Urbanization mediates the effects of water quality and climate on a model aerial insectivorous bird

S. MAŽEIKA P. SULLIVAN1, JOSEPH W. CORRA, AND JEFFRY T. HAYES

Schiermeier Olentangy River Wetland Research Park, School of Environment & Natural Resources, The Ohio State University, 2021 Coffey Road, Columbus, Ohio 43210 USA

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Abstract. Aerial insectivorous birds have experienced alarming population declines in eastern North America. Meanwhile, urbanization continues to increase rapidly, with urban land use comprising 69.4 million acres (1 acre = 0.40 ha), or 3.6% of total land area, in the contiguous United States. Multiple environmental changes are associated with urbanization, including alterations to local climate, changes in habitat structure, and potential shifts in both terrestrial and emergent aquatic flying insects on which aerial insectivorous birds rely. Here, we investigated the linkages between urbanization, water quality, and Tree Swallow (Tachycineta bicolor) reproductive success and body condition at seven river-riparian sites representing urban and protected land use in Columbus, Ohio (USA) over five consecutive years (2014–2018). Tree Swallows at urban and protected sites relied on emergent aquatic insects for 37.4% and 30.8% (SD = 28.4% and 24.1%) of their nutritional subsidies, respectively. Despite the loss of environmental quality generally attributed to cities, Tree Swallows exhibited greater reproductive success in urban settings where climate was more amenable to egg and nestling survival, and the breeding season was longer. Urban-nesting Tree Swallows initiated laying 7.9 d earlier and fledged 35% more young per nest than those at protected sites. Multiple characteristics of urban sites appeared to drive these patterns, including differences in mean and extreme air temperatures and measures of water quality (e.g., water temperature, nutrient concentrations, turbidity). However, chronic effects of elevated Hg concentrations, which were 482% greater in adult swallow blood at urban sites than at protected sites where swallows exhibited a 17.4% lower trophic position, may disadvantage individuals in other ways. Further, although Tree Swallows are a good model aerial insectivore bird species, characteristics of urban landscapes that benefit Tree Swallows may not advantage other aerial insectivorous birds owing to differences in life-history and foraging strategies. These findings implicate urbanization, local climate, and water quality as important considerations in the conservation of aerial insectivorous birds.

Key words: aerial insectivores; climate; conservation; cross-boundary ecosystems; streams; urbanization.

INTRODUCTION

Aerial insectivorous birds, a guild comprising swallows, nightjars, swifts, and flycatchers, have experienced alarming population declines in North America, with population losses outpacing declines observed in any other avian group (Nebel et al. 2010, North American Bird Conservation Initiative Canada 2012). Population trends among species in the guild exhibit spatial and temporal variation, but there is broad evidence for intensified declines for most species beginning in the 1980s (Smith et al. 2015). Population declines are likely in response to a complex set of conditions, including loss of suitable breeding habitat (MacHunter et al. 2006), predation (Bohning-Gaese et al. 1993), and environmental degradation or habitat loss on wintering grounds (Fraser et al. 2012, Michel et al. 2016) and migration stopover sites (Rioux-Paquette et al. 2014). Furthermore, comparable declines observed across multiple, taxonomically diverse species in the guild implicate changes in the availability and quality of flying insect prey (Nebel et al. 2010).

Riparian zones are often hotspots of aerial insectivorous bird diversity (Naiman et al. 1993), where the condition of aquatic-riparian ecosystems can influence individual health (Smiths and Fernie 2013) and reproductive success (McCarty and Secord 1999, Sullivan et al. 2006). In particular, aquatic insects that emerge from the water as winged adults (hereafter, “emergent insects”) provide a critical nutritional subsidy to many riparian aerial insectivorous bird species (Jackson and
Fisher 1986, Nakano and Murakami 2001). For instance, Kautza and Sullivan (2016b) showed that 41% of riparian swallows’ energy was derived from aquatic primary production via emergent insects. Emergent insects may provide nutritional advantages over terrestrial insects; Twining et al. (2016) experimentally showed that Tree Swallow (Tachycineta bicolor) nestlings fed a diet high in long-chain omega-3 polyunsaturated fatty acids, found in greater concentrations in aquatic insects, exhibited faster growth rates and better body condition than nestlings fed non-enriched diets.

Anthropogenic landscape changes in a watershed, such as urbanization, can have strong impacts on aquatic ecosystems (Roth et al. 1996, Allan 2004, Meyer et al. 2005). Urban land accounts for 69.4 million acres (1 acre = 0.40 ha) of land (3.6% of total) in the contiguous United States and represents an increase of 470% since 1945 (Brown et al. 2005, Bigelow and Borchers 2012). Further, urban land use is expected to triple worldwide between 2000 and 2030, outpacing human population growth (Seto et al. 2012). Urban encroachment into riparian zones is associated with changes in avian community composition, distribution, and reproductive success (Blair 1996, Rodewald and Bakermans 2006, Rodewald et al. 2013), commonly associated with the removal of riparian vegetation (Lussier et al. 2006), habitat fragmentation and altered vegetation structure (Crooks et al. 2004), and the increased presence of invasive biota (Rottenborn 1999). The Urban Stream Syndrome (Walsh et al. 2005) synthesizes the collective impacts of urbanization on streams flowing through urbanized catchments (e.g., channelization, increased runoff, flashier hydrographs, elevated concentrations of nutrients and contaminants; Meyer et al. 2005, Vietz et al. 2015).

