

Quantifying avian nest survival along an urbanization gradient using citizen- and scientist-generated data

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Abstract. Despite the increasing pace of urbanization little is known about the factors that limit bird populations (i.e., population-level processes) within the urban/suburban land-use matrix. Here, we report rates of nest survival within the matrix of an urban land-use gradient in the greater Washington, D.C., USA, area for five common songbirds using data collected by scientists and citizens as part of a project called Neighborhood Nestwatch. Using program MARK, we modeled the effects of species, urbanization at multiple spatial scales (canopy cover and impervious surface), and observer (citizen vs. scientist) on nest survival of four open-cup and one cavity-nesting species. In addition, artificial nests were used to determine the relative impacts of specific predators along the land-use gradient. Our results suggest that predation on nests within the land-use matrix declines with urbanization but that there are species-specific differences. Moreover, variation in nest survival among species was best explained by urbanization metrics measured at larger “neighborhood” spatial scales (e.g., 1000 m). Trends were supported by data from artificial nests and suggest that variable predator communities (avian vs. mammalian) are one possible mechanism to explain differential nest survival. In addition, we assessed the quality of citizen science data and show that citizens had no negative effect on nest survival and provided estimates of nest survival comparable to Smithsonian biologists. Although birds nesting within the urban matrix experienced higher nest survival, individuals also faced a multitude of other challenges such as contaminants and invasive species, all of which could reduce adult survival.

Key words: *artificial nests; citizen science; land-use matrix; MARK; nest survival; predation pressure; urbanization.*

INTRODUCTION

Since the early 1970s, the extent of urban area in the United States has more than doubled (Heimlich and Anderson 2001). As a result, concerns for the persistence of wildlife populations, such as birds, within the urban to forest land-use gradient has motivated research to understand the human impact (e.g., Marzluff 2001, DeStefano and DeGraaf 2003, Blair 2004). Generally, studies of urban birds have focused on how land development impacts diversity, abundance indices, and community organization (Marzluff 2001, Chen et al. 2002, Blair 2004, Porter et al. 2005). Although such studies integrate habitat and landscape variables into analyses, using diversity and abundance metrics as dependent variables has limited utility for understanding underlying mechanisms driving population dynamics of birds (Brawn and Robinson 1996, McKinney 2002, DeStefano and DeGraaf 2003). Understanding how birds are affected by urbanization requires examination of demographic parameters that regulate population growth (Marzluff 2001, Thorington and Bowman 2003).

Moreover, this research needs to be conducted within the urban/suburban matrix as well as in remaining patches of natural vegetation. Given that nest predation is the primary cause of nest failure (Ricklefs 1969, Martin 1992) and can play an important role in driving population dynamics (Lack 1954), studying nest predation along a land-use gradient can provide powerful insights into the effects that urbanization may have on important demographic parameters (Gering and Blair 1999, Jokimäki and Huhta 2000).

To date, too few studies of nest predation in human-dominated landscapes have been conducted to establish whether nest predation rates consistently increase (Jokimäki and Huhta 2000, Thorington and Bowman 2003), decrease (Gering and Blair 1999, Blair 2004), or show negligible impacts (Reale and Blair 2005, Rodewald and Shustack 2008) with increasing urbanization. Differing results may be due to several reasons. First, many of the nest survival studies conducted within urban areas have used only artificial nests (e.g., Gering and Blair 1999, Jokimäki and Huhta 2000, Thorington and Bowman 2003) with only recent work examining survival of real nests (e.g., Borgmann and Rodewald 2004, Marzluff et al. 2007, Rodewald and Shustack 2008). It is now widely accepted that artificial nests may not provide accurate survival estimates because they lack parental influence and are known to differentially attract nest predators using scent cues (Major and Kendal 1996, Moore and

