contributes to fitness. Our models demonstrated that underutilization of habitat may explain distributional patterns generally attributed to habitat quality alone. Further empirical data are required to make specific quantitative predictions as to the magnitude of difference that might be expected under the hypotheses we considered. However, the key qualitative prediction to differentiation these two hypotheses (low quality urban forest hypothesis" versus "underutilized urban forest hypothesis") was that individuals of similar quality should do better in the underutilized habitat than the preferred habitat.

Field data. Based on our analysis of seven years of field data of the Neotropical migratory bird, Acadian Flycatcher, we found little evidence to suggest that urban areas are underutilized by this species. While five of the six fitness components examined showed one or more coefficient in the direction predicted by the underutilization hypothesis, none of these parameter estimates were significant. Further, of the seven coefficients that had $P<0.5$ and additional five with $P<0.1$ none were in the direction predicted by the underutilization hypothesis. The finding of significant additive effect of

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urbanization in the opposite direction as that predicted by the underutilization hypothesis suggests that urban forests may even be used more than they should be. In combination, these results indicate that forests in more urban areas are indeed low quality habitat for Acadian flycatchers and that the Acadian flycatchers appropriately avoid these habitats thus leading to lower densities in these areas (Rodewald and Bakermans 2006). These results support our previous suggestion (Rodewald and Shustack 2008) that lower quality individuals may be relegated to these urban habitats either the through competitive exclusion in a despotic manner from higher quality rural forests or because they naively select these low quality forests or are unable to select better forests.

In our analysis we considered five commonly measured (or calculated) individual morphological variables that displayed variation in our population. We assumed that these individual variables were related to the fitness components we also considered. Several of the regression coefficients for these variables had $P<0.05$ supporting a relationship between morphology and fitness components. However, it is possible that these or other measures of bird quality are also important for Acadian flycatchers. In general little is known about which factors contribute to variation in individual quality in birds and even less for Acadian flycatchers. The lack of information on what constitutes individual bird quality may be one reason why individuals are often assumed to be equal in modeling studies (Fretwell and Lucas 1970, Pulliam and Danielson 1991, Rodenhouse et al. 1997, Donovan and Thompson 2001, Kokko and Sutherland 2001, Kristan 2003). Nevertheless, wild populations display variation in morphology, genetic composition, and behavior that is likely related to fitness. For example, bill shape in the great tit (*Parus*

major) is related to food handling efficiency and birds with different shaped bills were better with some foods than others (Gosler 1987). Survival in the Galapagos *Geospiza* spp. finches was related to bill size (Grant 2003). Another key insight from the Galapogos finches, however, is that the morphological features that contribute to fitness in one year may not be the same in subsequent years (Grant 2003). Murphy (2007) found relationships between morphology and lifetime reproductive success in another flycatcher species, the Eastern Kingbird, with smaller birds having larger clutches and greater lifetime reproductive success although not all studies have found relationships between morphology and fitness (Bouwman et al. 2007). Larger birds may be able to directly out-compete smaller individuals for breeding sites, territories or mates (Jonart et al. 2007, Ost et al. 2007). Bird behavior including foraging ability and nest attentiveness may contribute to bird quality (Lewis et al. 2006). For instance nest defense may be important in preventing nest predation and bird size, agility, or temperament may be important in such encounters (Olendorf and Robinson 2000). Larger or smaller females may be preferred by males for their potential to produce larger offspring, egg volumes (Neto and Gosler 2005), or larger clutches (Murphy 2007), although larger eggs may not translate into more fit offspring (Krist et al. 2004). Larger individuals may be able to collect larger food items for themselves or their offspring (Grigera and Trejo 2007). Bird size may be related to over winter survival (Schulter and Smith 1986). On a genetic level, some studies have indicated that heterozygozity within an individual is related to clutch size and laying date (Tomiuk et al. 2007, Ortego et al. 2007).

The fitness components we considered did not indicate that urban habitats were underutilized, but it is possible that effects of other fitness components might vary. We assume that the fitness components we considered are related to the genetic contribution by individuals to future generations. Although more direct measures of fitness (e.g. fledglings recruited to the population) would be preferred (Coulson et al. 2007) we did not have this information. There are other potentially relevant fitness components that we did not consider including egg mass, clutch size, fledgling mass or size, fledgling survival, timing of fledging, and foraging efficiency. Tradeoffs in these fitness components (Chalfoun and Martin 2007) and scale dependency (Pidgeon et al. 2006) further add to difficulty in testing the "underutilization hypothesis".

This study expands our understanding of the ecology of urbanizing systems in two important ways. First, our model demonstrates that perceptual errors leading to underutilization of a habitat can, in fact, generate patterns of lower density and lower fitness, even in the absence of differences in habitat quality among sites. Not only does our model affect the way we conceptualize landscapes, but it also provides a useful tool for evaluating underutilization of habitats by considering the fitness of birds of equal quality across habitats. Second, we provide strong empirical evidence showing that urban habitats in an urbanizing Midwestern landscape are not underutilized and may indeed represent lower quality habitats for Neotropical migrants. In light of this, we urge conservation biologists to continue research that seeks to identify and restore those habitat features that most strongly constitute habitat quality for sensitive and declining species in urbanizing landscapes.

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4.9 Literature Cited

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Table 4. 1 Parameter inputs and summary outputs for two simulated hypotheses to account for distributions of birds across urban and rural patches. Subscripts U and R refer to urban and rural; q:relative contribution of individual quality versus habitat quality; θ:value defining habitat quality function based on $f(x)= \theta e^{-\theta x}$; P: reduced perception of habitat quality; N: average number of individuals; F: patch average fitness from 100 simulations; $P_{(FR\ vs\ RU)}$:P value from nonparametric t-test comparing F urban and rural from 100 simulations; Q: patch-average individual quality; $P_{(QR\ vs\ QU)}$: P value from nonparametric t-test comparing Q between urban and rural for 100 simulations; $N_{(ave)}$: average number of individuals meeting that had $Q_i < |0.25sd|$ from 100 simulations; $F_{(ave)}$: average from 100 simulations of fitness of individuals with $Q_i < |0.25sd|$; $P_{(FR(ave)\ vs\ RU(ave))}$: P value from nonparametric t-test comparing $F_{(ave)}$ between urban and rural for 100 simulations; $Q_{(ave)}$: average from 100 simulations of the average quality of individuals $Q_i < |0.25sd|$; $P_{(QR(ave)\ vs\ QU(ave))}$: P value from nonparametric t-test comparing $Q_{(ave)}$ between urban and rural; slope estimate:patch: slope estimate for a patch effect on the relationship between fitness and bird quality; $P_{(slope\ estimate)}$: P value for significance of slope estimate.

Table 4.1	"low urban habitat quality"		"underutilization"	
	mean	st.dev.	mean	st.dev.
q	0.500	*n/a*	0.500	*n/a*
θ_R	0.100	*n/a*	0.100	*n/a*
θ_U	0.400	*n/a*	0.100	*n/a*
st. dev. of q	5.000	*n/a*	5.000	*n/a*
P_R	1.000	*n/a*	1.000	*n/a*
P_U	1.000	*n/a*	0.500	*n/a*
N	100.000	*n/a*	100.000	*n/a*
N_R	65.430	1.305	61.000	0.000
N_U	34.570	1.305	39.000	0.000
F_R	5.754	0.167	6.305	0.175
F_U	3.496	0.231	5.659	0.240
$P_{(FR\ vs\ RU)}$	0.008	0.013	0.272	0.131
Q_R	0.988	0.444	2.112	0.541
Q_U	-1.901	0.563	-3.211	0.577
$P_{(QR\ vs\ QU)}$	0.009	0.013	0.000	0.000
$N_{R(ave)}$	6.480	1.667	10.710	2.249

Table 4.1 continued

$N_{U(ave)}$	13.160	2.863	8.590	2.738
$F_{R(ave)}$	4.783	0.321	4.417	0.428
$F_{U(ave)}$	4.684	0.401	8.856	0.293
$P_{(FR(ave)\ vs\ RU(ave))}$	0.580	0.265	0.005	0.008
$Q_{R(ave)}$	0.055	0.204	-0.026	0.282
$Q_{U(ave)}$	-0.010	0.278	0.043	0.282
$P_{(QR(ave)\ vs\ QU(ave))}$	0.580	0.265	0.450	0.329
slope estimate:patch	-0.110	0.126	3.724	0.112
$P_{(slope\ estimate)}$	0.480	0.307	0.000	0.000

	females			males		
	r	*P*	N	*r*	*P*	N
body size	-0.247	0.080	51	-0.157	0.154	84
condition	0.203	0.157	50	-0.166	0.134	83
tarsus	-0.203	0.153	51	-0.060	0.589	84
wing chord	-0.162	0.243	54	-0.203	0.035	108
weight	0.183	0.190	53	-0.199	0.043	104

Table 4. 2: Pearson correlations (*r*) between the urban index and individual morphology variables for males and female Acadian flycatchers breeding in central Ohio, USA between 2001-2007.

Table 4. 3 Parameter estimates relating individual morphology variables and urbanization to the number of fledglings produced over the season (negative binomial regression) and the natural logarithm of day of the year of clutch initiation (least squares regression). Parameter estimates, standard errors, and P values for significance tests of the regression coefficients are shown. N is the sample size used in each regressions. C refers to the value of the Pearson chi-square value divided by the degrees of freedom. For clutch initiation, the $P_{(normal)}$ is the P value of a Shapiro-Wilks test for normality of the residuals from the regression.

Table 4.3	# seasonal fledglings	se	*P*	N	C	clutch initiation	se	*P*	N	*P*(normal)
Intercept	4.093	4.50	0.36	66	0.90	5.164	0.18	0.00	63	0.838
tarsus female	-0.255	0.30	0.40			-0.008	0.01	0.49		
urban	-0.087	0.22	0.70			0.006	0.01	0.48		
dispersion	0.489	0.27								
Intercept	0.034	0.34	0.92	66	0.94	5.013	0.01	0.00	63	0.840
body size:female	-0.223	0.23	0.32			-0.025	0.01	0.01		
urban	-0.109	0.23	0.63			0.001	0.01	0.89		
dispersion	0.476	0.27								
Intercept	0.362	0.19	0.06	65	1.00	5.042	0.01	0.00	62	0.874
condition:female	-0.203	0.09	0.03			-0.007	0.00	0.08		
urban	0.021	0.21	0.92			0.012	0.01	0.15		
dispersion	0.340	0.24								
Intercept	4.474	5.49	0.42	68	0.93	6.002	0.21	0.00	64	0.935
wing:female	-0.060	0.08	0.45			-0.014	0.00	0.00		
urban	-0.063	0.22	0.78			-0.004	0.01	0.61		
dispersion	0.470	0.26								
Intercept	2.810	1.21	0.02	67	1.01	5.149	0.05	0.00	63	0.922
weight:female	-0.186	0.09	0.04			-0.008	0.00	0.04		
urban	0.028	0.21	0.89			0.012	0.01	0.17		
dispersion	0.341	0.23								
Intercept	-1.547	2.42	0.52	141	0.89	5.223	0.12	0.00	127	0.141
tarsus:male	0.115	0.15	0.45			-0.011	0.01	0.17		
urban	-0.198	0.11	0.07			0.012	0.01	0.03		
dispersion	0.378	0.17								
Intercept	0.189	0.13	0.14	141	0.89	5.061	0.01	0.00	127	0.119
body:male	0.122	0.13	0.34			-0.009	0.01	0.17		
urban	-0.178	0.11	0.12			0.010	0.01	0.05		
dispersion	0.372	0.17								
Intercept	0.263	0.11	0.02	137	0.88	5.056	0.01	0.00	124	0.146
condition:male	0.020	0.11	0.86			0.001	0.01	0.90		
urban	-0.206	0.11	0.07			0.013	0.01	0.02		
dispersion	0.412	0.17								
Intercept	-0.944	3.74	0.80	172	0.88	5.081	0.17	0.00	151	0.040
wing:male	0.016	0.05	0.75			0.000	0.00	0.89		
urban	-0.165	0.11	0.12			0.016	0.01	0.00		

Table 4.3 continued

dispersion	0.415	0.16								
Intercept	0.271	1.33	0.84	166	0.88	5.030	0.07	0.00	147	0.152
weight:male	-0.001	0.10	0.99			0.002	0.00	0.69		
urban	-0.193	0.11	0.07			0.015	0.01	0.00		
dispersion	0.430	0.16								

Table 4. 4: Parameter estimates relating individual morphology variables and urbanization to the probability of nest survival (logistic exposure, Shaffer 2004) and the probability of renesting (logistic regression) within a season. Parameter estimates, standard errors, and P values for significance tests of the regression coefficients are shown. $N_{effective}$ is the effective sample size used in nest survival analysis (see Rotella et al. 2004) and N is the sample size for logistic regressions for renesting probability. $P_{(HL)}$ refers to the value of the P value from a Hosmer and Lemeshow (1989) tests.

