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Population demography of Gray Catbirds in the suburban matrix: sources, sinks and domestic cats

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Abstract Understanding factors that limit the productivity and survival of birds in rapidly changing human-dominated landscapes are key to managing future population persistence. To date, few studies have quantified both nest success and post-fledging survival for birds breeding within the suburban matrix. Here, we estimated nest success and juvenile post-fledging survival for Gray Catbirds (*Dumatella carolinensis*) and used those site-specific parameters to model source–sink dynamics at three sites in suburban Washington DC (USA). Cumulative nest success probability varied substantially among suburban sites and indicated that in some cases suburban habitats may provide suitable breeding sites for passerine birds. In addition, we documented the effects of sex and brood size on post-fledging survival rates and determined the role of predation on dispersing fledglings. Like nest success, estimates of post-fledging juvenile survival also varied among sites and highlight the importance of site-specific demographic estimates in urban habitats. Predation accounted for 79% of all mortalities, with 47% of known predation events attributable to domestic cats (*Felis catus*). Our models of source–sink dynamics underscore the importance of seasonal recruitment parameters for calculating population growth rate and subsequent persistence. This study provides parameter estimates for two critical life history stages in the avian annual cycle in the suburban matrix and posits that predation drives differential nest and post-fledging survival within human-dominated environments.

Zusammenfassung Um zu gewährleisten, dass Populationen in der Zukunft fortbestehen, liegt ein Schlüssel im Verständnis der Faktoren, die in sich rasant verändernden, menschendominierten Lebensräumen die Produktivität und das Überleben von Vögeln begrenzen. Bis heute haben nur wenige Studien sowohl den Bruterfolg als auch das Überleben nach dem Ausfliegen von Vögeln untersucht, die in der suburbanen Matrix brüten. Wir haben hier den Bruterfolg und die Überlebensrate von Jungvögeln der Katzendrossel (*Dumatella carolinensis*) nach dem Ausfliegen bestimmt und verwendeten diese ortsabhängigen Parameter für eine Modellierung der Quellen-Senken-Dynamiken an drei Standorten in Vorstädten von Washington DC (USA). Die kumulierte Bruterfolgswahrscheinlichkeit unterschied sich stark zwischen den Standorten und wies darauf hin, dass in einigen Fällen Vorstadthabitate durchaus passende Brutplätze für Singvögel bieten. Zusätzlich dokumentierten wir den Einfluss von Geschlecht und Brutgröße auf die Überlebensraten nach dem Ausfliegen und bestimmten die Rolle von Prädation auf dispergierende Jungvögel nach dem flügge werden. Ebenso wie der Bruterfolg variierten die Schätzungen der Überlebensraten der Jungvögel nach dem Ausfliegen zwischen den Standorten und unterstreichen die Bedeutung ortsspezifischer demographischer Bestimmungen in städtischen Lebensräumen. Prädation war in 79% die Todesursache, dabei gingen 47% der Prädationsereignisse auf Hauskatzen (*Felis

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catus) zurück. Unsere Modelle der Quellen-Senken-Dynamiken betonen die Bedeutung saisonaler Rekrutierungsparameter zur Berechnung von Wachstumsraten und darauf folgendem Fortbestehen von Populationen. Die vorliegende Arbeit erlaubt Parameterschätzungen für zwei kritische Lebensphasen im Jahreszyklus von Vögeln in der Vorstadtmatrix und stellt heraus, dass in menschendominierten Lebensräumen Prädation maßgeblich zu Unterschieden in der Überlebensrate im Nest und nach dem Ausfliegen führt.

Introduction

Urban areas cover over 100 million acres (c. 404.6 million ha) within the continental US and are spreading throughout the United States at an unprecedented rate, having increased by 48% from 1982 to 2003 (US EPA 2009). Urbanization has tremendous impacts on wildlife directly through land conversion or indirectly from human population pressure (Chace and Walsh 2004). Unfortunately, ecologists know relatively little about the factors that limit the productivity and survival of birds breeding in urban/suburban environments (Chamberlin et al. 2009). To date, most studies have focused on nest success along an urban gradient using artificial nest studies (e.g., Gering and Blair 1999; Jokimäki and Huhta 2000; Thorington and Bowman 2003; Blair 2004), or less commonly, real nests (Blair 2004), although some have measured bird productivity in undeveloped fragments within urban environments (e.g., Leston and Rodewald 2006; Marzluff et al. 2007; Reidy et al. 2008). Only two studies have quantified nesting (Ryder et al. 2010) or post-fledging survival (Whittaker and Marzluff 2009) for birds within the urban/suburban matrix.

Nest success, defined as the probability that a brood will survive both incubation and nestling stages, is a common metric used to estimate avian reproductive success (Ricklefs 1969). Nest success, however, is only a partial estimate of reproductive output because it fails to account for survival during the post-fledging period for birds (i.e., survival between departure from the nest and migration). The post-fledging phase is key to population recruitment and persistence yet remains one of the least understood stages of the avian life cycle for all species (Whittaker and Marzluff 2009), largely because relocating fledglings to estimate survival has been limited by applicable techniques. Fortunately, the application of radio telemetry for tracking small passerines has advanced considerably making studies of post-fledging survival feasible. Cumulatively, radio telemetry estimates of habitat use and post-fledging survivorship of young birds indicate that despite species-specific variation, the post-fledging period accounts for a significant portion of juvenile mortality in birds. (e.g., Anders et al. 1997; Vega Rivera et al. 1998). Identified causes of fledgling mortality include predation, starvation, collisions and disease (Anders et al. 1997; Vega Rivera et al. 1998). To date, the only study on Gray Catbirds (Dumatella carolinensis) post-fledging survival found that brood size, age of the parent, date of fledging and fledgling condition affected fledgling survival time (Maxted 2001).