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Robinson 2004). As such, more studies on natural nests are needed to help elucidate the trends of avian nest survival along the urbanization gradient. Second, many studies focus on Neotropical migrants that nest in larger-scale patches of forest or other contiguous habitats embedded within urban environments rather than within the matrix itself. Given the role of predator communities on nest survival probability and their likely spatial variability (Marzluff et al. 2007), it is unclear if large urban parks accurately represent the predators present in the urban and suburban matrix. As such, a study focusing on the “winners” of the urbanization process (i.e., those that nest in small parks and backyards) can provide information about predator communities and the subsequent nest predation pressure within the urban/suburban matrix. Third, most nest predation studies have used either percentages of successful vs. depredated nests or regression techniques with binary metrics of success to model nest survival across the gradient. Such estimates of apparent nest survival do not account for exposure time and are often positively biased relative to true nest survival (see Mayfield 1961). Unbiased nest survival estimators that account for exposure time and allow researchers to rigorously assess the importance of biological covariates on survival provide stronger resolution of how predation varies along the urban to rural land-use gradient. Last, most studies to date have taken a single species approach yet species are likely to show different responses to urbanization. As such, a multispecies approach may better characterize how human land use affects nest survival across avian communities.

Here we used both scientists and citizens to investigate avian nest survival in five common species that breed along an urbanization gradient in the greater Washington, D.C./Baltimore, Maryland region. We modeled daily survival rates of nests using program MARK (White and Burnham 1999) and built competing models to test for the effects of species, observer (scientist vs. citizen), and urbanization at multiple spatial scales. To our knowledge this is the first study to rigorously determine if citizen-generated data can accurately estimate demographic parameters of interest (e.g., nest survival). In addition to our use of natural nests, we conducted an experiment with artificial nests and plasticine eggs to identify predator types and to examine their relative impact on open-cup nesters.

METHODS

Study sites and land-use characterization

We studied nesting success along an urban to wild land gradient in the Washington, D.C. and Baltimore, Maryland metropolitan region. A significant portion of the data was collected in conjunction with Neighborhood Nestwatch (hereafter referred to as NN; *available online*).³ NN is a citizen science program administered

by the Smithsonian Migratory Bird Center (SMBC) at the National Zoological Park (see Evans et al. 2005). As such, artificial and natural nests were located along the gradient using two sets of localities: (1) at the properties of NN participants ($n = 71$), and (2) at properties and small suburban parks adjacent to established NN participant sites ($n = 75$).

Geographic Information Systems (GIS) were used to analyze landscape-scale land-use characteristics for nest locations. We used 30-m resolution National Land Cover Data 2001 (NLCD; Homer et al. 2004) impervious surface and canopy density as proxies to characterize the degree of urbanization around natural and artificial nest sites (McKinney 2002). The locations of nest sites were recorded using a Garmin 12 XL GPS unit (Garmin, Olathe, Kansas, USA). Using ArcGIS 9.2 (ESRI, Redlands, California, USA), landscape metrics were determined using a point buffer from each nest location at multiple spatial scales (100, 200, 500, and 1000 m radii).

Because several Nestwatch sites in the Chesapeake Bay region included open water within one or all radii, this land-use type was excluded from the analyses (Alberti et al. 2001). Cells designated as “Open Water” in the classified NLCD 2001 data set were reclassified and converted from raster to vector format using ArcGIS Spatial Analyst and extracted from the point buffers. Given that larger radii overlapped spatially, our data set created the potential for spatial nonindependence among explanatory variables. To test for spatial autocorrelation in our data, we performed simple and partial Mantel tests using the *ecodist* package (Goslee and Urban 2007) in R version 2.8.1 (R Development Core Team 2008). Simple Mantel tests were used to examine how environmental variables (canopy and impervious) and binary nest success were spatially structured. Partial Mantel tests were used to compare environmental effects on nest success, while controlling for spatial structure in the data. Our metrics of canopy cover and impervious surface were highly correlated ($r = -0.811$, $P = 0.0001$). Despite this, we included both canopy cover and impervious surface in this study because these metrics characterize land use in different ways and many rural sites had both low canopy cover and impervious surface.