Table 4.4	nest survival	se	*P*	N	P(HL)	prob. renesting	se	*P*	N	P(HL)
Intercept	9.327	4.42	0.03	2373	0.47	2.876	6.18	0.64	129	0.979
tarsus female	-0.405	0.29	0.16			-0.195	0.41	0.64		
urban	0.131	0.23	0.56			0.038	0.31	0.90		
day of year	0.002	0.01	0.70							
Intercept	2.977	1.07	0.01	2373	0.58	-0.258	0.43	0.55	129	0.975
body size:female	-0.355	0.20	0.08			-0.202	0.31	0.51		
urban	0.091	0.23	0.69			0.012	0.32	0.97		
day of year	0.002	0.01	0.77							
Intercept	3.375	1.08	0.00	2355	0.13	-0.036	0.28	0.90	128	0.944
condition:female	-0.161	0.09	0.08			0.010	0.14	0.94		
urban	0.227	0.23	0.32			0.089	0.32	0.78		
day of year	0.002	0.01	0.73							
Intercept	10.921	5.21	0.04	2477	0.54	4.345	7.50	0.56	131	0.940
wing:female	-0.110	0.07	0.13			-0.063	0.11	0.56		
urban	0.090	0.22	0.68			0.021	0.32	0.95		
day of year	0.002	0.01	0.73							
Intercept	5.394	1.70	0.00	2459	0.29	-0.075	1.81	0.97	130	0.992
weight:female	-0.162	0.09	0.08			0.003	0.13	0.98		
urban	0.217	0.23	0.34			0.093	0.31	0.77		
day of year	0.003	0.01	0.66							
Intercept	2.825	2.68	0.29	4782	0.76	3.485	3.74	0.35	217	0.890
tarsus:male	-0.059	0.16	0.71			-0.214	0.24	0.37		
urban	0.058	0.12	0.61			0.156	0.17	0.35		
day of year	0.010	0.00	0.04							
Intercept	1.880	0.86	0.03	4782	0.70	0.243	0.21	0.24	217	0.980
body:male	-0.001	0.13	0.99			-0.198	0.20	0.31		
urban	0.063	0.12	0.60			0.123	0.18	0.48		
day of year	0.010	0.00	0.03							
Intercept	2.131	0.87	0.01	4708	0.58	0.175	0.18	0.32	210	0.912
condition:male	-0.033	0.12	0.79			0.141	0.19	0.45		
urban	0.057	0.12	0.64			0.215	0.18	0.22		
day of year	0.009	0.00	0.07							
Intercept	2.552	3.95	0.52	5956	0.39	3.191	5.75	0.58	267	0.850
wing:male	-0.009	0.05	0.86			-0.041	0.08	0.60		

Table 4.4. continued

urban	0.028	0.11	0.80			0.195	0.17	0.24		
day of year	0.010	0.00	0.02							
Intercept	2.631	1.59	0.10	5814	0.32	-0.978	2.07	0.64	257	0.993
weight:male	-0.043	0.11	0.68			0.089	0.16	0.57		
urban	0.037	0.11	0.74			0.254	0.17	0.13		
day of year	0.009	0.00	0.04							

Table 4. 5 Parameter estimates relating individual morphology variables and urbanization to the probability of resighting (logistic regression) an individual in a future year and the number of nesting attempts made within a season (dispersion adjusted Poisson regression).   Parameter estimates, standard errors, and P values for significance tests of the regression coefficients are shown. N is the sample size used in each regressions. $P_{(HL)}$ refers to the value of the P value from a Hosmer and Lemeshow (1989) test and C refers to the value of the Pearson chi-square value divided by the degrees of freedom (Note that C<1 therefore the use of the scale parameter. See text for details).

	prob. resight	se	*P*	N	P(HL)	# nesting attempts	se	*P*	N	*C*
Intercept	-6.835	10.07	0.50	54	0.33	-0.496	1.78	0.78	61	0.337
tarsus female	0.510	0.68	0.45			0.081	0.12	0.50		
urban	0.032	0.53	0.95			-0.028	0.09	0.75		
scale						0.581	0.00			
Intercept	0.548	0.76	0.47	54	0.59	0.836	0.13	0.00	61	0.331
body size:female	-0.145	0.50	0.77			0.107	0.09	0.23		
urban	-0.126	0.54	0.82			-0.011	0.09	0.91		
scale						0.576	0.00			
Intercept	0.609	0.46	0.19	53	0.25	0.713	0.08	0.00	60	0.330
condition:female	0.305	0.22	0.16			0.000	0.04	1.00		
urban	-0.148	0.52	0.78			-0.056	0.09	0.52		
scale						0.574	0.00			
Intercept	19.671	12.85	0.13	56	0.49	-2.073	2.14	0.33	62	0.322
wing:female	-0.273	0.19	0.14			0.040	0.03	0.19		
urban	-0.236	0.53	0.66			-0.013	0.09	0.88		
scale						0.567	0.00			
Intercept	-3.203	2.82	0.26	55	0.21	0.675	0.47	0.15	61	0.324
weight:female	0.297	0.21	0.16			0.003	0.03	0.94		
urban	-0.145	0.52	0.78			-0.058	0.09	0.50		
scale						0.570	0.00			
Intercept	-0.501	5.23	0.92	108	0.36	-0.985	1.00	0.33	110	0.297
tarsus:male	0.002	0.33	1.00			0.103	0.06	0.10		
urban	-0.063	0.23	0.78			-0.078	0.05	0.09		
scale						0.545	0.00			
Intercept	-0.517	0.28	0.06	108	0.03	0.583	0.06	0.00	110	0.295
body:male	0.066	0.27	0.81			0.096	0.05	0.07		
urban	-0.048	0.24	0.84			-0.065	0.05	0.16		
scale						0.543	0.00			
Intercept	-0.315	0.23	0.17	104	0.84	0.628	0.05	0.00	107	0.315
condition:male	0.496	0.26	0.06			-0.040	0.05	0.38		
urban	0.042	0.24	0.86			-0.096	0.05	0.04		
scale						0.561	0.00			
Intercept	-2.687	7.58	0.72	139	0.42	-0.855	1.55	0.58	138	0.285
wing:male	0.033	0.10	0.75			0.020	0.02	0.34		

Table 4.5

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Table 4.5 continued

urban	0.007	0.21	0.97			-0.094	0.04	0.03		
scale						0.534	0.00			
Intercept	-4.734	2.87	0.10	133	0.37	0.933	0.51	0.07	133	0.294
weight:male	0.341	0.22	0.12			-0.025	0.04	0.53		
urban	0.004	0.21	0.99			-0.113	0.04	0.01		
scale						0.542	0.00			

Figure 4. 1: We ordered and numbered the territories for urban and rural patches in descending habitat quality. In both models individuals select the available territory with the best perceived habitat quality. However, in A, the "lower quality urban forest hypothesis," the perceived habitat quality ($P\beta$) is equal to the actual habitat quality (β) but the urban patch is of lower quality (β, dashed curved line) than the rural patch (solid upper curved line). Thus, individuals sequentially select territories from the best available territories resulting in higher densities in the rural patch (N_R) than the urban patch (N_U). The horizontal dotted line shows the final densities (i.e., N=100 individual total) and habitat quality of the last individuals to select a territory from both the urban and rural patch. In B, the "underutilized urban forest hypothesis," urban and rural habitat quality is similar (solid upper line) but the perceived habitat quality of the urban is P_U lower (e.g., P_U=0.5 in this example). Individuals sequentially select territories based on the perceived habitat quality so that final distribution (the lower dotted line, when N=100 total individual) contains more individuals in the rural (N_R) than the urban habitat (N_U) but the actual habitat quality experienced by the last individuals to select each site experience similar perceived habitat quality, yet the individual in the urban habitat

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"lower quality urban forest hypothesis" A

habitat quality

$\beta_U = \beta_R = P_U\beta_U = P_U\beta_R$

— rural habitat quality (actual)

- - - urban habitat quality (actual)

N_U

N_R

territory number (density)

"underutilized urban forest hypothesis" B

habitat quality

β_U

$\beta_R = P_U\beta_U = P_U\beta_R$

— rural and urban habitat quality (actual)

- - - urban habitat quality (perceived)