Despite advances in our understanding of avian post-fledging survival, we still know next to nothing about this stage of the avian life cycle in human-modified landscapes. Moreover, estimating survival in these contexts is important because factors that affect the survival of nestlings and fledglings may differ substantially along urbanization gradients. For example, in some instances, species may benefit from urbanization via reduction in native predators (Gering and Blair 1999); increased supplemental food (bird feeders) (Brittingham and Temple 1986; Fuller et al. 2008), availability of nest sites (nest boxes) (Gaston et al. 2005) and altered microclimates (Marzluff et al. 2000). Conversely, urban environments have a host of factors that could negatively impact species persistence including competition with exotics (Chace and Walsh 2006); introduced predators (Churcher and Lawton 1987; Sorace 2005), and contaminants and toxins (Roux and Marra 2007). In particular, novel predators like the domestic cat (Felis catus) may disproportionately impact avian populations because they are subsidized enabling them to exist at densities exceeding any native predator (Lepczyk et al. 2003; van Heezik et al. 2010). Given that nest predation and subsequent post-fledging survival limit avian populations, quantifying which factors impact survival probability in variable environmental contexts remains crucial to understanding avian population demography (Anders et al. 1997; Vega Rivera et al. 1998). Although recent work has begun to quantify how urbanization impacts avian nest predators and subsequent nest success (see Marzluff et al. 2007; Ryder et al. 2010), little is understood about how novel predators present in the urban/suburban matrix impact post-fledging survival (Whittaker and Marzluff 2009).

Research on the population dynamics of birds has taken a variety of approaches to differentiate sources from sinks. Studies have used the number of female offspring per adult female, adult survival and juvenile survival (both apparent and simulated estimates) to categorize populations (e.g., Donovan et al. 1995). Moreover, given the challenges of estimating recruitment, many studies have applied the constant post-fledging survival probabilities (see Temple and Cary 1988), regardless of species or habitat type (e.g., Noon and Sauer 1992; Donovan et al. 1995). If the post-fledging period is characterized by low survival then use of constant values may limit our ability to assess population viability. Indeed, if species-specific post-fledging and

nest success estimates were incorporated in population models, the source–sink status of the populations changed from sources to sinks (Anders et al. 1997). Given that habitat use, post-fledging survival and dispersal patterns may be species-specific and clearly affect source–sink categorization; research should focus on this life stage along habitat gradients.

Here, we studied the nesting success and post-fledging survival of Gray Catbirds in suburban Washington DC. We specifically asked two questions: (1) how do rates of nest success and juvenile post-fledging survival vary among sites within the suburban matrix, and (2) how do intrinsic demographic variables (sex and brood size) and extrinsic (predation pressure) factors influence the post-fledging survival probabilities of birds in human dominated landscapes. Lastly, we use the demographic data generated here to parameterize source–sink models and determine the sensitivity of population growth (λ) to juvenile recruitment.

Methods

Study area and field methods

Gray Catbirds are medium-sized passerine birds that breed from southern Canada to the southeastern US and winter from the southeastern US to the Caribbean and Panama (Cimprich and Moore 1995). Catbirds are found along the urban gradient, and nest in open canopy areas with low, dense shrubs, making them frequent summer residents in the suburban matrix. They feed primarily on insects and fruit, and forage largely on the ground. Behaviorally, they often run or hop, rather than fly when threatened, and are known to confront predators, making them especially susceptible to terrestrial predation (Cimprich and Moore 1995).

Research was conducted from May to September 2004 at three suburban sites in the greater Washington DC metropolitan area. Two sites, Spring Park (SP) and Opal Daniels Park (OD) were located in the city of Takoma Park, Maryland (38 58′48″N, 77 0′8″W), which has a population density of 1,308.9/km^2 (United States Census Bureau 2000). The third site was located in Bethesda (B), Maryland (38 58′50″N, 77 6′2″W) which has a population density of 716.0/km^2 (United States Census Bureau 2000). Individual properties within the sites varied in size and landscaping, though the majority contained extensive vegetation (A.L. Balogh, personal observation). House size tended to be larger at the Bethesda site, with more structured gardens and a larger percentage of lawn. Takoma Park sites had smaller and more densely clustered homes, with plentiful gardens and limited lawn areas (A.L. Balogh, personal observation). All three sites retained large, old

trees, though Takoma Park appeared to have more areas of green space in the form of parks or empty lots. The primary tree species on private property and in remnant woods were American beech (*Fagus grandifolia*), Virginia pine (*Pinus virginianus*), tulip poplar (*Liriodendron tulipifera*), several species of oaks (*Quercus* spp.), maples (*Acer* spp.) and sycamore (*Platinus* spp.). Yards contained a mix of native and non-native shrubs including multiflora rose (*Rosa multiflora*), grape (*Vitis* spp.), bamboo (*Phyllostachys aurea*) and Japanese honeysuckle (*Lonicera japonica*).

Study sites were centered around the properties of participants in a Smithsonian Institution citizen science program called Neighborhood Nestwatch (http://nationalzoo.si.edu/goto/nestwatch; see Evans et al. 2005). We searched for nests in a 500-m^2 area centered on these properties. We located nests using systematic searches of yards or by observing adults with nesting material or food. Catbirds build large, bulky nests, placed 0.5 to >15 m up (typically $\sim$2 m, personal observation) in dense vegetation, making them fairly easy to locate. We checked the nest contents in every nest found every 2–4 days during the 12-day incubation (mean $= 11.57 \pm 0.14$) and 11-day nestling stage (mean $= 11.69 \pm 0.16$), until they either failed or nestlings fledged (Martin and Geupel 1993). At each nest visit, we recorded the number of eggs and nestlings. Nests that produced at least one fledgling were categorized as successful, otherwise as failed (Burke et al. 2004). On the eighth or ninth day of the nestling stage, all nestlings were banded using USFW aluminum bands and weighed to the nearest 0.1 g using a digital scale. We also took a $\sim$50-μl blood sample from the brachial vein to determine nestling sex. Blood samples were placed on Permacode bloodcards and sent to Avian Biotech for molecular sexing analysis (www.Avianbiotech.com).

To document survival and movement during the post-fledging stage, we fitted the nestlings from 30 nests with radio-transmitters ($n = 47$). In addition, we caught recently fledged juvenile catbirds using mist-nets and fitted these individuals with transmitters ($n = 22$). Model BD-2 transmitters (1.4 g, 9 weeks; Holohil Systems, Ottawa, Canada) were attached using a harness with 1-mm elastic thread (Rappole and Tipton 1991). We located radio-tagged fledglings every other day using a hand-held receiver and a 3-element Yagi antenna. Individuals were tracked until we saw the target bird and then each bird's location was recorded using a GPS (global positioning system).

Individuals were tracked in a 5-km radius area around the original tagging location until they died or departed the study area. When a bird died, we categorized the death as predation when the transmitter was tracked to a predator, found underground, or was associated with consumed remains (Maxted 2001). When possible, we assigned the type of predator based on direct observation or

characteristics symptomatic of specific predators (see "Results"). In cases where we lost a subject's signal, we searched by car the area around the individual's last-known location in a widening radius. If a signal was not found after 3 weeks of subsequent visits, we assumed that the bird left the area.