Natural nests

During the breeding seasons (April through July) 2000–2008 nests of all focal species were found and subsequently monitored by either Smithsonian biologists or NN participants. Species include the American Robin, *Turdus migratorius* (AMRO); Northern Mockingbird, *Mimus polyglottos* (NOMO); Northern Cardinal, *Cardinalis cardinalis* (NOCA); Gray Catbird, *Dumetella carolinensis* (GRCA); and House Wren, *Troglodytes aedon* (HOWR). Nests were found using two methods: (1) parental behavior (e.g., carrying nest material or provisioning offspring) and (2) systematic searches of nesting substrates within participant yards. All nests

³ (<http://nationalzoo.si.edu/goto/nestwatch>)

were systematically monitored on a two- to three-day rotation following Martin and Geupel (1993). On each visit, the numbers of eggs, nestlings, and fledglings, dates of clutch initiation, hatching, and fledging, and nest fate (e.g., fledged, abandoned, depredated) were recorded. For nests monitored by NN participants, data were either sent directly to the Smithsonian Migratory Bird Center in hard-copy form or were entered on the NN website. If a nest produced at least one fledgling, it was categorized as successful; otherwise it was categorized as failed (Burke et al. 2004). Nest attempts that failed prior to egg-laying and nests considered abandoned by adults were removed from the analysis.

Artificial nests

Despite the shortcomings of artificial nests for estimating survival under natural conditions, use of artificial nests with plasticine eggs can provide an inexpensive method to determine the relative contribution of different predators. Here, we deployed artificial nests across a land-use gradient during 2001 and 2002 to quantify predator suites in urban and rural landscapes and to determine the relative contribution of avian and mammalian predators to nest failure of open-cup nesting species. In addition, artificial nests provided us with unbiased independent estimates of apparent survival along the urbanization gradient. NN sites were chosen randomly from within each of the urban, suburban, or rural participant bases. Due to limited numbers of urban participants, additional urban sites were randomly selected from numbered atlas blocks in the urban centers of Washington, D.C. and Baltimore, Maryland. All forest sites were located randomly within a 2000-acre (809 ha) deciduous forest at the Smithsonian Environmental Research Station in Edgewater, Maryland.

To mimic natural nest placement and exposure times, two artificial wicker nests were placed at least 25 m apart at heights between 0.5 and 2.5 m and left for 14 days during early June. This time period corresponds to incubation periods for the focal species. Using latex gloves to minimize human odor, nests were baited using two Japanese quail (*Coturnix coturnix japonicus*) eggs and one plasticine egg. If quail or plasticine eggs were destroyed, marked by scratches or punctures, or missing from the nest, the nest was considered depredated (Thorington and Bowman 2003, Burke et al. 2004). Predator type was identified from the markings (e.g., tooth, bill) left on plasticine eggs (Major 1991, Matthews et al. 1999) and split into the following categories: avian (e.g., Blue-Jays and Crows), small mammal (e.g., mouse spp., rat spp., Eastern chipmunk, and gray squirrel), large mammal (e.g., gray and red fox, raccoon, and opossum), depredated without marks (e.g., egg out of nest), eggs missing, and other (e.g., unidentified marks). We calculated the percentage of nests in each portion of the gradient depredated by a specific predator class.

Nest survival analyses

Program MARK (White and Burnham 1999) allows users to build descriptive models and compare their fit to the data according to Akaike's Information Criterion (AIC; Akaike 1973). We built models of nest survival that incorporated combinations of individual covariates (species, observer, impervious surface, and canopy cover), and compared them to the null model of constant survival rate, $S(.)$. We assessed observer effect on nest survival by comparing nests monitored by Smithsonian biologists to those monitored by citizen scientists. We first looked for an observer effect with AMRO, GRCA, and NOCA and found no survival differences (see *Results*) so we pooled data across those species to increase our power to detect an observer effect. We examined our environmental variables (impervious and canopy cover) at multiple spatial scales (e.g., 100–1000 m) to determine which scale best explained variation in nest survival. Because of small sample sizes for some species in some years, data were pooled across years to increase power for detecting the effect of urbanization on nest survival. For species by year sample sizes see Appendix: Table A1. First we placed all open-cup nests into a cumulative analysis to examine what parameters best explained variation in nest survival. Our single cavity nesting species, House Wren, was excluded from this analysis because a priori survival differences were expected given nest architecture. Second, we ran species-specific models to determine the relative effect of our urbanization metrics on nest survival.