N_U

N_R

territory number (density)
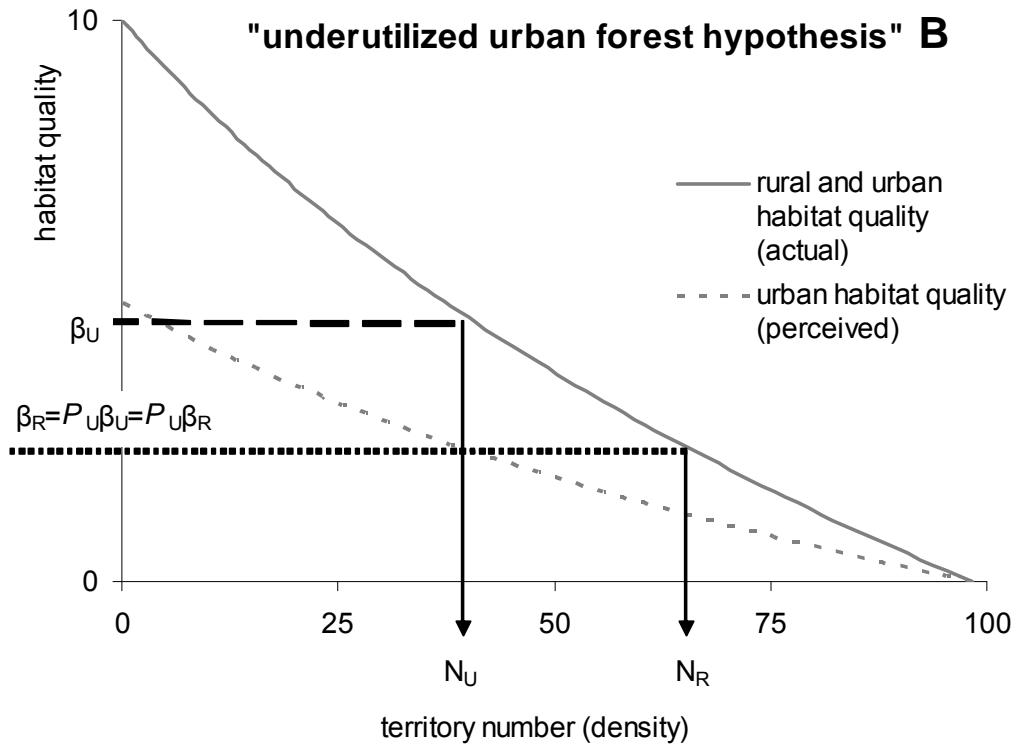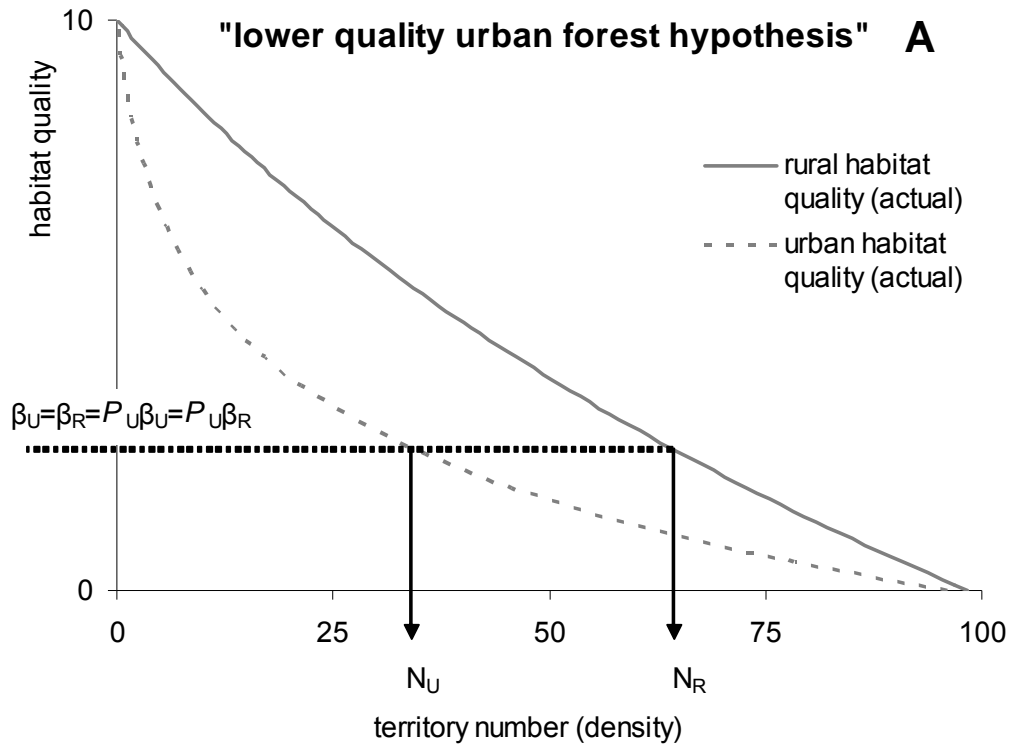
Figure 4. 2 Example output from one run of each simulation reflecting two hypotheses generating bird distributions. Notice that in the "low quality urban forest hypothesis" individuals of equal quality experience similar fitness values because they appropriately evaluate habitat quality and thus select available territory with the highest habitat quality, even though the urban patch has lower habitat quality. In the underutilized urban forest hypothesis, individuals select territories based on perceived habitat quality, which is lower for the urban forest even though both patches have equal habitat quality. Thus, individuals who end up in the rural patch experience a habitat quality than the perceived value resulting in higher fitness for those individuals.
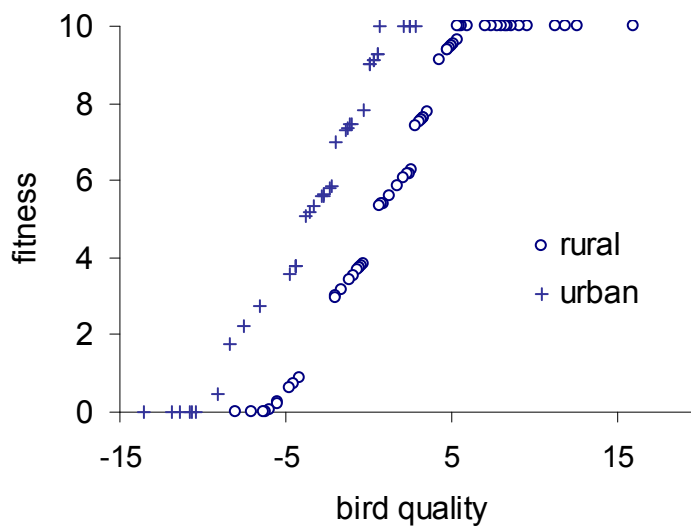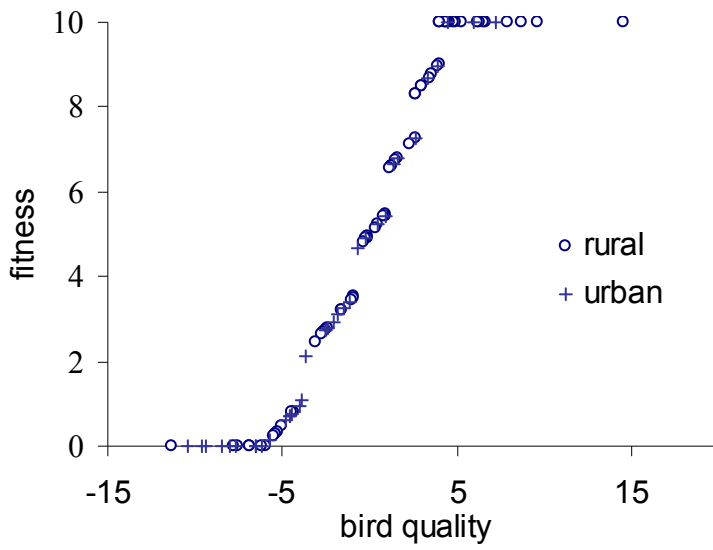
CHAPTER 5

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

5.1 Abstract

Earlier seasonal reproduction has been observed in urban compared to rural bird populations, but these observations are primarily of resident or short-distance migrants. To understand the relationship between urbanization and reproductive phenology or timing of a Neotropical migratory bird species we (1) described patterns and reproductive consequences of varied breeding phenology in a Neotropical migratory bird species across an urban to rural gradient and (2) evaluated the extent to which alternative factors might explain differences in reproductive phenology. Data were collected on Acadian flycatchers (*Empidonax virescens)* between 2001 and 2007 in 35 different forests spanning an urban to rural gradient in central Ohio, USA. The general pattern of breeding phenology was opposite that described for most resident and short-distance migrant birds. At higher levels of urbanization, arrival dates and clutch initiations were later and cessation of breeding was earlier than in forests within more rural landscapes. Collectively, these phenological shifts reduced the length of the nesting season in urban

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landscapes. This attenuated nesting season resulted in urban birds attempting fewer nests

and fledging fewer young than their rural-breeding counterparts. The underlying causes

of the phenological differences are less clear. One possibility supported by our data is

that urban forests were disproportionately settled by small females, which initiated the

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.

5.2 Introduction

Populations of native birds may be impacted by urbanization in various ways.

The most 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. In particular, advanced reproductive phenology has been documented in

several species inhabiting urban areas. Median nesting date for Woodpigeons (*Columba

palumbus*) nesting in London, England occurred about six days in advance of median

nesting of rural Woodpigeons (Cramp 1972). Florida Scrub-jays (*Aphelocoma

coerulescens;* Bowman and Woolfenden 2001), Australian Magpies (*Gymnorhina

tibicen*; Rollinson and Jones 2002), European Blackbirds (*Terdus merula*; Parktecke et al.

2005), and Cooper's Hawks (*Accipiter cooperii*; Boal and Mannan 1999) are among species noted to display advanced reproduction in urban compared to rural or suburban areas. Interestingly, the shift in breeding phenology does not seem dependent upon spatial extent. For example, magpies (*Pica pica*) nesting in urban areas of Sofia, Bulgaria, initiate clutches on average five days earlier than magpies in rural habitats that were within 1 km (Antonov and Atanasova 2003). In Britian, too, Perrins (1970) noted that "many species" breed earlier in gardens compared to neighboring woodlands.

Many studies have demonstrated that individuals breeding earlier in the year have higher reproductive success (Norris 1993, Verlhurst et al. 1995, Smith and Moore 2005). However, the fitness benefits associated with advanced breeding in urban areas are rarely investigated, and the few exceptions provide little evidence of a benefit to advanced breeding in urban systems. Although urban magpies (*Pica pica*) 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 magpies despite breeding almost two weeks earlier (Rollinson and Jones 2002). Nest success for Florida scrub-jays was highest earliest in the season when suburban jays were initiating nests in advance of wildland scrub jays (Bowman and Woolfenden 2001).

Various factors have been suggested to promote advanced reproduction in urban versus rural, suburban, or wild land populations. Among the most popularly suggested causes is elevated temperatures in urban areas (i.e. the urban heat island) (Erz 1966, Eden 1985, Rollinson and Jones 2002). Elevated temperatures might reduce energetic demands on overwintering birds thus leaving them in better condition early in the spring.

Further, temperature itself may be a cue that hastens physiological development thus allowing breeding to occur earlier (Jones 1986, Meijer et al. 1999). In addition, elevated urban temperatures may promote early development of both vegetation and food resources in the spring (Eden 1985). Abundant food supplies associated with human feeding, waste, and ornamental shrubs also may improve overwintering condition of birds, thus allowing them to reach breeding condition sooner in the spring (Cramp 1972, Schoech and Bowman 2003). High densities of conspecifics associated with urbanization may facilitate birds to reach breeding condition sooner (Jerzak 1995, Silverin and Westin 1995). Anthropogenic lighting also may accelerate reproduction through photoperiodic cues (Bartholomew 1949, Gorski and Kotlarz 1997).

Overwhelmingly, examples of bird species displaying advanced reproductive phenology in urban areas are those that either overwinter on breeding grounds (i.e., non-migrants or residents) or arrive on breeding grounds well in advance of actual nesting. Absent from these examples are Neotropical migratory songbirds which arrive on their breeding grounds and initiate breeding very quickly (Widmer and Bierback 2001, Smith and Moore 2003). Because long distance migrants do not experience the winter and early spring 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 (Ramenofsky and Wingfield 2006).

In order to understand the impact of urbanization on the reproductive phenology of Neotropical migratory birds, we studied an Acadian flycatcher (*Empidonax virescens*) population breeding in forests fragments in central Ohio, USA. The Acadian flycatcher migrates to Central and South America during the non-breeding season and breeds in the

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eastern North America. We used the Acadian flycatcher as a model species for

Neotropical migratory bird species because it breeds across the urban to rural gradient

and is present is sufficient numbers to allow for this analysis (Bakermans and Rodewald

2006). In this research we addressed the following questions: (1) What are the patterns

and reproductive consequences of varied breeding phenology in Neotropical migratory

bird species across an urban to rural gradient? And (2) To what extent do alternative

factors might explain differences in reproductive phenology?

5. 3 Methods

   Field methods.- Between 2001-2007 a total of 35 mature riparian forests in

central Ohio, USA, representing a gradient from highly urban to highly rural

(agricultural) land uses surrounding each forested site were monitored for Acadian

flycatcher activity, although nesting activity was found on only 22 of these sites.   Nine of

the original sites were not searched after 2004, in part because of the apparent absence of

breeding Acadian Flycatchers; two additional sites were added in 2005. By sampling

forests along this urban to rural gradient we were able to use a regression-based approach

in the analyses (see *Data Analysis* below). Beginning in early May each year, each site

was intensively searched for Acadian flycatchers. Throughout the breeding season,

assistants and we attempted to capture and band both male and female Acadian

flycatchers. We measured the length of the tarsus (mm), wing chord (mm), and mass of

each individual, later combining 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.

We attempted to locate and monitor all nesting attempts of every Acadian Flycatcher at each site. Nest searching efforts began two to three weeks before nesting began to ensure that the earliest nests were found. Once found, each nest was checked every two to five days by directly examining nest contents (e.g. eggs or nestlings). 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.

For each bird we determined its season-long reproductive activity including number of nesting attempts, nest fates, and number of fledglings. Individual birds were intensively monitored but there were some breeding pairs for which nesting attempts were missed. In addition, we 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). Consequently, we were able to use some nesting information from unmarked birds in addition to the individually marked birds. Therefore, 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.

Landscape quantification.- The methods we used to describe the landscape are described in detail elsewhere (Rodewald and Shustack 2008). Briefly, within a 1-km

radius of the center of each study site, we determined the proportions of different land

cover types and the number of buildings by inspection of digital orthophotos (2002–04).

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). We hereafter refer to this first component

as the 'urban index' (Table 1). 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).

Data analysis.- We determined the date the first egg was laid in each nest (e.g.,

clutch initiation date) 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, we 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 we used female behavior (i.e. nest building activity

and incubation) to indicate when eggs had been laid. We 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, we standardized the day of year for all years to the median clutch

initiation date in 2006.