Nest and post-fledging survival

We used program MARK (White and Burnham 1999) to build descriptive models of nest success. Competing models of nest success included nest height, nest age and site as covariates, and were compared to a model of constant survival rate $S_{(constant)}$. Models with the nest-age covariate were built following Rotella (2005), allowing daily survival rate (DSR) to vary with nest age. All covariates were unstandardized and logit link function and second part variance estimation were adopted. Cumulative survival probabilities were calculated by raising the daily survival rate to the number of days in the nesting cycle (i.e., ~23 days; 12 days incubation and 11 days nestling). Variance for cumulative survival probabilities and 95% confidence intervals were approximated using the delta method (see Powell 2007; Rotella 2005). Models were ranked according to Akaike's Information Criterion (AIC; Akaike 1973), where models within ΔAIC of 2.0 were considered equally supported (Burnham and Anderson 2002). Model selection was based on both AICc, which corrects for small sample sizes, and model normalized weights (w_i; Burnham and Anderson 2002). Post-hoc comparisons of survival between sites were done using CONTRAST (Hines and Sauer 1989).

Juvenile post-fledging survival was analyzed using the Kaplan–Meier (Kaplan and Meier 1958) procedure in JMP v8.0.1. Data were right-censored when a transmitter failed or an individual departed the site. We used the life-table function in SPSS v16.0 (Brown et al. 1979) to calculate weekly survival rates and daily hazard rates, the latter defined as the probability that a bird would encounter a threat. We tested whether sex, brood size or relative hatching date influenced post-fledging survival using Cox fit proportional hazards (Cox 1972). A previous study found that parents attended post-fledging juveniles for an average 18.1 days (Maxted 2001). As such, juveniles radio-tagged using mist-nets were assumed to be at least 18 days old because they were caught mid-way through the breeding season (July), were relatively strong fliers and were never observed being attended by, or in the proximity of, an adult. Here, we provide two separate estimates of post fledging survival for: (1) individuals fitted with transmitters before fledging (nestlings), and (2) both nestlings and juveniles (i.e., independent birds captured using mistnets) combined. Differences in site-specific predator abundance were compared using a chi-square goodness-of-fit test.

Source–sink models

To parameterize source–sink models we used site-specific estimates of cumulative nest success and post-fledgling survival from this paper. We specifically followed the source–sink model of Pulliam (1988, 1993), in which populations are considered sources when recruitment (i.e., mean number of female offspring per female × juvenile survival) is greater than adult mortality. We calculated the mean number of female offspring per female following Donovan et al. (1995) assuming that Gray Catbird pairs could raise two broods per breeding season (Martin 1995) and would re-nest up to three times in an effort to successfully raise two broods. Estimates of apparent survival of adults Gray Catbirds ($\phi = 0.69 \pm 0.09$, $n = 734$) are from Cormack-Jolly-Seber capture–recapture models (accounting for transients) constructed with 10 years of Neighborhood Nestwatch data (Marra et al., in preparation). Because we chose to use all catbird captures (as opposed to only those sites in this study) to estimate apparent survival and increase confidence in model parameters, we had to assume constant survival across sites. Juvenile survival (i.e., recruitment rate) was estimated by multiplying our site-specific estimate of post-fledging survival by overwinter survival. Given that juveniles may have lower survival than adults during migration and overwintering periods (Marra and Holmes 2001; Latta and Faaborg 2002) and that uncertainty in this parameter can impact source–sink categorization, we modeled population growth for a range of hatch-year over-winter survival values (e.g., 0.30–0.70). Lastly, population growth rate (λ) is calculated as adult survival + (mean number of female offspring per female) × (recruitment rate).

Predator surveys

To assess predator abundance, we walked four, parallel 100-m-long and 50-m-wide transects at each site a total of three times in September from 0700 to 1200 hours. Given the limitations of conducting line transects in residential areas dominated by private property, we utilized roads as transect lines. Along each transect, we recorded the quantity of all potential diurnal nest and post-fledging predators, such as hawks, Eastern Chipmunks (*Tamias striatus*), Gray Squirrels (*Sciurus carolinensis*), Blue Jays (*Cyanocitta cristata*), Domestic Cats (*Felis catus*), and American Crows (*Corvus brachyrhynchos*). One potential limitation of our diurnal census technique is inability to detect cryptic or nocturnal urban species such as owls, snakes, and rats

(*Rattus norvegicus*). Given the low numbers of predators and small number of detections per replicate (see "Results"), we were unable to calculate estimates of density corrected for detectability. As such, we compare total predator counts summed across replicates as an index of site-specific predator abundance. Differences in site-specific predator abundance were compared using a chi-square goodness-of-fit test and a Bonferroni corrected p value was used to account for multiple comparisons. All statistics were done using program JMP v8.0.1. We report means ± 1 standard errors unless otherwise noted.

Results

Nest success

We monitored 68 nests at three sites within the suburban matrix (B, $n = 15$; OD, $n = 27$; SP, $n = 26$) for a total of 791 exposure days. Mean brood size was 2.8 (0.2, range:1–3) at Bethesda, 3.0 (0.2, 1–4) at Spring Park and 2.9 (0.1, 2–5) at Opal Daniels and did not significantly differ among sites ($F_{2,65} = 0.776$, $P = 0.46$). Likewise, the mass of the heaviest nestling in each brood on days 8 or 9 did not significantly differ among sites ($F_{2,65} = 0.523$, $P = 0.60$), but ranged from 17.3 g to 34.2 g, with a mean of 27.7 (0.7 g) at Bethesda, 27.5 (0.6 g) at Spring Park and 28.3 (0.6 g) at Opal Daniels.

Variation in nest success was best explained by a model that included site ($S_{(site)}$: $\Delta AICc = 0.00$, $w_i = 0.46$), but the fit of this model could not be differentiated from a model that also included nest height ($S_{(site + nest\ height)}$: $\Delta AICc = 1.94$, $w_i = 0.17$) (Table 1). These models were, however, better fit than a model of constant survival ($S_{(constant)}$ $\Delta AICc = 2.08$, $w_i = 0.16$) or a model, which allowed nest success to vary with nest age ($S_{(nest\ age)}$: $\Delta AICc = 3.38$, $w_i = 0.08$) and nest height ($S_{(nest\ height)}$ $\Delta AICc = 3.83$, $w_i = 0.07$) (Table 1). Likewise, models with additive and multiplicative interaction terms did not improve overall fit to the data (Table 1). Cumulative survival varied among sites, with nests at Bethesda having the highest probability of successfully fledging offspring (Fig. 1). Post-hoc comparisons of site-specific survival show significant differences between Bethesda and Opal Daniels ($\chi^2 = 5.60$, $df = 1$, $P = 0.018$), Bethesda and Spring Park ($\chi^2 = 5.87$, $df = 1$, $P = 0.015$) but no differences between Opal Daniels and Spring Park ($\chi^2 = 0.03$, $df = 1$, $P = 0.85$).