All covariates were unstandardized and logit link function and second part variance estimation were adopted. Daily survival estimates were obtained from specific model beta parameters and back transformed following Dinsmore et al. (2002) and Rotella (2005). Cumulative survival probabilities were calculated by raising daily survival rate (DSR) to the appropriate species-specific number of days in the nesting cycle (i.e., incubation days + nestling days). We approximated variance for cumulative survival probabilities and calculated 95% CIs using the delta method (see Rotella 2005, Powell 2007). We compared model support using AIC_c , which corrects for small sample sizes and evaluated the strength of evidence for each model using normalized weights, w_i (Burnham and Anderson 2002). We selected the model with the smallest AIC_c as the best among all models being compared, where models within a ΔAIC_c of 2.00, were considered equally supported (Burnham and Anderson 2002). Post hoc comparisons of survival rates among species were made using program CONTRAST (Hines and Sauer 1989). We used Bonferroni-adjusted P values for multiple comparisons. Differences in the rates of predation among treatments for artificial nests were compared with a chi-square goodness-of-fit test. Means and estimates are presented \pm standard error.

TABLE 1. A summary of model selection results for four open-cup nesting bird species along an urbanization gradient in Washington, D.C., USA.

Model†	Deviance‡	K§	ΔAIC_c ¶	w_i
S(species + canopy1000m)	835.76	5	0.00	0.51
S(species + impervious1000m)	837.05	5	1.29	0.27
S(species)	840.21	4	2.45	0.15
S(canopy1000m)	847.47	2	5.70	0.03
S(impervious1000m)	848.86	2	7.09	0.01
S(canopy500m)	849.94	2	8.17	0.00
S(canopy200m)	850.76	2	8.99	0.00
S(impervious500m)	850.82	2	9.05	0.00
S(impervious200m)	851.13	2	9.36	0.00
S(impervious100m)	851.87	2	10.10	0.00
S(.)	855.26	1	11.49	0.00
S(canopy100m)	854.50	2	12.73	0.00
S(citizen)	855.19	2	13.42	0.00

† Nest survival models for all open-cup nesting species with the incorporation of covariates and compared with the null model of constant survival S(.). Model components include: impervious, average percentage impermeable surface in a given radius (100–1000 m) around each nest measured in ArcGis 9.2 using 30-m resolution National Land Cover Data (NLCD); canopy, average percentage canopy cover in a given radius (100–1000 m) around each nest measured in ArcGis 9.2 using 30-m resolution NLCD; citizen, a measure of observer effect for those nests monitored by citizen scientists.

‡ A measure of model fit where deviance is measured as the difference in $-2 \log$ -likelihood of the current model and the $-2 \log$ -likelihood of the saturated model.

§ Number of parameters.

¶ The lowest AIC_c value was 845.7.

RESULTS

Species, urbanization, and observer effects

A total of 405 natural nests were monitored from 2001 to 2008 ($n = 302$ open-cup nests for a total of 17 526 exposure days; $n = 103$ cavity nests for a total of 592 exposure days). The model that included species and canopy cover at the largest spatial scale was the best overall fit [S(species + canopy1000m): $\Delta AIC_c = 0.00$, $w_i = 0.51$] but could not be differentiated from the model with species and impervious surface [S(species + impervious1000m): $\Delta AIC_c = 1.29$, $w_i = 0.27$], i.e., $\Delta AIC_c < 2$ (Table 1). Models at smaller spatial scales (e.g., 100–500 m) were poorer predictors of nest survival regardless of the environmental variable than were models incorporating covariates measured at larger (1000 m) spatial scales (Table 1). Overall, the canopy cover model had a negative slope ($\beta_{can} = -0.014 \pm 0.007$) indicating that as canopy cover increased daily nest survival decreased. Conversely, impervious surface had a positive slope ($\beta_{imp} = 0.011 \pm 0.006$), indicating that as impervious surface increased, daily survival also increased. Models that incorporated an observer effect across open-cup nesters were poorly fit (S(citizen): $\Delta AIC_c = 13.42$, $w_i = 0.00$) and ranked below the null model (S(.): $\Delta AIC_c = 11.49$, $w_i = 0.00$) (Table 1). Moreover, our most powerful test for an observer effect (all open-cup nests) showed no significant difference in DSR between nests monitored by Smithsonian biologists and citizen scientists ($\chi^2 = 0.02$, $df = 1$, $P = 0.897$)

(Fig. 1). In addition, our failure to detect differences in an observer by species analysis, AMRO ($\chi^2 = 0.12$, $df = 1$, $P = 0.735$), GRCA ($\chi^2 = 0.71$, $df = 1$, $P = 0.399$), and NOCA ($\chi^2 = 2.10$, $df = 1$, $P = 0.147$), suggests that citizens provide reliable survival estimates.