Patterns of reproductive phenology.- We described several components of

Acadian flycatcher reproductive phenology relative to the urban index. First, on a site

level, we used nonparametric correlation to look for a relationship between the order of

detection for the first male at a site and the site order of urbanization for each year

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separately (2004-2007, PROC CORR). Using all nests that we found within one 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 (PROC REG). In order to achieve normality of the residuals we performed a natural log transformation on number of days between 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 due to cryptic nest predation, sensu Maddox and Weatherhead (2006)), because of high nest predation rates in our study system.

On a site level we related the date of the very first clutch initiation, median clutch initiation, absolute last clutch initiation, and average length of time between first and last clutches to the urban index using PROC GENMOD. In order to improve normality of the variables and the residuals, we transformed the urban index (sqrt(urban index+1.28)) and the date of clutch initiations (natural log transformation) for the regression with absolute first clutch initiations and median clutch initiations. The remainder of the variables and regressions satisfied the assumptions for least-squares regression and we did not transform variables for those regressions. We averaged the length of time between first and last clutches at a site over all years. For first, median, and last clutches we included year as a class variable. We then separated sites into urban (greater than zero on urban index) and rural (less than zero on urban index) in order to test for differences in patterns of nesting activity between the start and completion of all female nesting activity (i.e. initiation of first clutch through completion, failed or success of final nest) based on an urban/rural dichotomy (Kolmogorov-Smirnov tests, Proc NPAR1WAY).

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For each nest we determined whether the female renested following completion (failed=abandoned, depredated, or fledged a brown-headed cowbird, or successful-fledged host young) of that nest. We used logistic regression to relate probability of renesting to prior nest fate, the urban index, and the day of the year of the completion of the previous nest (PROC GENMOD). Further, we determined if there was a difference in when fledglings were produced based on an urban/rural dichotomy (described above) by testing the cumulative distribution functions of when chicks fledged with Kolmogorov-Smirnov tests (Proc NPAR1WAY).

Consequences of reproductive phenology.- We described the potential consequences of altered reproductive phenology in four ways. First, we used the individual clutch initiation dates from all females from all years to determine if clutch initiation date was related to the number of fledglings a female produced over the course of a breeding season (negative binomial regression, PROC GENMOD). Second, we used logistic exposure (Shaffer 2004) to examine temporal patterns in nest survival to examine the pattern between day of the year and nest survival. Third, we related the number of nesting attempts a female initiated to the day of year of the clutch initiation date of a female's first nest (PROC GENMOD). Fourth, we used logistic regression (PROC LOGISTIC) to determine if clutch initiation date was related to the probability of resighting a female or male in a subsequent breeding season.

Causes of reproductive phenology.- We considered several possible factors that might influence reproductive phenology. Because older, more experienced individuals may be able to reproduce earlier, we examined if older, more experienced birds initiated clutches earlier comparing clutch initiation dates in year t to year $t + 1$. Because arrival

date limits clutch initiation date, we looked to see if the length of time between when the first singing male was detected at a site and the median clutch initiation date for that site varied over the urban index (PROC GENMOD). Based on results from a complementary study (Chapter 5; Shustack and Rodewald, unpub. manuscript) we knew that females that were smaller in size, wing chord and weight tended to initiate clutches later in the season. We added to this information in this current study by further examining the independent effect of female body size, wing chord and weight on clutch initiation date. To do this, we first regressed clutch initiation date of each individual female on the urban index and calculated the residuals. We then regressed the residuals on female body size, wing chord, and weight to determine the independent effects of female morphology. All analyses were performed in SAS 9.1 (2002).

5.4 Results

Patterns of reproductive phenology.- In all years the first singing male was detected progressively later as the urban index increased, but this was only significant in three of four years (2004: $r = 0.660$, $P < 0.001$, N = 23; 2005: $r = 0.305$, $P = 0.180$, N = 21; 2006: $r = 0.5458$, $P = 0.006$, N = 24; 2007: $r = 0.490$, $P = 0.009$, 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 day of year of initiation of nest building ($F_{2,167}$ = 48.98, $P < 0.0001$; intercept $\beta = 3.617$, $t = 18.98$, $P < 0.0001$; ln(day of year): $\beta = -0.011$ $t = -9.80$, $P < 0.0001$; urban index: $\beta = -0.0338$ $t = -1.16$, $P = 0.248$). As the season progressed, the length of time between the initiation of nest building and the first

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egg laid in that nest decreased from an average of ~8 days on May 20 to ~4 days on July 20th.

The urban index (square root transformed) was significantly related to the date of the very first clutch initiated at a site ($\beta = 0.0419$, $\chi^2 = 14.14$, $P < 0.001$), and this did not vary among years (all $Ps > 0.14$), with the exception of 2003 ($\beta = 0.089$, $\chi^2 = 21.70$, $P < 0.001$). Median clutch initiation date at sites (square root transformed) were also later in more urban forests ($\beta = 0.035$, $\chi^2 = 14.89$, $P < 0.001$) and there was no significant year effect (all $Ps > 0.06$). Nests were initiated later into the breeding season in more rural forests ($\beta = -7.347$, $\chi^2 = 21.59$, $P < 0.001$), again without a significant year effect (all $Ps > 0.09$). The average length of time between initiation of a female's first clutch and her last clutch decreased with increasing urbanization ($\beta = -6.780$, $\chi^2 = 14.79$, $P < 0.001$; Table 2.) The pattern of clutch initiations was different in rural (urban index < 0; N = 147 females) versus urban (urban index > 0; N = 37 females, D = 0.302, $P = 0.009$). However, landscapes were similarly distributed in timing of completion of nesting activity by females (D = 0.240, $P = 0.066$; Fig. 1). Three additional patterns also emerged from the data: (1) as the season progressed, birds were significantly less likely to renest ($\beta = 0.132$, $\chi^2 = 89.53$, $P < 0.001$), (2) birds renested with a lower probability in more urban forests ($\beta = 0.478$, $\chi^2 = 5.48$, $P = 0.019$), and (3) prior nest fate was not significantly related to renesting probability ($\beta = 0.1175$, $\chi^2 = 0.11$, $P = 0.738$; Fig. 2). There was no significant difference in the timing of fledging between urban (273 fledglings produced) and rural sites (56 fledglings produced; ($P = 0.258$; Fig. 3).

Consequences of reproductive phenology.-Earlier clutch initiation was related to producing more fledglings over the course of the breeding season ($\beta = -0.0193$, $\chi^2 = 7.62$,

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$P = 0.006$) with a bird initiating a first clutch ~May 20th expecting ~2 fledglings for the year and a bird initiating a month later only producing ~1 fledgling for the year (Fig. 4). Probability of nest survival increased over the season ($\chi^2 = 4.35$; $P = 0.037$; N = 2633 nest check intervals, effective sample size = 8526 [see Rotella et al. 2004]) with ~30% nest success (i.e., daily survival to the 28th power for a 28 day nest cycle) earliest in the season increasing to ~55% in early August (Fig. 5). The number of attempts that a female made decreased as she initiated her first clutch later in the season ($\beta = -0.026$, $\chi^2 = 84.69$, $P < 0.001$). A female initiating her first clutch ~May 20th made ~ 3 nesting attempts whereas a female which initiated her first clutch three weeks later made fewer than two attempts. The probability of resighting a male ($\beta = 0.0149$, $\chi^2 = 0.804$, $P = 0.370$) or female ($\beta = 0.022$, $\chi^2 = 0.428$, $P = 0.513$) in a subsequent breeding season was not related to when they initiated their nest in the previous year.

Causes of reproductive phenology.-Experience did not appear to be related to reproductive phenology. Eleven of 17 females that returned to breed in a subsequent year, on average initiated clutches about three days earlier, however, the confidence interval overlapped zero (6.6 days earlier to 0.9 days later in subsequent year). For males we recorded clutch initiation dates for 64 pair of confirmed clutch initiation in year *t* and *t*+1. The average clutch initiation dates were similar (0.6 days later) between years and the confidence interval included zero (2.2 days earlier to 3.4 days later in subsequent year). The average amount of time between detection of the first singing male and the median clutch initiation was 20.9 days (95% CI: 22.8-24.8 days). There was no relationship between the length of time between detection of the first singing male at a site and the median first clutch initiation date at the site ($\beta = -1.573$, $\chi^2 = 2.55$, $P = 0.110$)

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with no significant year effects. After controlling for the effect of urbanization (i.e.,

regressing residuals of first clutch initiation on urban index), there was still an effect of

female body size on timing of nest initiation with females with smaller bodies (β = -

3.212, t = -2.36, P = 0.021), shorter wing chords (β = -1.794, t = -3.77, P < 0.001) and

lower weights (β = -1.324, t = -2.20, P = 0.032) initiating first clutches later.

5.6 Discussion

Our results illustrate that tendency of urbanization to advance breeding is not

consistent across species. We showed that the Neotropical migrant Acadian Flycatcher

experienced delayed clutch initiation and earlier cessation of nesting as the amount of

urban development in the landscape increased. In contrast, previous studies of avian

breeding phenology in urban areas have demonstrated that birds in urban areas,

specifically resident and short-distance migrant species, tend to advance their breeding

phenology and extend their breeding seasons compared to rural populations (Erz 1966,

Eden 1985, Bowman and Wolfenden 2001, Rollinson and Jones 2002, Antonov and

Atanasova 2003, Schoech and Bowman 2003). To our knowledge, our study provides the

first example of the effects of urbanization on the breeding phenology of a Neotropical

migratory bird species.

Several 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 pattern that has been well documented (Norris 1993,

Verlhurst et al. 1995).   A female that initiated nesting in the earliest part of the season

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(e.g. mid-May) would 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 five ways. First, clutches laid earlier in the spring tend to be larger (Klomp 1970, Perrins 1970). Because a bird can not fledge more offspring than eggs it lays, laying larger clutch sizes maximizes the potential number of fledglings. However, clutch size must also be balanced with the ability to successfully feed and raise the young once they hatch (but see Vander Werf 1992). In our study, many nests were too high to view contents, so we were unable to adequately evaluate temporal patterns in clutch size. Second, the average number of young fledged per egg laid or the mass of nestlings may be higher earlier in the season (Arnold et al. 2006 but see Schwagmeyer and Mock 2008). Because we could not ascertain clutch size, we could not evaluate this potential benefit. Third, earlier nesting permits a greater amount of time available for renesting following either a successful or failed first nesting attempt (Barba et al. 1995, Ortega et al. 2006, Murray and Nolan 2007). Indeed, we found that earlier nesting birds made more nesting attempts (i.e., a decrease of one attempt for each 2 ½ week delay) and the day of the year was the most important variable predicting renesting probability. Fourth, early nesting allows fledglings from early nests to have more time to gain experience, improve body condition, and prepare for migration in the following autumn compared to young from later nests. 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 rural fledglings left nests earliest, there was not an overall significant pattern to the timing of when fledglings were produced based on urbanization. For

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instance, fledglings from a nest in late June would have two more months to prepare for migration than fledglings in late August. We found that the earliest fledglings were from rural sites, though there was not an overall significant pattern to the timing of when fledglings were produced. Because fledglings dispersed out of our study sites we were not able to detect this potential benefit to earlier breeding, however, other studies have documented higher survival rates among birds hatched early versus late in the season (Perrins 1970, Norris 1993, Barba et al. 1995, Møller et al 2006, Vitz 2008). A fifth benefit conferred to successful early-breeding adults is that they can have more time or energy for post-breeding 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 over-winter survival (Wiggins et al. 1998). Based on the timing of clutch initiations we did not find any patterns in return rates the following year and, therefore, we cannot conclude that early breeding leads to increased survival in this population.

Given these potential benefits of early breeding attempts, we found that nest success paradoxically was lowest early in the season – a pattern that likely dampened the effect sizes that we detected. Interestingly, despite early nests having the lowest success rates of the season, early-breeding pairs still derived some benefits from their early attempts. The pattern of increasing nest survival over the course of a season is not ubiquitous and many temporal patterns of nest survival have been observed (see references in Wilson et al. 2007).