Juvenile post-fledging survival

We sexed 47 nestlings, finding a 1:1 sex ratio (24 females:23 males). The Cox proportional hazards regression detected no

Table 1 A summary of model selection results for Gray Catbird (*Dumatella carolinensis*) nest survival (S) at three sites located within the suburban matrix of greater Washington, DC

Model	Deviance	K	$\Delta AICc$	w_i
$S_{(site)}$	222.31	3	0	0.46
$S_{(site + nest\ height)}$	224.24	4	1.94	0.17
$S_{(constant)}$	224.39	1	2.08	0.16
$S_{(nest\ age)}$	225.69	2	3.38	0.08
$S_{(nest\ height)}$	226.14	2	3.83	0.07
$S_{(nest\ age + nest\ height)}$	227.56	3	5.26	0.03
$S_{(site \times nest\ height)}$	228.17	6	5.86	0.02
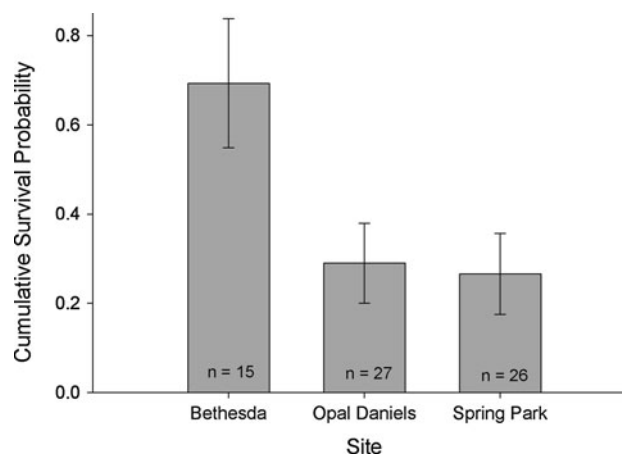
Fig. 1 Cumulative nest success shows site-specific variation for Gray Catbirds (*Dumatella carolinensis*) nesting at three sites in the suburban matrix of greater Washington, DC. Cumulative survival is the probability a nest will survive for both the incubation and nestling period. Standard errors were calculated using the delta method

significant effects of sex (Wald's $\chi^2 = 1.46$, $df = 1$, $P = 0.23$), brood size (Wald's $\chi^2 = 4.17$, $df = 2$, $P = 0.13$), nestling mass (Wald's $\chi^2 = 1.59$, $df = 1$, $P = 0.21$), or relative hatching date (Wald's $\chi^2 = 0.14$ $df = 1$, $P = 0.71$) on post-fledging survival. Survival did, however, vary by site (Wald's $\chi^2 = 6.15$, $df = 2$, $P = 0.046$). For catbirds radio-tagged as nestlings, cumulative survival from fledging to 9 weeks was 0.45 (0.14) at Bethesda ($n = 17$), 0.24 (0.12) at Opal Daniels ($n = 16$), and 0.10 (0.09) at Spring Park ($n = 14$) (Fig. 2a). Because brood level factors could influence survival probability, we recalculated estimates with a single fledging per brood and found no significant differences in survival rates (Bethesda, $n = 10$, 0.44 ± 0.18, $\chi^2 = 0.001$, $df = 1$, $P = 0.99$; Opal Daniels, $n = 8$, 0.19 ± 0.16, $\chi^2 = 0.068$, $df = 1$, $P = 0.79$; Spring Park, $n = 9$, 0.11 ± 0.11, $\chi^2 = 0.012$, $df = 1$, $P = 0.92$). As such, subsequent analyses used the complete dataset (see also below). Post-fledging survival was significantly different between Bethesda and Opal Daniels ($\chi^2 = 4.52$,

$df = 1$, $P = 0.03$), whereas Spring Park did not differ from either Bethesda ($\chi^2 = 1.42$, $df = 1$, $P = 0.23$) or Opal Daniels ($\chi^2 = 0.81$, $df = 1$, $P = 0.37$). Post-fledging juveniles were attended by parents for an average of 18.9 (2.0 days) with parents attending female fledglings for a significantly shorter period, 18.3 (0.6 days, $n = 7$), than male fledglings, 21.0 (0.9 days, $n = 3$), although sample sizes for this comparison were small, as many fledglings died before reaching independence and we did not always view parental activity when locating individuals ($F_{1,9} = 6.371$, $P = 0.04$).

When we included juvenile catbirds, captured after they achieved independence, in the analysis, cumulative survival to 9 weeks post-fledging was 0.55 (0.12) at Bethesda ($n = 21$), 0.20 (0.09) at Opal Daniels ($n = 27$), and 0.17 (0.08) at Spring Park ($n = 21$) (Fig. 2b). As above,