These urban-induced alterations to streams and rivers commonly lead to shifts in aquatic invertebrate communities, including reduced diversity (Gage et al. 2004, Urban et al. 2006) and increased relative abundance of dipterans and non-insect taxa (Roy et al. 2003), potentially limiting aquatic insect emergence in urban watersheds via shifts towards communities dominated by non-emergent taxa (e.g., Oligochaeta and Mollusca). Changes in the emergent insect community flux will, in turn, have implications for aerial insectivorous birds (Stenroth et al. 2015), yet are difficult to predict. For example, elevated nutrient concentrations may lead to a greater emergent insect flux density and thus advantage aerial insectivorous birds (Kautza and Sullivan 2015), yet ecosystem contamination may offset this nutritional benefit. Alberts et al. (2013) found that riparian swallows breeding in urban habitats were more dependent on emergent insects and fed at higher trophic levels than rural swallows, thereby increasing their exposure to aquatic contaminants. Avian foraging strategies may further complicate the interactions between water quality and aerial insectivorous birds. Stenroth et al. (2015) demonstrated that insectivorous birds were more associated with forested streams with large-bodied emergent insects vs. agricultural streams with a smaller body size of flying insects. Alberts et al. (2013) also observed that the biomass of emergent insect swallow prey was generally greater for urban vs. rural-breeding Tree Swallows, suggesting that, along with flux density, traits (e.g., body size) of the emergent insect flux must be considered.

Climatic conditions may also influence avian populations and phenology, including the timing of breeding and migration, reproductive success, and the ranges of individual species (McCarty 2001). Altered temperature regimes may influence birds directly (Pipoly et al. 2013, Becker and Weisberg 2015) or indirectly via changes to invertebrate assemblages (Jonsson et al. 2015) and insect activity (Nooker et al. 2005). For instance, 55% of Ohio’s bird species are projected to be climate threatened or climate endangered (i.e., in danger of losing more than 50% of their current range by 2080 or 2050, respectively), if present warming trends continue (Langham et al. 2014). Climate change is predicted to exert a similar influence on the phenology and range of flying insects (Hughes 2000). Indeed, analysis of long-term data (1959–1991) indicates a significant climate-related shift toward earlier nesting by Tree Swallows, likely influenced by temperature-driven insect availability (Dunn and Winkler 1999). Such shifts may impact reproductive success in complex ways (Monroe et al. 2008, Townsend et al. 2013), including a risk for significant adverse effects on insectivorous birds due to mismatch of lay dates with optimum food availability, as hatching may not align with peak insect abundance (Visser et al. 1998).

At local scales, the urban heat-island effect is a chief driver of localized climate variability, as urban environments typically experience elevated temperatures owing to reduced vegetation cover, diminished evapotranspiration, lower surface albedo, numerous reflective vertical surfaces, higher concentrations of suspended airborne particulate matter, and the presence of anthropogenic heat sources (Oke 1982, U.S. EPA 2008). At the regional scale, climate conditions may have additional impacts on aerial insectivorous birds at the population level. For instance, climate change may facilitate multiple broods per season, a phenomenon that has been observed with increased frequency at the southern end of the Tree Swallow’s breeding range (Monroe et al. 2008). On the other hand, increasing frequency of heat waves and other extreme climate events may reduce individual condition or even lead to mortality. Catry et al. (2015) reported that hyperthermia or acute dehydration led to 36% mortality of Lesser Kestrel (Falco naumanni) nestlings; exposure to high temperatures reduced body-mass gain and increased physiological stress levels among surviving nestlings. Thus, predicting the effects of climate, especially in the context of urbanization, will also be challenging.
HYPOTHESES AND PREDICTIONS

Considered together, the complex relationships among climate, water quality, and urbanization demand a broad perspective to adequately address their impacts on aerial insectivorous birds (see Appendix S1: Fig. S1 for conceptual model). Here, we investigated the potential impact of these factors on reproductive success and individual body condition of Tree Swallows over five years at a suite of urban and protected (i.e., forested or other natural vegetation) riparian study sites in and around Columbus, Ohio, USA. We hypothesized that water quality would mediate the effects of urbanization via changes in nutritional subsidies to Tree Swallows (i.e., the availability and composition of invertebrate prey assemblages).