What accounts for the pattern of abbreviated nesting activity in urban forests? Several explanations are possible. First, initiation of nesting is constrained by arrival time and the first singing males were detected later in more urban forests. Second, once

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settled at a site, individual birds may be delayed by the quality of the site. For instance, in more urban forests females may take longer to lay clutches find a suitable nest site, or build a nest. Because we lack individual arrival times, we were unable to determine if the period between settlement at a site and clutch initiations varied across the urban gradient. However, females in urban forests did not take longer to build nests but our results do indicate that urban forests lead to a "delay penalty" for birds which nest there.

The third factor that might constrain nesting seasons in urban forests is if birds settling in urban forests are less capable of reproducing (e.g., lower quality individuals) than individuals selecting more rural forests. This appears to be the main driver of the abbreviated nesting season in urban forests. We found evidence for heterogeneity among individuals that may be related to reproductive phenology and differential site use. Smaller females used more urban forests for nesting and smaller females tended to initiate nesting later. Further, after we controlled for the amount of urbanization we still found an effect of female size suggesting that not only does urbanization impose a delay on nest initiation, but at the same degree of urbanization smaller females initiated nesting later than larger females. However, we have mixed evidence that smaller females are lower quality birds. Information on the relationship between bird 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*). While smaller females initiated nesting significantly later in our study, productivity estimates including nest survival and number of fledglings per attempt indicated that smaller females were actually more successful in these aspects of breeding than larger females. This pattern may indicate that large females pre-empt

small females from the best nesting areas perhaps by earlier arrival after migration (Francis and Cooke 1986, Bowlin 2007) or through direct interactions over mates of territories (Jonart et al. 2007). These competitive interactions might force smaller females into less desirable habitats (i.e. more urban forests) leading to delayed reproductive timing through increased time to find a territory and a mate. However, once a breeding area is secured smaller females may have other advantages to breeding such as securing food for their young (Bowlin et al. 2004), increased clutch sizes (Murphy 2007) or possibly nest defense. The positive aspects of smaller females may be at least partially counterbalanced by the reduced probability of renesting and the lower productivity experienced in urban forests, a mismatch between fitness components that may not be uncommon (Chalfoun and Martin 2007). Elucidating the mechanisms responsible for these fine-level interactions and effects will require further study.

At least two other studies have found similar patterns to what we detected in the Acadian flycatchers, though only ours includes a landscape-scale context. Alatalo et al. (1986) showed that Pied flycatchers (*Fidedula hypoleuca*) had increased incidence of polygyny, larger clutches, more fledglings and higher densities in deciduous compared to coniferous forests. Interestingly, only males had larger wings and greater weights in the deciduous forest. The authors suggested that larger wings and weights allowed those males to occupy the preferred and higher quality habitat (deciduous forest) to the exclusion of smaller males (Alatalo et al. 1986). Ortega et al. (2006) showed that chipping sparrows (*Spizella passerina*) nesting in savannas invaded by an exotic forb had lower densities, delayed nest initiations, greater proportion of second year birds, lower site fidelity and fewer nesting attempts. Further, after accounting for differences in

age, Ortega et al. (2006) still found that birds in savannas with exotic forbs delayed in initiation of breeding, which is similar to the delay we describe based on female size along with an additional "urban penalty."

Clearly the effects of urbanization on bird populations are complex. Our results demonstrate that the effects of urbanization can not necessarily be generalized across species with different migratory strategies. While many previous studies have found advanced breeding phenology and extended breeding seasons associated with urbanization, our study documented delayed clutch initiation and truncated nesting by a Neotropical migratory bird species. To our knowledge, this is the first study to document this effect of urbanization on native bird species. The causes of this pattern of urbanization appear to be related to individual variation within the species coupled with variation in habitat quality between urban and rural forests.

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Table 5. 1 Urban index values for 35 sites surveyed for Acadian Flycatchers between 2001-2007 in Central, OH, USA. The index is the first component of a principal components analysis of five variables (number of building, % cover in agriculture, roads and pavement, lawn and agriculture) describing the landscape within 1-km of each site. See Rodewald and Shustack 2008 for details on data that generated the urban index.

Site	Urban Index
prindle	-1.73
ngalena	-1.27
klondike	-1.16
pubhunt	-1.15
prairie	-1.12
lock	-1.05
tnc	-0.96
chapman	-0.87
gardner	-0.87
kilbourn	-0.87
girlcamp	-0.82
creeks	-0.71
rocky	-0.68
sgalena	-0.57
galena	-0.48
sunbury	-0.42
highbank	-0.3
smith	-0.28
elkrun	-0.16
campmary	0.21
woodside	0.32
innis	0.33
heisel	0.36
whitehall	0.68
rushrun	0.75
cherry	0.76
kenny	0.89
bexley	1.23
casto	1.25
lou	1.26
bigwal	1.31
whetston	1.31
olentan	1.46
tuttle	1.61
osuwet	1.75

Table 5. 2 Day of year (standardized to 2006) of first clutch initiation (first) at a site, median clutch initiation (median) day of year, and last clutch initiation (last) at a site. N is number of confirmed first clutches for that site and year. "arr" is the day of year the first singing male was detected at the site (only collected in 2004-2007). Sites "Kenny" and "tuttle" were not surveyed until 2005. For all other sites, missing information indicates clutch initiation dates were not confirmed at the site, typically because Acadian Flycatchers were not breeding at the site in that year.

site	2001 first	med	N	last	2002 first	med	N	last	2003 first	med	N	last	2004 first	med	N	last	arr	2005 first	med	N	last	arr	2006 first	med	N	last	arr	2007 first	med	N	last	ar
bexley									171	171	1	183	162	162	1	162	146	154	155	3	186	130	159	169	2	192	128	164	164	1	172	12
bigwal	164	164	1	164									152	152	1	193	144	154	160	3	195	130	150	153	2	201	135	150	157	2	171	12
campmary	164	164	1	172									152	164	2	175	137	166			166	130	156	160	2	176	142	147	147	1	191	13
casto													168	168	1	190	152					139					147	155	160	2	178	14
cherry													160	184	1	184	164	157	157	1	199	146	164	164	1	164	133					12
creeks	146	148	2	192	151	153	2	176	164			199	152	153	3	212	132	150	154	6	201	129	151	153	4	191	128	144	149	3	193	12
elkrun																	153					150					136	167	167	1	167	14
galena	154	154	1	167	154	154	1	205	154	155	2	203	147	157	9	206	135	145	149	8	180	128	146	154	5	211	129	142	152	4	209	12
gardner	157	157	1	202									153	153	1	186	134	149	158	2	174	131	154	155	2	184	126	157	157	1	197	12
girlcamp													151	151	1	190	144	143	156	2	208	132	142	163	3	210	132	148	153	2	198	12
heisel																	144					129					150					13
kenny																																17
kilbourn	157	157	1	157	153	159	2	199	167			167	165	165	1	194	135	148	161	3	199	135	151	163	3	220	129	165	165	1	190	12
lockbourne																																
lou									171			171	157	157	1	178	146	151	157	3	186	137	157	157	1	157	135					12
ngalena	139	147	6	193	148	153	6	200	158			196	155	156	3	206	135	150	164	6	186	128	150	153	8	206	125	144	147	7	185	12
olentan																																15
prairie	148	159	3	176					166			195	146	146	3	193	134	150	158	2	196	135	155	155	2	197	132	145	149	3	188	12
pubhunt	155	158	4	180	156	156	2	185	171			189	152	153	3	199	134	153	156	5	194	138	148	153	5	217	123	155	160	2	188	12
rushrun																	180					136	167	167	1	168						15
sgalena													171	171	1	171	142	147	150	2	211	131	155	159	2	188	133	157	159	2	191	12
smith																						136	162				162					13
sunbury					144	150	2	195	145	154	2	198	156	156	1	202	135	150	158	3	179	131					125					12
tnc									193			193	154	161	2	190	134	146	150	3	211	128	149	153	4	153	136	143	143	1	185	12
tuttle																						139					138					14
whetston																																15
whitehal																											131	152	152	1	152	15
woodside	172	172	1	172									161	161	1	178	138	155			155	137	186			186	140	138	155	3	180	12
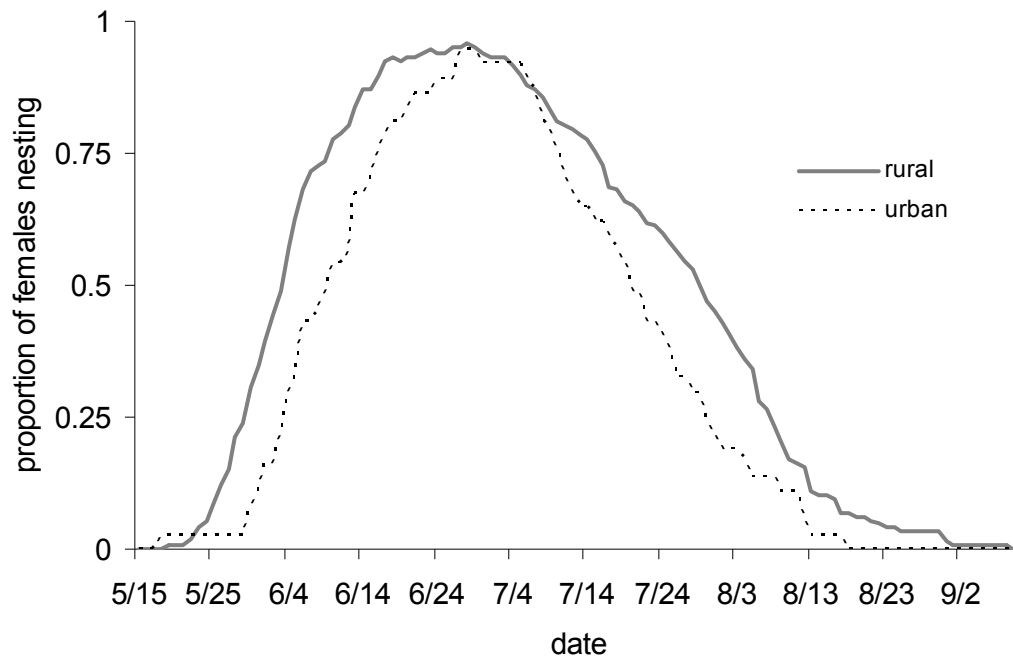
Figure 5. 1: Proportion of females nesting in rural (urban index<0) and urban (urban index>0) nesting (laying, incubating or tending nestlings) throughout the course of the breeding season. Notice that the urban females tend to initiate (significant different urban versus rural, P=0.009) and complete nesting sooner (non-significant difference urban versus rural, P=0.066) than rural females.
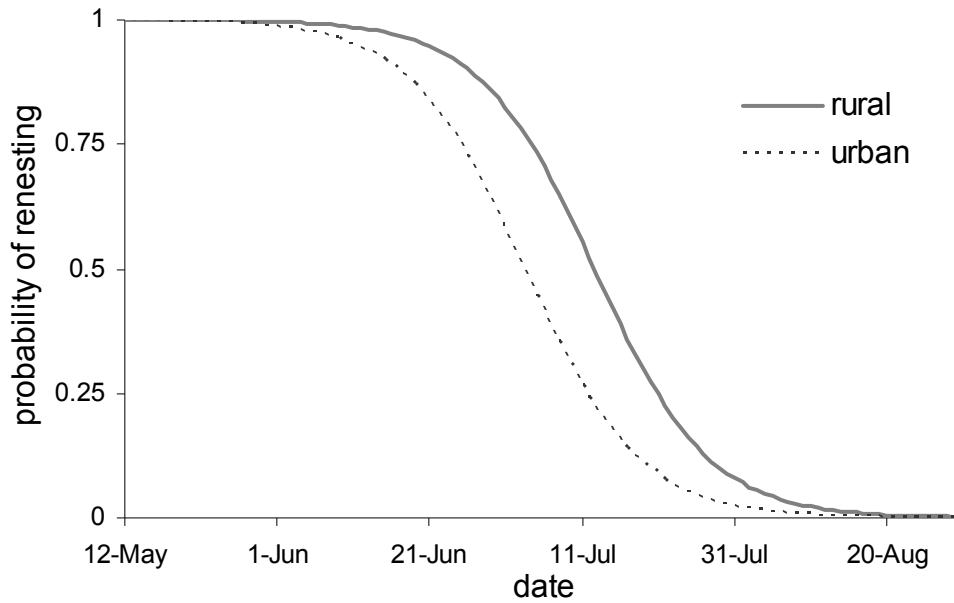
Figure 5. 2: Probability of renesting by Acadian Flycatchers over the course of the