Models that incorporated species performed better (S(species): $\Delta AIC_c = 2.45$, $w_i = 0.15$) than the null model (S(.): $\Delta AIC_c = 11.49$, $w_i = 0.00$) (Table 1). Daily survival rates differed significantly among species ($\chi^2 = 50.12$, $df = 4$, $P < 0.0001$) resulting in cumulative survival probabilities that ranged from 27% to 79% (Fig. 2). Pairwise comparisons among species showed significant survival differences between AMRO and NOCA ($\chi^2 = 9.44$, $df = 1$, $P = 0.002$), AMRO and HOWR ($\chi^2 = 11.94$, $df = 1$, $P < 0.001$), GRCA and NOCA ($\chi^2 = 9.52$, $df = 1$, $P = 0.002$), GRCA and HOWR ($\chi^2 = 20.71$, $df = 1$, $P < 0.0001$), and NOCA and HOWR ($\chi^2 = 25.57$, $df = 1$, $P < 0.0001$) (adjusted Bonferroni $P = 0.005$). All other pairwise comparisons were nonsignificant.

Species-specific models that incorporated the effects of our urbanization metrics showed that species were differentially impacted by urbanization. Model weights showed that canopy cover had the greatest explanatory power for GRCA ($\beta_{can} = -0.012 \pm 0.011$, $w_i = 0.22$) and NOCA ($\beta_{can} = -0.023 \pm 0.01$, $w_i = 0.43$) with both species showing a gradual decrease in nest survival with increasing canopy cover (Fig. 3A, B). As a result, cumulative survival probability was 25% to 45% higher in urban vs. rural environments for GRCA and NOCA, respectively. Impervious surface was a better predictor of nest fate for HOWR ($\beta_{imp} = 0.041 \pm 0.021$, $w_i = 0.31$) and NOMO ($\beta_{imp} = 0.032 \pm 0.022$, $w_i = 0.22$). Similarly, cumulative survival probabilities for HOWR and NOMO were 19% to 33% higher in urban vs. rural environments, respectively. Neither canopy cover nor impervious surface explained AMRO nest survival variation.

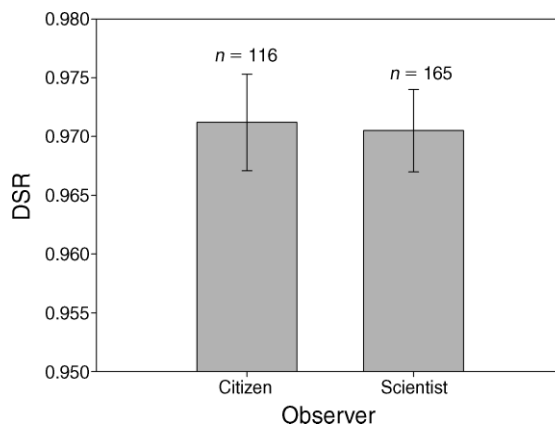


FIG. 1. Estimates (\pm SE) of daily survival rate (DSR) for three open-cup nesting species derived from citizens and scientists; n = number of nests observed. Our failure to detect differences between observer groups suggests that citizens had no negative impact on nest survival and provides reliable estimates of an important population parameter. Standard errors were calculated using the delta method.