survival estimates limited to one fledgling per brood produced equivalent estimates that did not significantly differ (Bethesda, $n = 14$, 0.57 ± 0.15, $\chi^2 = 0.012$, $df = 1$, $P = 0.92$; Opal Daniels, $n = 19$, 0.22 ± 0.11, $\chi^2 = 0.03$, $df = 1$, $P = 0.87$; Spring Park, $n = 16$, 0.13 ± 0.08, $\chi^2 = 0.016$, $df = 1$, $P = 0.69$). Survival differed significantly between sites ($\chi^2 = 6.14$, $df = 2$, $P = 0.046$) with Bethesda being significantly different from both Opal Daniels ($\chi^2 = 5.02$, $df = 1$, $P = 0.03$) and Spring Park ($\chi^2 = 5.07$, $df = 1$, $P = 0.03$). Opal Daniels and Spring Park were not different from each other $\chi^2 = 0.002$, $df = 1$, $P = 0.79$). Weekly survival and hazard rates did not differ between the three sites ($\chi^2 = 3.034$, $df = 2$, $P = 0.22$). Cumulative hazard rate data illustrate that the first (0.07) and third week (0.05) have the highest hazard rates for juvenile post-fledging catbirds, but rates only differ significantly between weeks 1 and 2 (0.07–0.01, $\chi^2 = 26.00$, $df = 2$, $P < 0.0001$).
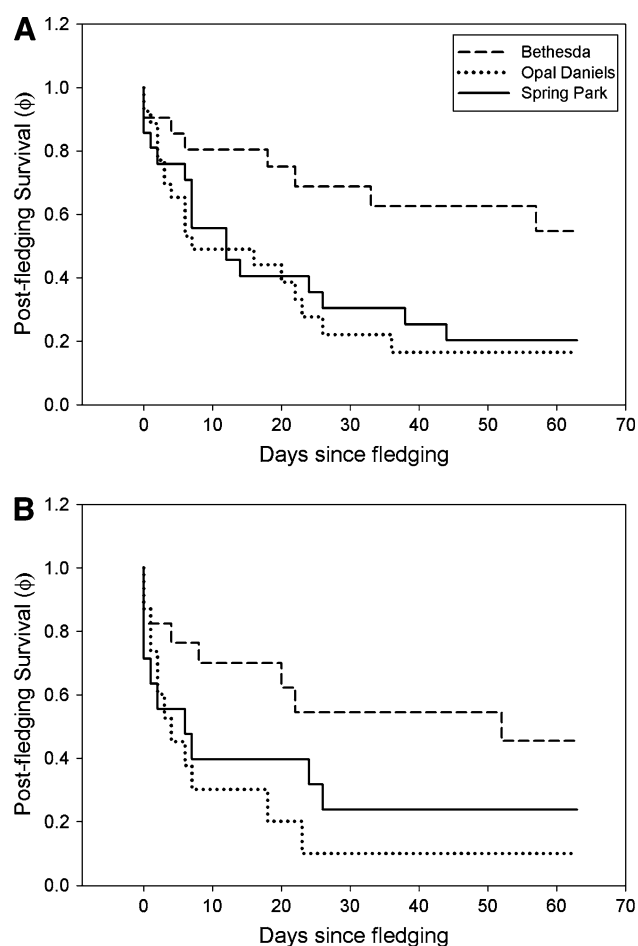
Causes of post-fledging mortality and predator surveys

During our study of post-fledging survival, 61% (42/69) of individuals died before reaching independence. Predation on juveniles accounted for 79% (33/42) of all mortalities (Bethesda 75% (6/8), Spring Park 75% (12/16), and Opal Daniels 83% (15/18) with the vast majority (70%) occurring in the first week post-fledging. Directly observed predation events involved domestic cats ($n = 6$; 18%), a black rat snake ($n = 1$; 3%), and a red-shouldered hawk ($n = 1$; 3%). Although not all mortalities could be clearly assigned, fledglings found with body damage or missing heads were considered symptomatic of cat kills ($n = 3$; 9%), those found cached underground of rat or chipmunk predation ($n = 7$; 21%) and those found in trees of avian predation ($n = 1$; 3%). The remaining mortalities ($n = 14$; 43%) could not be assigned to a specific predator. Mortality due to reasons other than predation (21%) included unknown cause ($n = 2$; 22%), weather related ($n = 2$; 22%), window strikes ($n = 2$; 22%) and individuals found close to the potential nest with no body damage ($n = 3$; 34%), suggesting premature fledging, disease or starvation.

Total counts of one potential nest predator (e.g., Gray Squirrels) varied significantly across our three suburban sites while the other two showed a trend (e.g., American Crows and Blue Jays) but were not significant after Bonferroni correction ($P = 0.013$) (Table 2). Most notable among nest predators were the higher counts of Gray Squirrels in two suburban neighborhoods (e.g., Opal Daniels and Spring Park). Domestic cats, one potential predator of post-fledging birds, also varied significantly among sites with both Spring Park and Opal Daniels having higher total counts (Table 2).

Fig. 2 Variable post-fledging survival of juvenile catbirds is evidenced by Kaplan–Meier estimates of daily survival for three suburban sites in the greater Washington, DC. a Estimates for catbirds tagged as nestlings, b combined estimates for catbirds tagged as nestlings and independent juvenile caught in mist-nets at the assumed age of 18 days (see "Methods")

Table 2 Total counts of four common predators of nests and post-fledgling juvenile birds at three suburban matrix sites in greater Washington, DC

	Bethesda $n = 12$	Opal daniels $n = 12$	Spring park $n = 12$	χ^2	P
Domestic cat	0	7	10	17.03	0.009
Gray Squirrel	7	34	27	34.74	<0.001
American Crow	3	5	1	13.99	0.029
Blue Jay	3	4	1	14.68	0.025
Total	13	50	39	21.34	<0.001

Source/sink designation

Our source–sink models indicate that the mean number of female offspring fledged per female (see "Methods") varied among sites due to differential predation rates and subsequent nests success (B = 1.67; OD = 0.84; SP = 0.76). Overall juvenile survival and subsequent recruitment was sensitive to hatch-year overwinter survival, changing source–sink categorization in our Bethesda population from a sink at lower overwinter survival rates to a source at higher overwinter survival rates (Fig. 3). Both Opal Daniels and Spring Park, however, remained categorized as sinks even when high overwinter survival was assumed (Fig. 3).
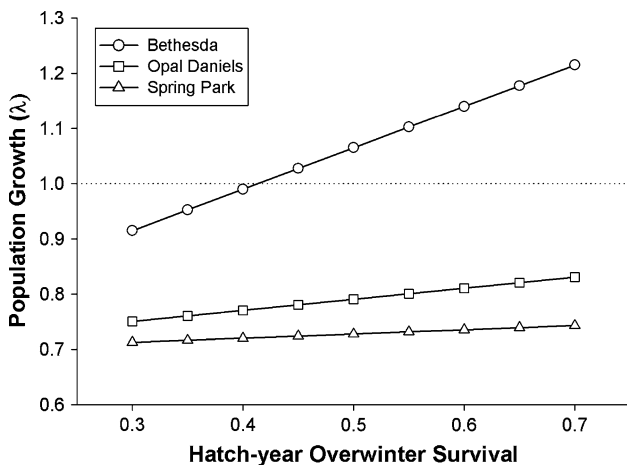
Discussion

To our knowledge, ours is the first study to document both rates of nest success and juvenile post-fledgling survival

Fig. 3 Site-specific population growth (λ) as a function of hatch-year overwinter survival. Model input parameters include adult survival (constant across sites, $\phi = 0.69$), site-specific number of female fledglings per adult female (B = 1.67; OD = 0.84; SP = 0.76), and site-specific post-fledgling survival (B = 0.45; OD = 0.24 SP = 0.10). The *dotted line* denotes ($\lambda = 1$) with populations above the line categorized as sources and those below the line categorized as sinks. Note that both Opal Daniels and Spring Park are insensitive to hatch-year overwinter survival because low post-fledgling survival keeps these sites below the source threshold

among passerine birds breeding directly in the suburban matrix (but see Whittaker and Marzluff 2009). One site, Bethesda, had significantly higher nest success and post-fledging survival for Gray Catbirds than the other two sites, Opal Daniels and Spring Park, indicating suburban habitats show substantial site-specific variation in factors that can limit avian productivity.