breeding season in the most rural site and more urban site on which flycatchers were

detected. Model included fate of previous nest but was non-significant (see text) and

figure shows probabilities when prior nest was successful. Notice that the probability of

renesting declines sooner in more urban sites.
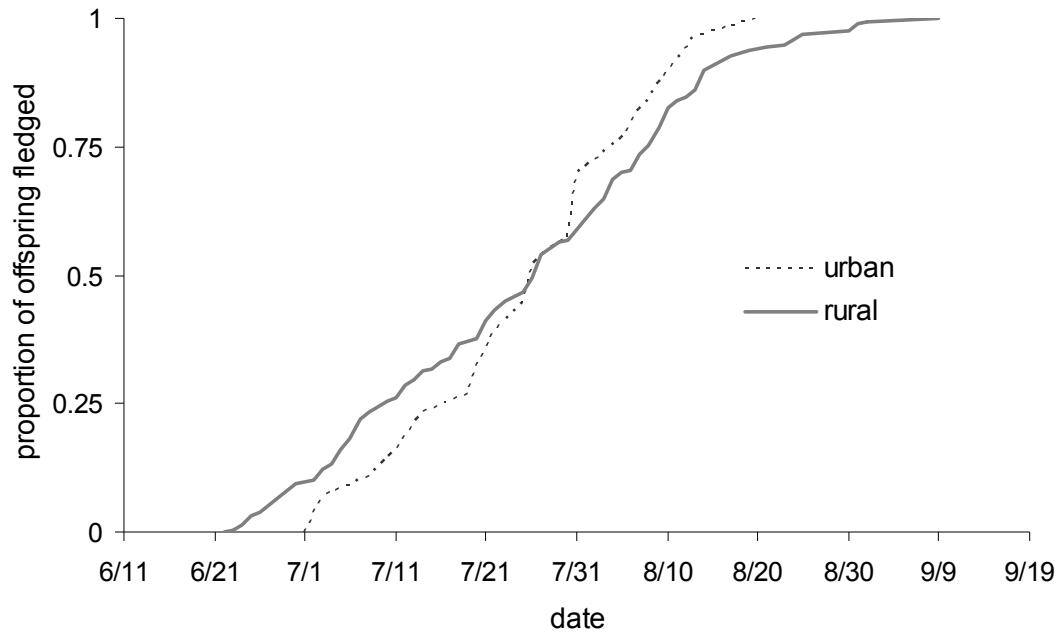
Figure 5. 3: Proportion of fledglings produced over the course of the breeding season based on rural (urban index<0) and urban (urban index>0). Difference in timing is non-significant, but not pattern of urban fledglings being produced over a narrow period of time than rural fledglings.

Figure 5. 4: Number of fledglings produced by Acadian Flycatchers over the breeding season based on the date of initiation of the first clutch of the season. Bold line is negative binomial regression line and dashed lines show upper and lower 95% confidence interval for regression line.
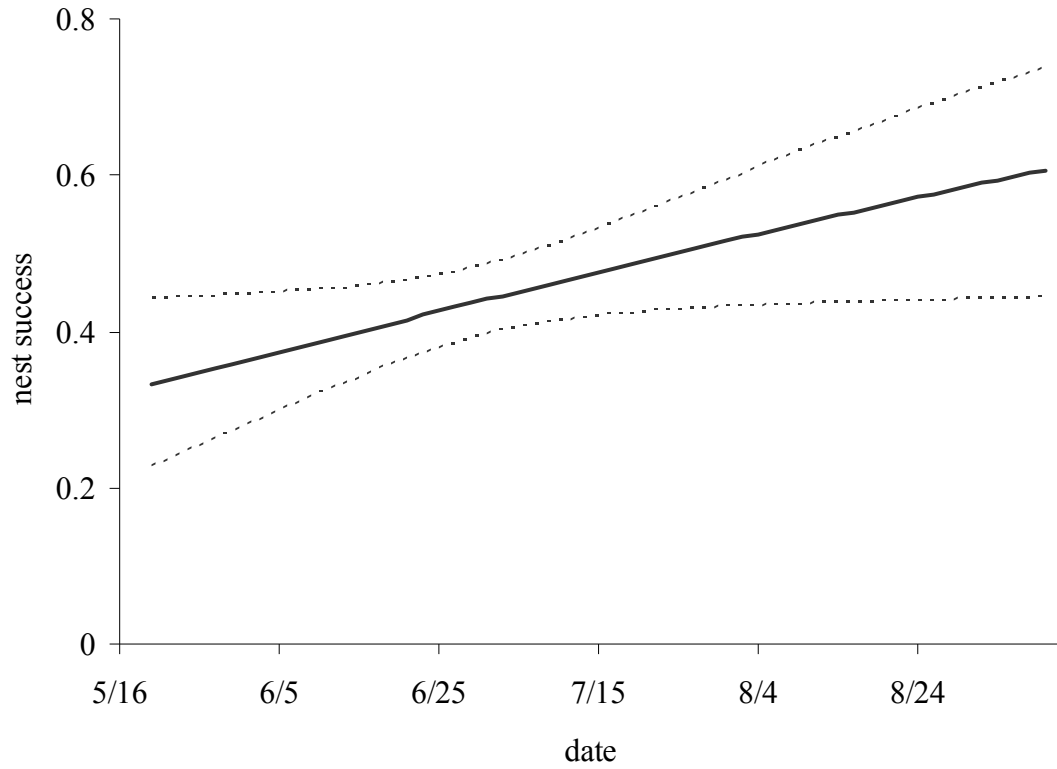
Figure 5. 5: Nest success (daily survival probability to the 28th power) over date for Acadian Flycatcher nests in central Ohio, USA from 2001-2007. Estimates are based on a logistic exposure model (Shaffer 2004) from 469 nests and 2633 nest check intervals.

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APPENDIX A List of riparian forest study sites and their locations in central Ohio, USA, 2001-2007

Appendix A

Site	County	Latitude	Longitude
Chapmans Road	Delaware	40N 13'804''	83W 03'749''
Galena	Delaware	40N 12'939''	82W 52'734''
Highbanks	Delaware	40N 08'843''	83W 02'331''
Kilbourne	Delaware	40N 19'779''	82W 57'324''
Klondike	Delaware	40N 15'048''	83W 08'879''
North Galena Road	Delaware	40N 21'341''	82W 55'324''
Prindle Property	Delaware	40N 22'176''	83W 11'162''
Red Bank Road	Delaware	40N 08'706''	82W 51'448''
South Galena Road	Delaware	40N 14'210''	82W 53'675''
Sunbury	Delaware	40N 14'116''	82W 50'113''
Bexley Park	Franklin	39N 58'378''	82W 56'736''
Big Walnut Park	Franklin	39N 56'658''	82W 51'361''
Camp Mary Orton	Franklin	40N 07'282''	83W 01'848''
Casto Park	Franklin	40N 04'966''	82W 55'327''
Cherrybottom Park	Franklin	40N 03'860''	83N 53'913''
Darby Girl Scout Camp	Franklin	39N 58'125''	83W 14'748''
Darby Public Hunting	Franklin	39N 50'834''	83W 12'168''
Elk Run Park	Franklin	39N 53'835''	82W 53'894''
Gardner Road	Franklin	39N 53'695''	83W 13'003''
Heisel Park	Franklin	39N 54'615''	82W 53'160''
Innis Park	Franklin	40N 02'129''	82W 56'013''
Kenny Park	Franklin	40N 03' 55''	83W 01' 48''
Lockbourne	Franklin	39N 48'638''	82W 58'484''
Lou Berliner Park	Franklin	39N 56'183''	83W 00'071''
N. Olentangy Parkland	Franklin	40N 06'337''	83W 02'087''
OSU Wetlands	Franklin	40N 01'119''	83W 00'973''
Prairie Oaks Metro Park	Franklin	39N 59'177''	83W 14'752''
Rocky Creek	Franklin	40N 01'993''	82W 50'383''
Rush Run	Franklin	40N 04'598''	83W 01'862''
Smith Farm Metro Park	Franklin	39N 54'164''	82W 55'020''
Three Creeks Metro Park	Franklin	39N 52'901''	82W 54'272''
TNC	Franklin	39N 56'690''	83W 13'890''
Tuttle Park	Franklin	40N 00' 39''	83W 00' 00''
Whetstone	Franklin	40N 02'408''	83W 01'763''
Whitehall Park	Franklin	39N 59'003''	82W 51'863''
Woodside Green Park	Franklin	40N 02'734''	82W 52'854''
Westfall	Pickaway	39N 33'467''	82W 59'687''

APPENDIX B Location of riparian forest study sites in Cetral Ohio, USA

Urban
Agriculture/Open Urban Areas
Shrub/Scrub
Wooded
Open Water
Non-Forested Wetlands
Barren (Strip Mine, Quarries, S & G Pits
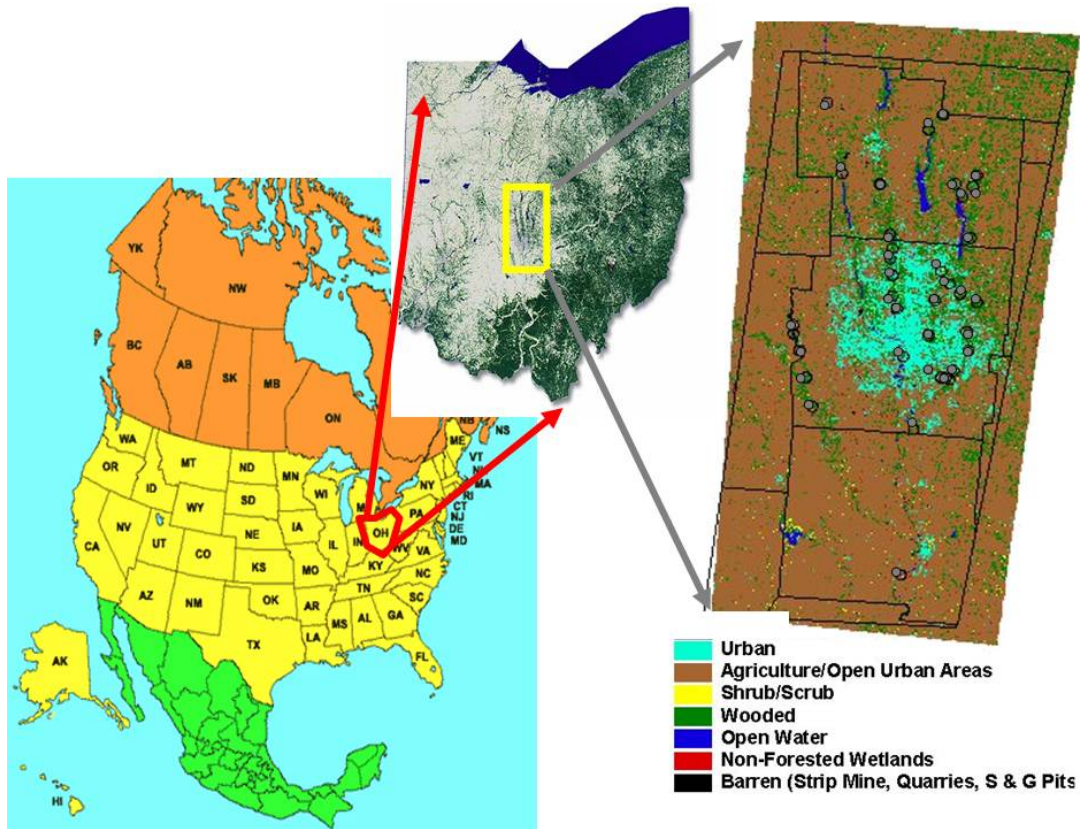
APPENDIX C Supplementary figures

Figure C. 1 A-C. Trends in phenology for *Acer negundo* (A)*, Aesculus glabra* (B)*, and Lonicera maackii* (C), for bud break (open circle and light line, left axis), leaf expansion (open squares and dashed line, left axis), and shoot length (closed circles and dark line, right axis) from eleven forests in central Ohio, USA. Notice the trends for earlier bud break, earlier leaf expansion and for longer shoot lengths with increasing urbanization.