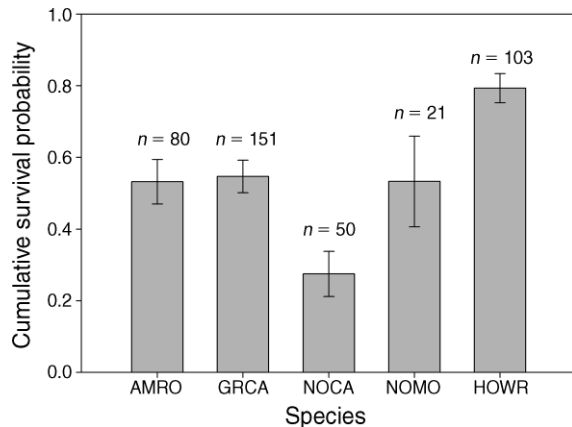


FIG. 2. Variable nest survival among common birds in the greater Washington, D.C. area is evidenced by cumulative survival probabilities (\pm SE). Cumulative survival probability is the probability a nest will survive to fledge at least one offspring and is calculated by raising DSR to the power of the nest exposure days (incubation + nestling). Standard errors were calculated using the delta method. Species are: American Robin, *Turdus migratorius* (AMRO); Gray Catbird, *Dumetella carolinensis* (GRCA); Northern Cardinal, *Cardinalis cardinalis* (NOCA); Northern Mockingbird, *Mimus polyglottos* (NOMO); and House Wren, *Troglodytes aedon* (HOWR). Sample sizes are the numbers of nests monitored.

Spatial distributions

Simple Mantel tests for autocorrelation between environmental variables at the 1000 m radius scale show that while both canopy cover and impervious surface were significantly autocorrelated for some species (e.g., NOMO and GRCA), only impervious surface was significant in a cumulative analysis across species (Mantel $r = 0.147$, $P = 0.009$; Table 2). Likewise, binary nest success was spatially autocorrelated for only two species (e.g., HOWR and NOMO) but was not significant in a cumulative open-cup analysis (Mantel $r = -0.0121$, $P = 0.75$). In a partial Mantel that controlled for the effects of distance, canopy cover was still predictive of binary reproductive success across our four open-cup species (Mantel $r = 0.042$, $P = 0.018$). Variation in binary success of House Wren nests, however, was not predicted by impervious surface after controlling for spatial proximity (Mantel $r = -0.048$, $P = 0.68$). Although these tests are not as nuanced as DSR estimates that account for exposure time, they corroborate our result that canopy cover was predictive of nest survival.

Artificial nests

Overall, 178 (55.6%) nests were depredated at all sites combined. Predation ranged from 37.5% to 77.5% showing a gradual increase from urban to rural sites (Table 3). These predation rates mirror survival trends for natural nests; however, they are apparent survival estimates and prone to upward bias. Nest predator identification from plasticine eggs revealed a shift in the types of nest predators preying on artificial nests along

the land-use gradient (Table 3). In urban areas, significantly more avian predators depredated nests, while nests in rural locations were more likely to be depredated by small mammals (Table 3). Other predator classes failed to show significant differences between habitat types.

DISCUSSION

The rapid conversion of forest into urban and suburban land use has made understanding the impacts of an urbanizing landscape on wildlife, in our case birds, an imperative for conservation biology (Blair 1996). Given the extent of the threat, native wildlife are often faced with existing in a “novel” and modified habitat. Here, we examined how avian nest survival, a key demographic parameter for understanding overall population dynamics, varied along an urbanization gradient. In addition, we assessed the quality of citizen- vs. Smithsonian biologist-generated data for estimating a population parameter. Our results show two important findings: (1) that data from citizens and scientists are equivalent and

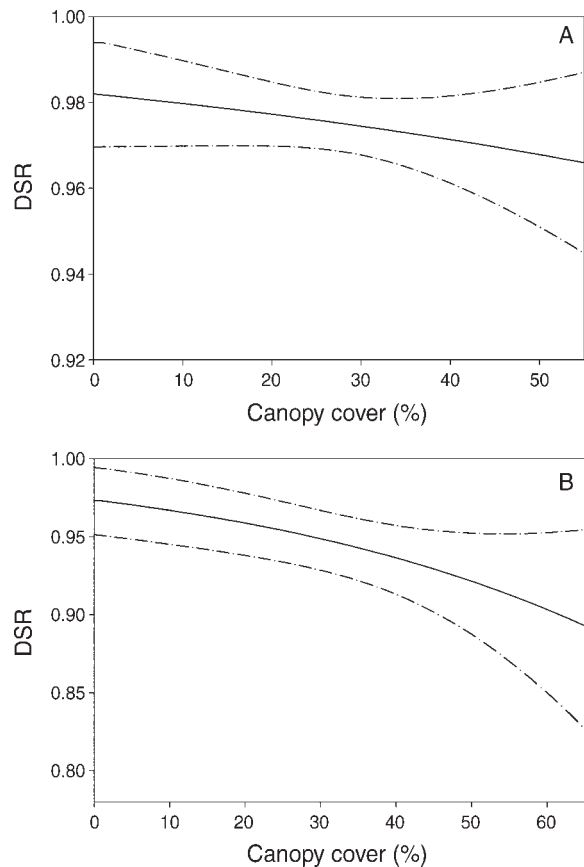


FIG. 3. Daily nest survival of (A) Gray Catbirds and (B) Northern Cardinals shows a gradual decrease with increasing canopy cover. Solid lines represent DSR estimated using beta parameters from the best-fit model. Dashed lines represent upper and lower 95% confidence intervals for the estimated DSR calculated using the delta method.

