



Consequences of urbanizing landscapes to reproductive performance of birds in remnant forests



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ARTICLE INFO

Article history:

Received 8 August 2012

Received in revised form 8 October 2012

Accepted 19 December 2012

Keywords:

Brood parasitism

Nest predation

Nest survival

Productivity

Urban

ABSTRACT

In contrast to the well-documented changes in avian community structure in urbanizing areas, the demographic consequences of urbanization remain less understood. As such, we examined the extent to which an urbanizing landscape matrix affected avian reproductive performance in forests. From 2001 to 2011, we studied five songbird species in 19 forested sites in Ohio, USA and monitored 4264 natural nests to determine rates of daily nest survival and brood parasitism by brown-headed cowbirds (*Molothrus ater*). We also tracked the annual number of fledglings produced by color-banded pairs of two focal species, the synanthropic northern cardinal (*Cardinalis cardinalis*, $n = 974$ breeding pairs between 2003 and 2011) and the urban-avoiding Acadian flycatcher (*Empidonax vireescens*, $n = 350$ breeding pairs between 2001 and 2011). Over the 10-year period, neither daily nest survival nor brood parasitism rates in remnant forests were consistently related to the amount of urbanization in the surrounding landscape matrix for focal species, with the sole exception of Acadian flycatcher for which the percentage of nests with brood parasitism increased with urbanization. Annual reproductive output of cardinals was comparable across the rural–urban gradient, but Acadian flycatchers produced fewer fledglings as urbanization increased. These findings demonstrate that urban-associated patterns of annual reproduction cannot necessarily be inferred from nest survival data alone. Moreover, we show that avian community changes are not the simple consequence of nest predation. Understanding ecological processes that operate within metropolitan areas is critical if we are to conserve biological diversity on our urbanizing planet.

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1. Introduction

Understanding ecological processes that operate within cities is critical if we are to conserve biological diversity in a world where 60% of the world's population is projected to live in metropolitan areas by 2030 (Grimm et al., 2008). From a conservation perspective, one particularly worrisome consequence of burgeoning urban populations is that the footprint of cities will continue to expand and increasingly envelop protected natural areas (McDonald et al., 2008; Wade and Theobald, 2010). Protected areas have long served as the cornerstone of conservation (Soule and Terborgh, 1999), but within urbanizing landscapes, protected areas may be ill-equipped to sustain viable populations of many native species (Forman, 2008). Ecologists must evaluate how external pressures from urbanization influence the ecological performance of protected areas within a conservation context (Gaston et al., 2008). Though some consequences of urban development may reflect

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the well-known consequences of fragmentation (e.g., Forman et al., 1976; Ambuel and Temple, 1983; Blake and Karr, 1987; Robinson et al., 1995), others result squarely from land use changes within the landscape matrix. Indeed, characteristics of the matrix can alter movement rates (Brown and Kodricbrown, 1977; Gascon et al., 1999; Bender and Fahrig, 2005), provide alternative habitat (Foster and Gaines, 1991; Jules and Shahani, 2003), serve as a source of invaders (Laurance, 1991; Pysek et al., 2002), and determine the severity of edge and area effects (Andren, 1994; Aberg et al., 1995; Donovan et al., 1997). A recent meta-analysis showed that 95% of 104 studies found distinct matrix effects (Prevedello and Vieira, 2010), and, in particular, avian communities may be more sensitive to attributes of the matrix than to area and isolation (Andren, 1994; Kennedy et al., 2010, 2011).

Urbanizing landscape matrices are strongly associated with pronounced shifts in avian community structure and tend to support fewer Nearctic–Neotropical migratory bird species compared to less developed landscapes (e.g., Mills et al., 1989; Friesen et al., 1995; Rodewald and Bakermans, 2006). Changes in bird communities in human-dominated landscapes have been attributed to concomitant changes in reproductive performance due to patterns of nest predation and/or brood parasitism (Wilcove, 1985; Crooks and Soule,

1999). For example, high densities of some species (i.e., urban adapters) could partly result from higher nesting success in cities, either due to lower numbers of specialist predators and/or lower impact of food-subsidized generalist predators (Gering and Blair, 1999; Faeth et al., 2005; Shochat et al., 2006). Alternatively, because cities are known to host abundant populations of generalist nest predators, nest predation may be higher in cities (Thorington and Bowman, 2003; Phillips et al., 2005), thereby contributing to low numbers of urban avoiders. However, there are few long-term and large-scale empirical studies of avian reproduction in urban systems that allow evaluation of these possibilities. Well-documented is that urban landscapes typically support a diverse and abundant community of generalist predators (Jokimaki and Huhta, 2000; Sorace, 2002; Chace and Walsh, 2006). Yet recent evidence shows that numbers of generalist predators may be poor predictors of nest predation rates, likely because urban predators are often subsidized by anthropogenic foods (Rodewald et al., 2011; Stracey, 2011).