Figure C.1

Continued

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Figure C.1

C. *Lonicera maackii*
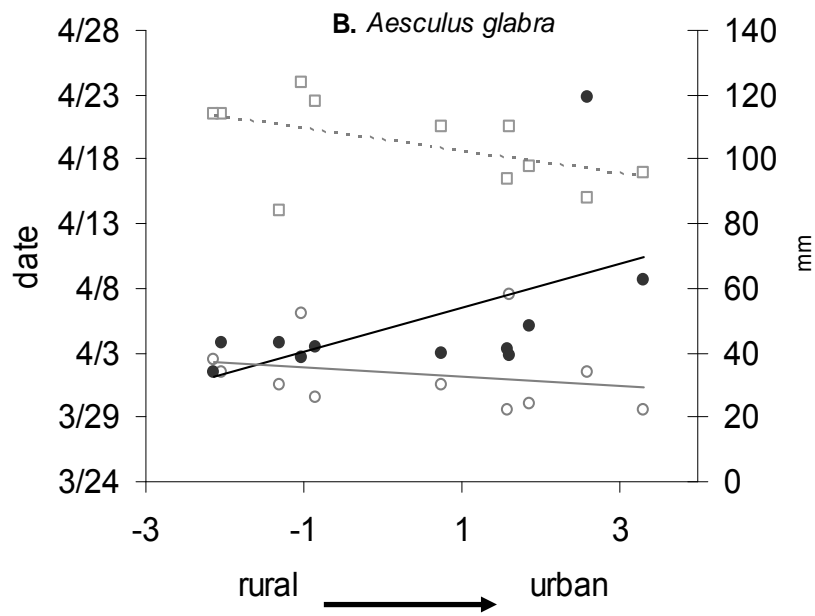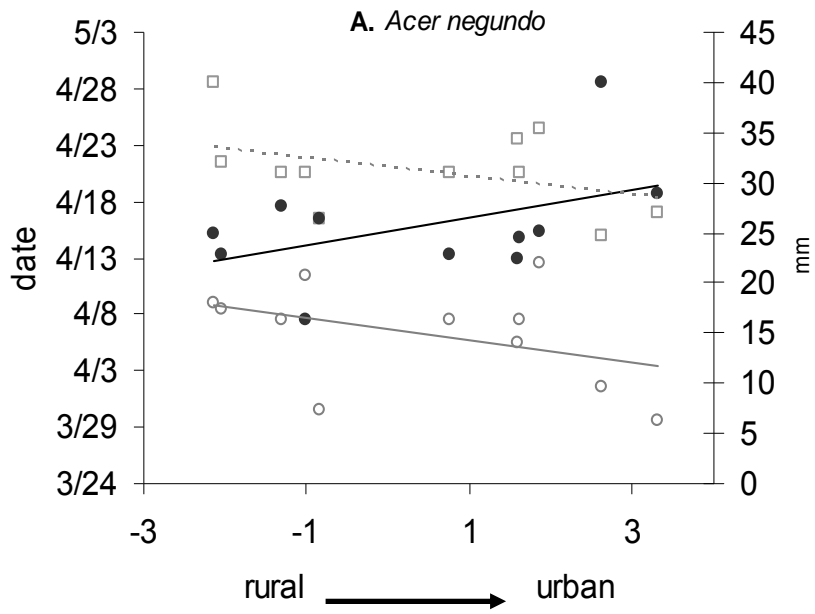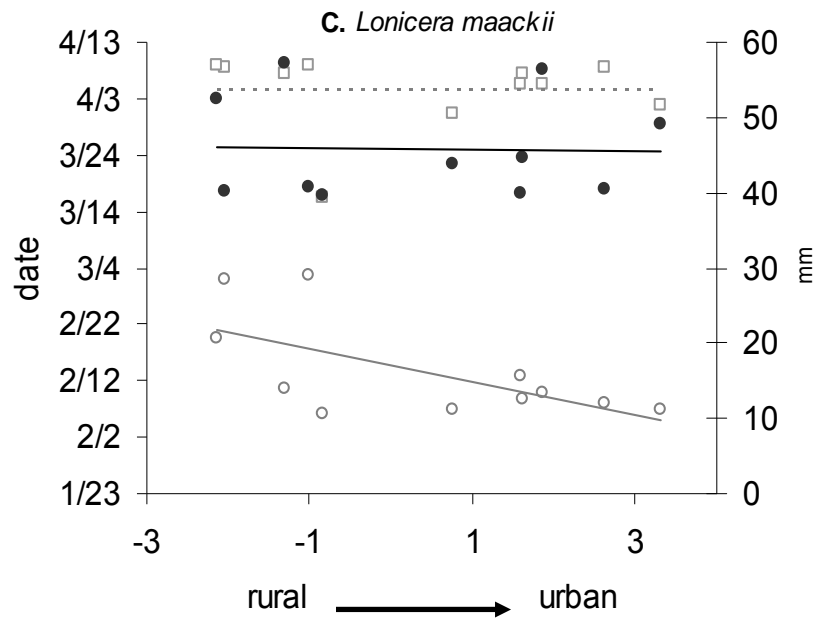
APPENDIX D Supplementary tables

	box elder			Ohio buckeye			Amur honeysuckle		
site	bud[a]	leaf[b]	shoot[c]	bud[a]	leaf[b]	shoot[c]	bud[a]	leaf[b]	shoot[c]
cherry	4/7	4/20	24.5	4/7	4/20	38.8	2/8	4/7	44.7
creeks	4/7	4/20	27.6	3/31	4/14	43.2	2/10	4/7	57.1
galena	3/30	4/16	26.3	3/30	4/22	41.6	2/6	3/16	39.5
kenny	4/12	4/24	25.1	3/30	4/17	48.1	2/10	4/5	56.4
lou	4/1	4/15	40.0	4/1	4/15	119.3	2/8	4/8	40.4
prairie	4/8	4/21	22.8	4/1	4/21	43.3	3/2	4/8	40.3
pubhunt	4/9	4/28	25.0	4/2	4/21	33.7	2/19	4/9	52.5
rush	4/5	4/23	22.4	3/29	4/16	41.1	2/13	4/5	39.8
sgalena	4/11	4/20	16.4	4/6	4/24	38.4	3/2	4/8	40.7
tuttle	3/29	4/17	28.9	3/29	4/17	62.8	2/7	4/2	49.3
woodside	4/7	4/20	22.8	3/31	4/20	39.8	2/7	3/31	43.7

[a] median date of bud break

[b] median date of leaf expansion

[c] average shoot length in centimeters

Table D. 1 Site median and average leafing phenology variables for the eleven forest sites sampled in central Ohio, USA, in 2006.

Table D. 2 Temperature variables from 11 sites in 2006 on which vegetation phenology was measured.

Table D.2

	January				February				March			
Site	max[a]	min[b]	dd[c]	ddzero[d]	max[a]	min[b]	dd[c]	ddzero[d]	max[a]	min[b]	dd[c]	ddzero[d]
cherry	9.1	0.7	151.7	170.2	5.4	-3.8	21.5	87.2	10.3	0.0	158.4	190.4
creeks	10.5	1.3	183.5	199.2	7.1	-3.3	53.6	111.6	11.7	0.7	191.2	217.7
galena	8.6	0.2	136.3	156.3	5.3	-4.1	16.8	85.1	10.4	-0.4	155.7	190.1
kenny	10.1	0.4	161.6	181.6	7.1	-3.9	44.4	107.2	11.6	-0.1	178.7	209.6
lou	9.7	1.6	174.5	186.6	6.6	-2.8	54.0	106.4	11.5	1.1	195.9	216.9
prairie	8.8	0.3	141.5	162.9	5.6	-4.2	19.0	90.6	10.7	-0.4	158.7	193.6
pubhunt	9.9	-0.2	151.6	174.5	6.2	-4.5	24.4	94.6	11.3	-0.5	167.5	201.5
rush	9.5	0.6	157.6	176.0	6.6	-3.7	41.0	103.3	11.5	0.0	177.1	208.8
sgalena	9.9	0.1	154.7	176.6	6.6	-4.6	27.4	100.0	11.1	-0.6	163.5	201.3
tuttle	9.5	1.5	170.6	183.6	6.1	-3.1	42.3	99.9	11.2	0.7	185.4	209.3
woodside	9.6	0.6	158.4	176.4	6.4	-3.8	35.5	98.9	11.5	-0.1	176.7	208.9

Table D.2 continued

| Site | April | | | | May | | | | June | | | |
	max[a]	min[b]	dd[c]	ddzero[d]	max[a]	min[b]	dd[c]	ddzero[d]	max[a]	min[b]	dd[c]	ddzero[d]
cherry	21.1	7.0	422.2	424.3	20.9	9.9	477.6	477.6	25.3	14.3	595.3	595.3
creeks	21.9	7.7	443.9	444.9	22.0	10.9	510.3	510.3	25.9	15.2	617.0	617.0
galena	21.1	6.7	415.9	418.1	20.7	10.0	475.6	475.6	24.4	14.2	578.3	578.3
kenny	21.3	6.8	421.6	422.9	21.4	10.0	487.4	487.4	25.1	14.6	595.1	595.1
lou	22.8	8.5	468.8	469.5	21.3	11.8	513.0	513.0	25.3	16.2	621.7	621.7
prairie	21.3	6.6	418.6	421.3	21.3	9.8	481.6	481.6	24.9	14.4	590.0	590.0
pubhunt	21.6	6.4	419.9	422.1	21.4	9.8	483.0	483.0	25.7	14.5	602.3	602.3
rush	22.3	6.9	437.7	440.0	21.2	10.2	486.4	486.4	24.3	14.6	583.5	583.5
sgalena	22.2	6.2	425.5	428.7	22.3	9.8	497.4	497.4	25.3	13.8	586.4	586.4
tuttle	21.9	7.8	445.2	446.0	22.1	11.1	514.9	514.9	25.9	15.0	614.1	614.1
woodside	22.0	7.2	437.1	439.3	21.8	10.2	494.5	494.5	25.5	14.7	603.5	603.5

a maximum daily temperature average for the month

b minimum daily temperature average for the month

[c] temperature accumulations for the month, no minimum threshold

[d] temperature accumulations for the month, no minimum threshold

	2006[a]			2007[b]		
site	estimate[c]	95% CI		estimate[c]	95% CI	
casto				52.3	46.7	58.5
cherry	137.9	120.8	157.5	71.4	63.8	79.9
creeks	19.8	17.4	22.7	27.7	24.8	31.0
elkrun				59.2	52.9	66.3
galena	49.8	43.6	56.9	30.0	26.8	33.6
kennynorth	112.8[d]	98.8	128.9	73.9	66.1	82.7
kennysouth	112.8[d]	98.8	128.9	57.1	51.0	63.8
lounorth	41.4	36.2	47.3	35.4	31.6	39.6
lousouth	38.6	33.8	44.0	33.3	29.8	37.3
ngalena				4.8	4.3	5.4
prairie	59.6	52.2	68.1	32.2	28.8	36.0
pubhunt	42.5	37.2	48.6	69.6	62.2	77.8
rushrunnorth	39.8	34.9	45.5	27.3	24.4	30.6
rushrunsouth	144.3	126.4	164.9	44.1	39.4	49.3
sgalena	84.5	74.0	96.5			
tuttlenorth	65.3	57.2	74.6	12.5	11.2	14.0
tuttlesouth				39.7	35.5	44.4
woodside	18.8	16.5	21.5	20.0	17.8	22.3

[a] estimated cluster size = 4.3

[b] estimated cluster size = 3.6

[c] Pearson correlation between 2006 and 2007 estimates, r = 0.59

[d] only one estimate for kennynorth and south in 2006

Table D. 3 Estimates for potential pre-leafout nest site availability for Northern Cardinals based on Distance sampling. Pre-leafout nests sites were those that would provide nesting cover for nests without any leafy cover. Examples include dense vine and brush piles.