Our estimates of cumulative nest success in suburban neighborhoods indicate that, although some sites may offer adequate breeding habitat, others suffer from high nest predation. Overall, our nest success estimates are comparable to previous work on Gray Catbirds in Indiana (0.26; Maxted 2001), Iowa (0.44; Best and Stauffer 1980) and Pennsylvania (0.52; Yahner 1991; see also Martin 1995). Interestingly, one of our sites, Bethesda, had the highest recorded nest success (0.69) for Gray Catbirds and shows that in some cases suburban/urban habitat may provide better quality breeding sites than undisturbed native scrub habitat (see also Ryder et al. 2010). While we realize our nest survival estimates are limited by sample size and temporal scope, recent demographic work on Gray Catbirds in 2008–2009 corroborates low cumulative nest survival and a lack of site-specific differences between Spring Park and Opal Daniels (cumulative nest survival = 0.34 ± 0.09, $n = 98$; Ryder et al., unpublished data). Ultimately, future demographic work at all sites will help corroborate the consistency of the patterns observed in this study.

Recent studies of nest predation pressure in urban/suburban habitats suggest that differences in predator communities may be the primary driver of differential nest success (Marzluff et al. 2007; Ryder et al. 2010). Crows, jays and raptors are common, native, urban nest predators (Jokimäki and Huhta 2000; Reidy et al. 2008), but our surveys did not indicate higher avian predators at the two sites with low nest success. Predator transects did, however, suggest higher abundances of cats and Gray Squirrels at our two sites with lower nest success (Opal Daniels and Spring Park). While evidence for squirrels as nest predators is fairly well established (Newson et al. 2010), the role of cats as nest predators remains unclear (Gillies and Clout 2003; Jokimaki et al. 2005). In addition, limitations in our sampling design preclude us from addressing the relative role of cryptic and nocturnal predators on nest survival or

how detectability might impact abundance estimates. Although cats and squirrels are fairly conspicuous, the larger yards at our Bethesda site could have limited detection and downwardly biased our estimates of predator abundance at that site. Ultimately, while our study lacks detailed information on the relative contributions of predators to nest predation, our correlative data on nest survival probability and predators are consistent with the hypothesis that diurnal predator abundance affects cumulative nest survival probability among habitats in the suburban matrix.

A previous study of Gray Catbird post-fledging survival in native habitats reported higher survival (0.60; Maxted 2001) than our estimates in the suburban matrix. Unlike Maxted (2001), who found that factors of parental age and fledging date affected post-fledging survival, smaller nestlings had a higher risk of death, and larger brood sizes significantly increased Gray Catbird post-fledging survival. Here, we failed to find evidence linking these factors and post-fledging survival. Our data did, however, show significant site-specific differences in post-fledging survival. More specifically, two of our sites had lower post-fledging survival rates than those reported for species with various life-history strategies and breeding habitats (e.g., Lark Buntings, *Calamospiza melanocory,* 0.37; Adams et al. 2001; European Starlings, *Sturnus vulgaris*, 0.53–0.59; Stromborg et al. 1988; Yellow-breasted Chats, *Icteria virens*, 0.40, Maxted 2001; Wood Thrush, *Hylocichla mustelina,* 0.42, Anders et al. 1997; and Eastern Meadowlarks, *Sturnella magna*, 0.56–0.69, Kershner et al. 2004). Like these previous studies, predation accounted for 79% of juvenile post-fledging mortality in our human-dominated environments.

Overall, our data show that while predation rates of fledglings were similar among sites (Bethesda 75%, Spring Park 75%, Opal Daniels 83%), post-fledging survival probability showed substantial variation. Most post-fledging survival studies have attributed predation mortality to native predators, such as snakes, hawks and chipmunks (Anders et al. 1997; Vega Rivera et al. 1998; Maxted 2001). Our data, however, suggest that novel predators (e.g., cats and rats) have the potential to substantially impact post-fledging survival in the suburban matrix. While our predator transects were not effective for detecting secretive or nocturnal predators (e.g., owls, etc.), a large proportion of nestlings were found cached underground, 37% (7/19), a behavior symptomatic of nocturnal avian predation events by rats (see Townsend et al. 2009). Although we cannot rule out chipmunks in our cached mortalities, rats are known to be common residents in human-dominated environments while chipmunks are rare urban/suburban residents preferring woodland habitats (Henderson et al. 1985).

Likewise, nearly half of our assignable predation events, 47% (9/19), were attributed to domestic cats in only two of our suburban neighborhoods. While some of these predation events were based on symptomatic kills, several lines of evidence suggest cats had a disproportionate impact on post-fledging survival in the suburban matrix. First, domestic cats were never detected during predator surveys at Bethesda while they were frequently seen during both surveys and telemetry session in both Opal Daniels and Spring Park. Second, we are unaware of any other native or non-native predator that regularly decapitates birds while leaving the body uneaten. Moreover, we acknowledge that these data are only correlative and not causal yet we believe the observed differences in cat abundance between our sites, and first-hand observations of cat predation on Gray Catbirds are consistent with the hypothesis that cats are likely regulating post-fledging survival in some urban environments.

Our data show higher levels of predation during the first week after fledging than had previously been reported for Gray Catbirds (Maxted 2001), but are consistent with post-fledging studies on other species (Anders et al. 1997; Naef-Daenzer et al. 2001; Kershner et al. 2004). High predation during the first week is not particularly surprising given constant parental attendance, loud begging and predator naïveté of fledglings during this time period (Anders et al. 1997). These characteristics might make fledglings in suburban environments particularly prone to visual predators such as domestic cats. Moreover, while feral domestic cats may have large ranges in excess of 5.0 km^2 (Fitzgerald and Karl 1986), owned domestic cats in suburban environments may have small home ranges (Kays and Dewan 2004) and spend the majority of time in their own or adjacent yards (Barratt 1997; Kays and Dewan 2004). As such, domestic cats are likely able to intensively monitor, locate, and hunt inexperienced juvenile birds.