An examination of the literature also shows that the putative link between urbanization and increased nest predation has surprisingly weak empirical support (Chamberlain et al., 2009). Published studies based on natural nests have found evidence of both no relationship (Reidy et al., 2009; Burhans and Thompson, 2006), negative association (Ryder et al., 2010), and positive association between predation rate and urban development (Phillips et al., 2005; Vigallon and Marzluff, 2005; Bakermans and Rodewald, 2006). Some studies of artificial nests also tend to show higher rates of predation in urban environments (Jokimaki and Huhta, 2000; Thorington and Bowman, 2003; Jokimaki et al., 2005; Lopez-Flores et al., 2009). In contrast, other artificial nest studies suggest that highly developed urban centers might provide a refuge from predation (Gering and Blair, 1999; Jokimaki et al., 2005). Part of the variability in patterns may be a consequence of comparing studies conducted in habitat remnants to those in the urban matrix itself. In addition, many previous studies had shortcomings that include short duration (most are 1–3 years), use of artificial nests, emphasis on single-species, and, importantly, failure to control for both landscape composition and configuration in study design (i.e., fragmentation and habitat loss increase with urbanization).

We applied our 10-year dataset on multiple species of songbirds breeding in protected forests in fragmented landscapes across an urban-to-rural gradient to answer the following still-unresolved question that ultimately determines the value of urban habitat for bird conservation: How does an urbanizing landscape matrix affect avian reproductive performance? We specifically examined nest survival and brood parasitism rates, as well as annual reproductive output of two focal species.

2. Methods

From 2001 to 2011, we monitored 4264 nests of five forest-breeding songbird species in 19 mature riparian forests in central Ohio, USA (Table 1). Forests were located along a rural-to-urban gradient, where landscapes shared similar land use history prior to urbanization as well as amount and spatial configurations of natural areas. All of our landscapes were highly fragmented and human-dominated systems. Because riparian forests in our study area were linear and highly connective over many kilometers along waterways, width of forest was used to characterize the amount of habitat available to forest-breeding birds. Although sites varied in forest width (115–565 m for >300 m of length), the width of the forest was not confounded with the amount of surrounding urban development ($r = -0.015$, $P = 0.546$). Thus, sites located along the rural–urban gradient differed primarily in the dominant land use type (i.e., either agriculture or urban development), not the amount of forest or forest edge, within the landscape matrix.

We derived an urban index to represent the amount of urbanization surrounding each forest site. We quantified landscape composition within a 1-km radius area centered on each study site using recent (2002–2004) digital orthophotos (Table 1). This 1-km scale has been shown to be strongly associated with bird communities in other studies (Tewksbury et al., 1998; Rodewald and Yahner, 2001), is commonly used in conservation efforts, and far exceeds average territory size of birds breeding at our sites. As part of a complementary study, we performed a principal components analysis on landscape metrics across study sites (Rodewald and Shustack, 2008a). The first principal component (hereafter termed the “urban index”) explained 80% of the variation among sites and loaded positively for number of buildings (0.92), percent cover by roads (0.94), pavement (0.90), and lawn (0.88), but loaded negatively for percent cover by agriculture (−0.83). Rural landscapes were dominated by cropland, pasture, managed grassland, and farms. Urban landscapes, in contrast, were dominated by residential areas, commercial development, and roads. Building densities in our landscapes ranged from 0.1 to 7.3 buildings per ha (10–727 buildings/km²).

2.1. Field methods

From March–September 2001–2011, we searched forest remnants for nests of five understory-nesting songbird species that nest in understory and midstory strata – one resident (northern cardinal, *Cardinalis cardinalis*, $n = 2532$), one temperate migrant (American robin, *Turdus migratorius*, $n = 696$), and three Neotropical migratory species (Acadian flycatcher, *Empidonax vireescens*, $n = 574$; gray catbird, *Dumetella carolinensis*, $n = 238$; wood thrush, *Hylocichla mustelina*, $n = 224$; Table 2). Though the breeding season began in late March for cardinals, the main pulse of nesting was May through August. Our previous work in this system indicated that robins and cardinals (and catbirds, to a lesser extent) respond positively to urbanizing landscapes, whereas the flycatcher and wood thrush respond negatively (Rodewald and Bakermans, 2006).

Each located nest was checked at 2–4 day intervals by viewing nest contents or by observing parental behavior to track nest stage (e.g., onset of incubation behavior) and locate young fledglings, when possible. To avoid exposing nests to predators as a consequence of our visits, we observed nests from as far a distance as possible (often >10 m), for as brief a time as possible, and from different routes each time. If a predator was observed in the vicinity, we delayed checking the nest. We attempted to check all nests for cowbird eggs, though this was not always possible due to early nest failures and inaccessible nests (i.e., too high or over water). Our research with video-cameras at nests shows that the suite of nest predators is diverse, including corvids, raptors, squirrels, common grackles (*Quiscalus quiscula*), brown-headed cowbirds (*Molothrus ater*), raccoons (*Procyon lotor*), opossum (*Didelphis virginiana*), and domestic cats (*Felis catus*) (Rodewald and Kearns, 2011). We also have documented that nearly all species of nest predator increase in relative abundance as landscapes become more urban (Rodewald et al., 2011).

Annual reproductive output (i.e., total number of fledglings) of flycatchers and cardinals was estimated by monitoring successive nest attempts of pairs breeding at sites. Whenever possible, flycatchers and cardinals were individually marked with a USGS band and a unique combination of color bands. We used information on territory locations combined with banded individuals to identify all pairs breeding at sites. Because we were not able to band every individual breeding at sites, the pair focus still allowed us to estimate the reproductive output for each territory. Moreover, low within-season turnover rates of banded individuals suggested that territories and pairs were stable within each breeding season. For each pair, all known nesting attempts were monitored from late

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