Table D. 4 Monthly temperature values between January and June 2007 in riparian

forests in central Ohio, USA

Table D.4

site	month	dd[a]	dd(zero)[b]	min[c]	max[d]
casto	Jan	32.3	92.5	-2.6	9.1
casto	Feb	-112.4	128.5	-6.6	5.5
casto	Mar	143.9	415.2	-3.6	13.5
casto	Apr	471.6	752.2	-1.6	18.8
casto	May	1061.4	1342.0	1.3	25.5
casto	Jun	1708.6	1989.2	3.8	30.1
cherry	Jan	38.4	95.9	-2.4	9.5
cherry	Feb	-107.5	131.5	-6.6	5.7
cherry	Mar	148.9	418.7	-3.5	13.5
cherry	Apr	470.7	750.6	-1.6	18.7
cherry	May	1064.4	1344.4	1.2	25.7
cherry	Jun	1708.5	1988.5	3.6	30.4
creeks	Jan	43.7	99.0	-2.1	9.6
creeks	Feb	-107.6	130.1	-6.3	5.2
creeks	Mar	159.5	422.5	-3.1	13.2
creeks	Apr	493.7	764.9	-1.0	18.4
creeks	May	1090.6	1361.8	1.8	25.2
creeks	Jun	1737.8	2009.0	4.3	29.8
Clintonville[e]	Jan	41.5	99.4	-2.3	9.7
Clintonville[e]	Feb	-93.6	136.4	-6.2	5.9
Clintonville[e]	Mar	186.7	446.9	-3.1	14.3
Clintonville[e]	Apr	541.4	809.1	-0.9	19.8
Clintonville[e]	May	1175.2	1442.8	1.9	27.2
Clintonville[e]	Jun	1862.7	2130.4	4.5	32.1
elkrun	Jan	49.6	101.5	-1.9	9.9
elkrun	Feb	-92.6	135.3	-6.1	5.8
elkrun	Mar	179.9	432.7	-3.0	13.9
elkrun	Apr	527.1	787.6	-1.0	19.4
elkrun	May	1118.3	1378.8	1.9	25.8
elkrun	Jun	1757.2	2017.7	4.3	30.1
galena	Jan	24.3	86.4	-2.8	8.4
galena	Feb	-137.9	117.3	-7.1	4.6
galena	Mar	105.8	392.2	-4.0	12.6
galena	Apr	416.9	713.5	-2.0	17.8
galena	May	979.2	1275.8	0.8	24.2

Table D.4 continued

galena	Jun	1589.0	1885.6	3.3	28.5
kennynorth	Jan	39.8	95.5	-2.3	9.4
kennynorth	Feb	-105.2	130.4	-6.3	5.4
kennynorth	Mar	153.1	418.8	-3.4	13.5
kennynorth	Apr	478.1	751.7	-1.4	18.6
kennynorth	May	1059.4	1333.0	1.5	25.1
kennynorth	Jun	1700.5	1974.1	3.9	29.6
kennysouth	Jan	36.5	94.1	-2.4	9.3
kennysouth	Feb	-110.7	129.8	-6.5	5.3
kennysouth	Mar	142.5	415.0	-3.6	13.4
kennysouth	Apr	468.7	750.2	-1.6	18.7
kennysouth	May	1071.1	1352.6	1.2	26.0
kennysouth	Jun	1737.6	2019.0	3.6	31.1
lounorth	Jan	56.7	99.6	-1.1	9.2
lounorth	Feb	-89.1	126.3	-5.3	4.4
lounorth	Mar	169.8	404.9	-2.2	11.9
lounorth	Apr	502.3	744.8	-0.3	17.2
lounorth	May	1109.2	1351.7	2.5	24.2
lounorth	Jun	1779.6	2022.1	5.0	29.3
lousouth	Jan	43.2	96.9	-2.0	9.2
lousouth	Feb	-100.0	129.2	-6.0	5.0
lousouth	Mar	168.5	423.1	-2.8	13.0
lousouth	Apr	501.3	764.1	-0.8	18.2
lousouth	May	1112.1	1374.9	2.2	25.0
lousouth	Jun	1784.4	2047.2	4.7	29.9
ngalena	Jan	6.6	83.8	-3.8	8.2
ngalena	Feb	-167.3	121.4	-8.1	4.7
ngalena	Mar	57.2	380.9	-4.8	12.1
ngalena	Apr	364.3	700.2	-2.7	17.5
ngalena	May	933.0	1269.0	0.1	24.4
ngalena	Jun	1548.8	1884.8	2.6	29.1
prairie	Jan	26.5	92.8	-2.9	8.9
prairie	Feb	-142.6	126.9	-7.3	4.7
prairie	Mar	110.8	411.9	-3.9	12.7
prairie	Apr	435.0	746.7	-1.8	18.0
prairie	May	1018.8	1330.5	1.0	24.9
prairie	Jun	1645.0	1956.7	3.4	29.4

Table D.4 continued

pubhunt	Jan	26.1	88.6	-2.8	8.7
pubhunt	Feb	-141.9	124.4	-7.4	5.0
pubhunt	Mar	109.6	407.0	-4.1	13.1
pubhunt	Apr	443.8	750.8	-2.0	18.7
pubhunt	May	1025.9	1332.9	0.8	25.5
pubhunt	Jun	1654.6	1961.6	3.3	30.0
rushrunnorth	Jan	30.9	91.5	-2.6	9.0
rushrunnorth	Feb	-119.6	126.3	-6.7	5.1
rushrunnorth	Mar	131.6	409.4	-3.7	13.1
rushrunnorth	Apr	449.8	736.4	-1.6	18.2
rushrunnorth	May	1027.5	1314.1	1.2	24.9
rushrunnorth	Jun	1665.5	1952.1	3.7	29.4
rushrunsouth	Jan	35.2	95.4	-2.6	9.4
rushrunsouth	Feb	-112.3	130.6	-6.6	5.4
rushrunsouth	Mar	150.3	423.2	-3.5	13.5
rushrunsouth	Apr	480.6	761.7	-1.4	18.7
rushrunsouth	May	1070.4	1351.5	1.4	25.5
rushrunsouth	Jun	1714.7	1995.8	3.9	30.0
sgalena	Jan	16.9	87.1	-3.4	8.6
sgalena	Feb	-158.6	122.4	-7.9	4.9
sgalena	Mar	81.2	397.6	-4.7	12.9
sgalena	Apr	408.1	735.9	-2.6	18.7
sgalena	May	995.9	1323.8	0.3	25.8
sgalena	Jun	1593.5	1921.4	2.7	29.8
tuttlenorth	Jan	41.0	95.9	-2.1	9.2
tuttlenorth	Feb	-80.9	143.4	-5.8	6.0
tuttlenorth	Mar	194.9	444.3	-2.7	14.0
tuttlenorth	Apr	543.3	799.8	-0.7	19.3
tuttlenorth	May	1164.3	1420.8	2.2	26.3
tuttlenorth	Jun	1835.4	2091.9	4.8	31.0
tuttlesouth	Jan	50.4	101.0	-1.7	9.7
tuttlesouth	Feb	-66.7	149.8	-5.6	6.6
tuttlesouth	Mar	210.0	450.7	-2.6	14.3
tuttlesouth	Apr	556.0	802.4	-0.5	19.4
tuttlesouth	May	1170.6	1417.0	2.4	26.1
tuttlesouth	Jun	1841.5	2087.9	4.9	30.8
woodside	Jan	36.6	96.2	-2.6	9.5
woodside	Feb	-113.3	128.6	-6.7	5.5

Table D.4 continued

woodside	Mar	138.1	411.5	-3.7	13.4
woodside	Apr	462.8	745.5	-1.7	18.7
woodside	May	1042.9	1325.7	1.1	25.3
woodside	Jun	1678.6	1961.3	3.6	29.8

[a] temperature accumulations (C) based daily average
temperature [i.e., (min+max/2)] summed over the month

[b] same as [a] but daily if min<0 then min=0 and if max<0 then max=0

[c] average monthly minimum temperatures (C)

[d] average monthly maximum temperatures (C)

[e] one backyard location in Clintonville neighborhood,Columbus, OH

site	N[a]	estimate[b]	standard error	95% confidence interval	
casto	21	0.660	0.091	0.467	0.811
cherry	20	0.686	0.104	0.460	0.849
creeks	15	0.745	0.092	0.532	0.883
elkrun	18	0.729	0.089	0.526	0.867
galena	26	0.386	0.097	0.220	0.582
kenny[c]	36	0.783	0.076	0.599	0.897
lou[c]	40	0.617	0.074	0.465	0.749
ngalena	10	0.666	0.127	0.394	0.859
prairie	17	0.524	0.115	0.309	0.730
pubhunt	25	0.505	0.103	0.313	0.696
rushrun[c]	39	0.662	0.081	0.492	0.799
sgalena	23	0.736	0.087	0.537	0.870
tuttle[c]	48	0.664	0.070	0.516	0.785
woodside	16	0.695	0.106	0.461	0.859

[a] Number of adults Northern Cardinals captured at each site between 2003-2007.

[b] Estimates based on capture and resighting histories for each site individually using program MARK. Detection probability(p) was constant across sites and sex. A model with site*sex was >20 AIC_c more than the site only model.

[c] Sites with 4 ha grids (i.e., north and south subgrids) were merged for site survival estimates.

Table D. 5 Site-level Northern Cardinal survival estimates, standard errors, and confidence intervals generated from resighting histories between 2003 and 2007 with Program MARK

Table D. 6 Julian dates of the Northern Cardinal breeding phenology at 14 study riparian

forests in central Ohio, USA.

Table D.6

site	year	firstact[a]	first egg[b]	nthact[c]
casto	2004	108	110	112
casto	2005	103	102	117
casto	2006	103	110	112
casto	2007	89	98	99
cherry	2004	114	114	114
cherry	2005	102	104	115
cherry	2006	103	106	107
cherry	2007	101	114	106
creeks	2004	122	114	122
creeks	2005	102	108	102
creeks	2006	105	108	105
creeks	2007	96	115	96
elkrun	2004	115	115	119
elkrun	2005	102	102	116
elkrun	2006	101	104	143
elkrun	2007	94	106	109
galena	2004	109	117	118
galena	2005	104	125	110
galena	2006	112	111	112
galena	2007	111	120	114
kenny	2005	97	103	105
kenny	2006	96	104	107
kenny	2007	92	104	114
lou	2004	118	103	118
lou	2005	88	98	104
lou	2006	96	97	102
lou	2007	91	115	94
ngalena	2004	124	130	124
ngalena	2005	117	115	117
ngalena	2006	112	117	112
ngalena	2007	123	135	123
prairie	2004	112	117	112
prairie	2005	116	108	116
prairie	2006	105	109	105
prairie	2007	90	108	90
pubhunt	2004	117	116	117

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Table D.6 continued

pubhunt	2005	111	105	116
pubhunt	2006	102	104	108
pubhunt	2007	90	97	102
rushrun	2004	111	113	117
rushrun	2005	98	105	106
rushrun	2006	98	110	105
rushrun	2007	102	104	109
sgalena	2004	114	117	118
sgalena	2005	116	109	123
sgalena	2006	101	109	109
sgalena	2007	102	120	104
tuttle	2005	101	101	109
tuttle	2006	97	100	99
tuttle	2007	89	96	89
woodside	2004	106	111	113
woodside	2005	102	105	109
woodside	2006	101	110	103
woodside	2007	103	108	103

[a] Julian date of the first detection of nesting activity at the site.

[b] Julian date of the first clutch initiation at the site

[c] Julian date of the density-adjusted nesting activity activity (see text).