Cats can occur at high densities as subsidized predators, without the typical constraints of limited food availability, disease and intraspecific competition (Coleman and Temple 1993). This suite of characteristics combined with a cat's opportunistic hunting behavior (Coman and Brunner 1972) and unnaturally high density in urban environments creates a scenario in which cat-catch can exceed local recruitment and dramatically impact the population persistence (van Heezik et al. 2010). This scenario, however, assumes that the effects of cat predation on juvenile recruitment are additive in nature. An equally plausible alternative is that cat predation acts in a compensatory fashion removing weaker juveniles that would not have survived in the absences of predation pressure. Regardless, future research should aim to differentiate the additive versus compensatory nature of cat predation on avian population dynamics.

The concept of source–sink dynamics is well integrated into ecological theory and a large number of studies have aimed to categorize populations as sources or sinks (Runge et al. 2006). Understanding habitat-specific demography and source sink dynamics in rapidly changing human-dominated landscapes is the key to managing population persistence. Avian studies often couple single, estimated parameters, with others obtained from the literature (e.g., Donovan et al. 1995; Anders et al. 1997; Vierling 2000). Here, the majority of our model input parameters (e.g., adult survival, nest success and post-fledging survival) were population specific. Our data suggest that despite high adult survival, and at some sites high nest success, recruitment rates can easily change source habitats into sink habitats. Despite finding no effect of mass on post-fledging survival, our study used only the two heaviest nestlings per brood and this could have resulted in over-estimates of post-fledging survival and subsequent recruitment. As such, our models should be considered an optimistic scenario for Gray Catbirds breeding in suburban/urban landscape matrix. Regardless, it is likely that hatch-year individuals do not survive migration and overwintering at the same rate as adults (Marra and Holmes 2001; Latta and Faaborg 2002) and so future models should consider the importance of each demographic parameter for categorizing populations as sources or sinks. In particular, gaps in our knowledge about the first year in a bird's life needs addressing, as variables on the wintering range may significantly affect recruitment and thus, site-specific population demography.

Here, our findings document both variable nest and post-fledging survival for Gray Catbirds in three suburban neighborhoods. Our data suggest that suburban environments present significant variability in habitat suitability for breeding Gray Catbirds. Given the short duration of the study, the small number of suburban replicates and limited geographic scope, we cannot currently elucidate the exact causes of differential nest and post-fledging survival probabilities among suburban environments. Despite these limitations, our data are consistent with the general hypothesis that differences in predator communities, be they native or introduced, have the capacity influence survival probabilities during both nesting and post-fledging stages of the annual cycle.

Finally, this study highlights that source–sink models must account for the seasonal components of recruitment (e.g., overwinter survival) because ultimately it is the additive effects across stages that drive population demography.

References

Adams AAY, Skagen SK, Adams RD (2001) Movements and survival of lark bunting fledglings. Condor 103:643–647

Akaike H (1973) Information theory and an extension of the maximumlikelihood principle. In: Petrov BN, Csaki F (eds) SecondInternational Symposium on Information Theory. Budapest: Akademiai Kiado, pp 267–281

Anders AD, Dearborn DC, Faaborg J, Thompson FR III (1997) Juvenile survival in a population of neotropical migrant birds. Conserv Biol 11:698–707

Barratt DG (1997) Predation by house cats Felis catus (L.), in Canberra, Australia. I. Prey composition and preference. Wildl Resour 24:263–277

Best LB, Stauffer DF (1980) Factors affecting nesting success in riparian bird communities. Condor 82:149–158

Blair R (2004) The effects of urban sprawl on birds at multiple levels of biological organization. Ecol Soc 9(5):2. http://www.ecologyandsociety.org/vol9/iss5/art2/

Brittingham M, Temple S (1992) Use of winter bird feeders by black-capped chickadees. J Wildl Manage 56:103–110

Brown BW, Walker H, Schimek M, Wright PR (1979) Life table analysis package for SPSS. Am Stat 33:225–227

Burke DM, Elliott K, Moore L, Dunford W, Nol E, Phillips J, Holmes S (2004) Patterns of nest predation on artificial and natural nests in forests. Conserv Biol 18:381–388

Burnham KP, Anderson DR (2002) Model selection and inference: a practical information theoretic approach, 2nd edn. Springer, New York

Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urb Plan 74:46–69

Chamberlin DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ, Gaston KJ (2009) Avian productivity in urban landscapes: a review and meta-analysis. Ibis 151:1–18

Churcher PB, Lawton JH (1987) Predation by domestic cats in an English village. J Zool Lond 212:439–455

Cimprich DA, Moore FR (1995) Gray catbird (Dumetella carolinensis). The Birds of North America, No. 167. In: Poole A, Gill F (eds) The Birds of North America, Philadelphia, PA

Coleman JS, Temple SA (1993) Rural residents' free-ranging domestic cats: a survey. Wildl Soc Bull 21:381–390

Coman BJ, Brunner H (1972) Food habits of the feral house cat in Victoria. J Wildl Manag 36:848–853

Cox DR (1972) Regression models and life tables (with discussion). J R Stat Soc B 34:187–220

Donovan TM, Thompson FR III, Faaborg J, Probst JR (1995) Reproductive success of migratory birds in habitat sources and sinks. Conserv Biol 9:1380–1395

Evans E, Abrams E, Roux K, Salmonsen L, Reitsma R, Marra PP (2005) The Neighborhood Nestwatch Program: sense of place and science literacy in a citizen-based ecological research project. Conserv Biol 19:589–594

Fitzgerald BM, Karl BJ (1986) Home range of feral cats (Felis catus L.) in forest of the Orongorongo Valley, Wellington, New Zealand. N Z J Ecol 9:71–81

Fuller RA, Warren PH, Armsworth PR, Barbosa O, Gaston KJ (2008) Garden bird feeding predicts the structure of urban avian assemblages. Divers Distrib 14:131–137

Gaston KJ, Smith RM, Thompson K, Warren PH (2005) Urban domestic gardens (II): experimental tests of methods for increasing biodiversity. Biodivers Conserv 14:395–413

Gering JC, Blair RB (1999) Predation on artificial nests along an urban gradient: predatory risk or relaxation in urban environments? Ecography 22:532–541