TABLE 2. Tests for spatial autocorrelation in binary nest success and among environmental variables measured in 1000-m radii around the nests of five common species of birds nesting along the urbanization gradient in Washington, D.C.

Variable	HOWR		NOMO		NOCA		GRCA		AMRO		Open-cup	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Canopy	-0.04	0.67	0.31	<0.01	0.04	0.27	-0.04	0.67	0.14	0.09	0.07	0.12
Impervious	-0.03	0.62	0.24	0.02	0.01	0.38	0.14	0.03	0.07	0.19	0.15	<0.01
Nest success	0.31	<0.01	0.23	0.02	0.04	0.22	0.00	0.34	-0.03	0.59	-0.01	0.75

Notes: Values in bold denote significance ($P < 0.05$). Species are: House Wren, *Troglodytes aedon* (HOWR); Northern Mockingbird, *Mimus polyglottos* (NOMO); Northern Cardinal, *Cardinalis cardinalis* (NOCA); Gray Catbird, *Dumetella carolinensis* (GRCA); and American Robin, *Turdus migratorius* (AMRO).

provide reliable estimates of nest survival and (2) that variation in nest survival was explained by both species-specific differences and environmental variables that quantified the degree of urbanization (canopy cover and impervious surface). Ultimately, understanding the effects of urbanization on ecological processes and avian demography will help ameliorate human impacts while guiding proactive habitat management.

Overall, our results show that metrics of urbanization were predictive of nest survival. Contrary to our expectations, results from our models demonstrated that four of five species had higher nest survival in urban compared to rural environments. These results support the supposition that urban habitats may act as relative "safe zones," which suffer lower rates of nest predation than rural environments (Gering and Blair 1999, Blair 2004). Low predation in urban environments could result from changes in the composition and abundance of predators with increasing urbanization (Adams 1994). Snakes and rodents, for example, might be disproportionately affected by the novel threats of urban environments (e.g., cars and domestic animals) resulting in depressed populations and fewer nest losses. Although few studies have documented how urbanization impacts predator communities, recent work by Marzluff et al. (2007) showed that forest cover influences predator occurrence with some species increasing in urban environments (e.g., American Crows, *Corvus brachyrhynchos*) while others decreased (e.g., Douglas squirrel, *Tamiasciurus douglasii*). Work in riparian forests in central Ohio, on the other hand, has shown both avian and mammalian nest predators increase in more urbanized landscapes (Rodewald, *in*

press) creating the potential for higher nest predation. Data from our artificial nests suggest that avian predators such as American Crows and Blue Jays may cause significantly more nest failures in urban environments while small mammals including mice, chipmunks, and squirrels were significantly more likely to depredate nests in rural environments. Moreover, although we failed to detect a significant trend, larger mammals like foxes, raccoons, and opossums also appear more likely to depredate nests in the rural landscape. These results viewed cumulatively suggest predator responses to an urbanizing landscape show high spatial variability (Marzluff et al. 2007, Marzluff and Rodewald 2008). Ultimately, how nest predation pressure varies across the landscape gradient will be contingent on how predator species respond to landscape structure, novel threats (e.g., cars and domestic pets), and the relative impact those predators have on different avian species (Jokimaki and Huhta 2000).

Settlement patterns, nest site selection, and subsequent nest survival probability are intricately tied together, such that decisions early in the breeding season can dramatically influence seasonal reproductive output. Multiple factors are thought to drive predation risk on avian nests including but not limited to, habitat structure, nest type, predator abundance, nest placement, and substrate (Martin 1988, 1995). However, the aforementioned factors likely interact such that variation in nest survival within a species, among species, and across nesting guilds may be explained by different processes. Here, our results unequivocally show that species cumulative survival probabilities differ by a threefold difference. Clear differences existed among species with different nesting

TABLE 3. Percentages of artificial nests depredated by different kinds of predators along an urbanization gradient.