Gillies C, Clout M (2003) The prey of domestic cats (*Felis catus*) in two suburbs of Auckland City. N Z J Zool 259:309–315

Henderson MT, Merriam G, Wegner J (1985) Patchy environments and species survival: chipmunks in an agricultural mosaic. Biol Conserv 31:95–105

Hines JH, Sauer JR (1989) Program CONTRAST: a general program for the analysis of several survival or recovery rate estimates. U.S. Department of the Interior, Fish and Wildlife Service, Washington

Jokimäki J, Huhta E (2000) Artificial nest predation and abundance of birds along an urban gradient. Condor 102:838–847

Jokimaki J, Kaisanlahti-Jokimaki ML, Sorace A, Fernandez-Juricic E, Rodriguez-Prieto I, Jimenez MD (2005) Evaluation of the "safe nesting zone" hypothesis across an urban gradient: a multi-scale study. Ecography 28:59–70

Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. J Am Stat Assoc 53:457–481

Kays RW, DeWan AA (2004) Ecological impact of inside/outside house cats around a suburban nature preserve. Anim Conserv 7:273–283

Kershner EL, Walk JW, Warner RE (2004) Post-fledging movements and survival of juvenile eastern meadowlarks (*Sturnella magna*) in Illinois. Auk 121:1146–1154

Latta SC, Faaborg J (2002) Demographic and population responses of Cape May warblers wintering in multiple habitats. Ecology 83:2502–2515

Lepczyk CA, Mertig AG, Liu J (2003) Landowners and cat predation across rural-to-urban landscapes. Biol Conserv 115:191–201

Leston LFV, Rodewald AD (2006) Are urban forests ecological traps for understory birds? An examination using Northern cardinals. Biol Conserv 131:566–574

Marra PP, Holmes RT (2001) Consequences of dominance-mediated habitat segregation in American redstarts during the non-breeding season. Auk 118:92–104

Martin TE (1995) Avian life history evolution in relation to nest sites, nest predation, and food. Ecol Monogr 65:101–127

Martin TE, Geupel GR (1993) Nest-monitoring plots—methods for locating nests and monitoring success. J Field Ornithol 64:507–519

Marzluff JM, Withey JC, Whittaker KA, Oleyar MD, Unfried TM, Rullman S, DeLap J (2007) Consequences of habitat utilization by nest predators and breeding songbirds across multiple scales in an urbanizing landscape. Condor 109:516–534

Maxted AM (2001) Post-fledging survival, dispersal, and habitat use in two migratory shrubland bird species. MS thesis, Purdue University, Purdue

Naef-Daenzer B, Widmer F, Nuber M (2001) Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. J Anim Ecol 70:730–738

Newson SE, Leech DI, Hewson CM, Crick HQP, Grice PV (2010) Potential impact of grey squirrels (*Sciurus carolinensis*) on woodland bird populations in England. J Field Ornithol 151:211–218

Noon BR, Sauer JR (1992) Population models for passerine birds: structure, parameterization, and analysis. In: McCullough DR, Barrett RH (eds) Wildlife 2001: populations. Elsevier, New York, pp 441–464

Powell LA (2007) Approximating variance of demographic parameters using the delta method: a reference for avian biologists. Condor 109:949–954

Pulliam HR (1988) Sources, sinks and population regulation. Am Nat 132:652–661

Pulliam HR (1993) Sources and sinks: empirical evidence and population consequences. In: Rhodes OE, Chesser RK, Smith MH (eds) Population dynamics in ecological space and time. University of Chicago Press, Chicago, pp 45–69

Rappole JH, Tipton AR (1991) New harness design for attachment of radio transmitters to small passerines. J Field Ornithol 62:335–337

Reidy JL, Stake MM, Thompson FR III (2008) Golden-cheeked warbler nest mortality and predators in urban and rural landscapes. Condor 100:458–466

Ricklefs RE (1969) An analysis of nesting mortality in birds. Smithson Contributions to Zool 9:1–48

Roux KE, Marra PP (2007) The presence and impact of environmental lead in passerine birds along an urban to rural land use gradient. Archiv Environ Contam Toxicol 53:261–268

Rotella J (2005) Nest success models. In: Cooch, E. and White, G. (eds). Program MARK: a gentle introduction, 5th edn. http://www.phidot.org/software/mark/docs/book/

Runge JP, Runge MC, Nichols JD (2006) The role of local populations within a landscape context: defining and classifying sources and sinks. Am Nat 167:925–938

Ryder TB, Reitsma R, Evans B, Marra PP (2010) Quantifying avian nest success along an urbanization gradient using citizen and scientist generated data. Ecol Appl 20:419–426

Sorace A (2002) High density of bird and pest species in urban habitats and the role of predator abundance. Ornis Fenn 80:60–71

Stromborg KL, Grue CE, Nichols JD, Hepp GR, Hines JE, Bourne HC (1988) Post-fledging survival of European sarlings exposed as nestlings to an organophosphorus insecticide. Ecology 68:590–601

Temple SA, Cary JR (1988) Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conserv Biol 2:340–347

Thorington KK, Bowman R (2003) Predation rate on artificial nests increases with human housing density in suburban habitats. Ecography 26:188–196

Townsend JM, Rimmer CC, Brocca J, McFarland KP, Townsend AK (2009) Predation of a wintering migratory songbird by introduced rats: can nocturnal roosting behavior serve as predator avoidance? Condor 111:565–569

United States Census Bureau 2000 http://www.census.gov/geo/www/ua/ua_2k.html and http://factfinder.census.gov

US EPA (2009) Report on the Environment. Urbanization and Population Change http://cfpub.epa.gov/eroe/index.cfm?fuseaction=detail.viewPDF&ch=50&lShowInd=0&subtop=210&lv=list.listByChapter&r=209832

van Heezik Y, Amyh A, Adams A, Gordon J (2010) Do domestic cats impose an unsustainable harvest on urban bird populations? Biol Conserv 143:121–130

Vega Rivera JH, Rappole JH, Mcshea WJ, Haas CA (1998) Wood Thrush post-fledging movements and habitat use in northern Virginia. Condor 100:69–78

Vierling KT (2000) Source and sink habitats of red-winged blackbirds in a rural/suburban landscape. Ecol Appl 10:1211–1218

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46(suppl): 120–139

Whittaker KA, Marzluff JM (2009) Species-specific survival and relative habitat use in an urban landscape during the post-fledging period. Auk 126:288–299

Yahner RH (1991) Avian nesting ecology in small even-aged aspen stands. J Wildl Manag 55:155–159