Type of predation	Habitat gradient				χ^2	<i>P</i>
	Urban (<i>n</i> = 80)	Suburban (<i>n</i> = 83)	Rural (<i>n</i> = 75)	Forest (<i>n</i> = 80)		
Avian	60.0	57.1	38.6	12.9	19.96	0.001
Small mammal	10.0	9.5	18.2	58.1	29.41	0.001
Large mammal	0.0	0.0	4.5	6.5	4.35	ns
Other	3.3	0.0	4.5	0.0	4.37	ns
Depredated without marks	6.7	7.1	11.4	11.3	0.86	ns
Eggs missing	20.0	26.2	22.7	14.5	2.56	ns
Total depredated	37.5	50.6	58.7	77.5		

strategies with our single cavity-nesting species, House Wren, having the highest survival probability. Moreover, this finding is consistent with recent experimental evidence that suggests predation risk is strongly determined by nest type (i.e., open vs. cavity), independent of parental behavior (Fontaine et al. 2007). Alternatively, differences in cumulative survival and the relative role of urbanization in nest predation probability could be attributed to nest placement and substrate (see Martin 1988, 1993). Our use of citizen scientists, however, precluded the ability to rigorously measure all variables of potential importance to nest survival.

Our approach did, however, afford us the opportunity to look at broadscale spatial patterns in nest survival. All open-cup and a single cavity-nesting species showed a similar nest survival pattern with respect to increasing urbanization. Nest survival was best predicted by environmental variables measured at a “neighborhood” spatial scale (e.g., 1000 m). Although we found a strong spatial signal for impervious surface, we believe our metrics accurately represent the urban environment and the characteristics its wildlife inhabitants encounter. Regardless, canopy cover did not suffer from autocorrelation and was a better predictor of nest survival for the majority of the species studied. The robust nature of our results is further evidenced by the fact that variation in nest survival was still explained by canopy cover after controlling for spatial autocorrelation. Most importantly, we believe our results highlight the importance of scale when studying nest predation. Marzluff et al. (2007) recently showed that nest predators and their prey were only associated at the largest spatial scale (e.g., 1 km²). Likewise, Kus et al. (2008) found that nest survival for Bell’s Vireo was explained by a broadscale environmental gradient. The associations between predators and prey at larger spatial scales may result from predators often having larger home ranges than their prey. Regardless, the combination of these results strongly suggests that larger scale perspectives may better account for predator responses (i.e., abundance and behavior) to environmental variation that then drive variation in nest survival. This suite of studies clearly identifies the need to make comparative examinations of predator communities and land-use variability to help understand the intricate relationships between the environment, predators, and their prey.

Nest success and the cumulative probability of fledging young are important parameters for understanding population dynamics, yet these metrics only partially quantify reproductive rates in birds. Our results suggest that birds have a higher probability of fledging young in urban environments, resulting in high potential reproductive output within the urban/suburban matrix. Moreover, there is increasing evidence that the urban environment can provide suitable habitat including, but not limited to, increased novel food resources and different thermal environments. Unfortunately, urban environments also contain a host of negative factors that

could impair total productivity. For example, birds in urban environments may face reduced post-fledging survival (A. Balogh and P. P. Marra, *unpublished manuscript*; but see Whittaker and Marzluff 2009), increased nest parasitism, fewer breeding attempts and fledged young (Rodewald and Shustack 2008), or reduced physical condition of young (Newhouse et al. 2008). Moreover, species living within the urban/suburban matrix are also subject to an array of other factors that could negatively affect various aspects of their life histories including increased noise pollution (Slabbekorn and Peet 2003), exposure to contaminants (Roux and Marra 2007), and exposure to novel predation pressures (e.g., cats; Baker et al. 2005). Given the potential role of life-history variation on species-specific responses to urbanization, future work would benefit from monitoring the reproductive ecology (e.g., nest, post-fledging periods) and survival (by age and sex) at multiple life stages.

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APPENDIX

Sample sizes of nests by year for five species of common backyard birds used to model nest survival across an urbanization gradient in the greater Washington, D.C./Baltimore area (*Ecological Archives* A020-011-A1).