Specifically, we predicted that increased landscape urbanization would be related to impaired water quality and reduced diversity (McKinney 2002, Walsh et al. 2005) and quality (Roy et al. 2003) of both emergent and terrestrial insects, resulting in lower reproductive success and body condition in Tree Swallows. We also anticipated that emergent insects would transfer contaminants from aquatic ecosystems to Tree Swallows ( Walters et al. 2008), with potential implications for swallow survival and reproduction (Sullivan and Rodewald 2012, Rowe et al. 2014). In particular, we predicted that mercury (Hg) blood concentrations would be elevated in urbanized landscapes in both adult and nestling swallows (Driscoll et al. 2007), both as a function of increased stream contamination and as a function of swallows feeding on larger-bodied predatory insects and at a higher trophic position at urban sites (Alberts et al. 2013). Further, we predicted that higher spring temperatures at urban sites would be related to earlier clutch initiation (Dunn and Winkler 1999, Russell 2003) and that greater variability in air temperatures (i.e., greater extremes) would be negatively associated with fledging success, clutch size, and nestling mass owing to both direct effects on individual condition (e.g., increased stress) and indirect effects via prey availability (Ardia et al. 2006, Winkler et al. 2013, Andrew et al. 2017).

METHODS AND ANALYSES

Study area and experimental design

The Tree Swallow was selected as a model aerial insectivore as this species readily makes use of artificial nest boxes, limiting external perturbations (e.g., predation, interspecific competition, and nest parasitism) and enabling capture of both juveniles and adults (Jones 2003). At the outset of the breeding season in late March each year (2014–2018), nest boxes were deployed at seven riparian study sites distributed across urban and protected land-cover types in the Scioto River system (Ohio, USA; Table 1, Fig. 1). The Scioto River watershed drains 16,868 km² as it flows south into the Ohio River (Ohio Environmental Protection Agency 2014). The middle Scioto River catchment lies within the Columbus Metropolitan Area. Our study sites were located on the Scioto River mainstem (sixth order), as well as on two major tributaries, the Olentangy River (fifth order) and Big Darby Creek (fourth order). The middle Scioto River basin is composed of developed (45%) and cultivated (40%) lands, with forests comprising only 6% of the total land cover (Ohio Environmental Protection Agency 2014). Each study site consisted of a 500-m river reach and the adjacent riparian zone, extending 500 m from each bank perpendicular to the river channel. This spatial extent was selected because (1) Tree Swallows generally forage within 500 m of their nest boxes (Quinney and Ankney 1985, Dunn and Hannon 1992) and (2) 500 m is considered sufficient to capture the influence of land use and land cover on stream water chemistry at the local scale (Strayer et al. 2003). Nest boxes were constructed according to Golondrinas de las Américas (2011), with identical interior dimensions (12.7 × 12.7 × 27.9 cm) to control for possible differences in clutch size due to cavity size (Rendell and Robertson 1993). Nest boxes were mounted on a combination of steel rebar and electrical conduit to deter predators; predator guards constructed from PVC pipe were installed at sites where predation was observed or suspected although such instances were very rare. Five to six nest boxes were deployed at each study site, spaced at moderate distance from one another (~20 m) to avoid territorial overlap (Muldal et al. 1985). All nest boxes were monitored at 2–3 d intervals from shortly before to the end of the breeding season each year. Nestlings were monitored and accessed via the swinging side door of the nest box, while adult birds were captured using the nest box’s “wig-wag” (i.e., trapdoor at the entrance hole) that can be closed from a distance with a length of monofilament fishing line, thus trapping the adult bird inside and facilitating capture via the side-door (Golondrinas de las Américas 2011). All captured birds were banded in accordance with North American Bird

### Table 1. Study sites with impervious surface cover (percentage of total within 500 m on each side of the stream channel) and land-use designation based on impervious surface cover (urban or protected).

| Reach       | Impervious surface (%) | Land use |
|-------------|------------------------|----------|
| Berliner    | 41.1                   | urban    |
| Darby       | 0.0                    | protected|
| Fawcett     | 48.3                   | urban    |
| Highbanks   | 14.2                   | protected|
| Mussel      | 14.4                   | protected|
| Restoration | 64.4                   | urban    |
| Wetlands    | 48.5                   | urban    |

*Note: Study sites were categorized by adapting the thresholds developed by Schueler (1994); those <25% impervious surface were categorized as protected, and those sites ≥25% impervious surface were designated as urban.*
Banding Program’s banding protocols (U.S. Geological Survey 2018).

Land use and land cover

Using Quantum GIS (QGIS Development Team 2017), the percentages of forested or wetland and developed land cover with impervious surfaces at each site were quantified. Land-use and land-cover (hereafter, "land use") data were obtained using the 2011 National Land Cover Database, which classifies land use for the continental United States at a 30-m spatial resolution (Homer et al. 2015). A 500-m buffer was delineated on each side of the stream channel as described above. Land-use percentage for each class (forest, developed, etc.) was then calculated for each delineated buffer. Additional GIS layers were added to calculate the percentage impervious surface (U.S. Geological Survey 2014a), percentage canopy cover (U.S. Geological Survey 2014b), and mean human population density (U.S. Census Bureau 2010).

Tree Swallow reproductive success and body condition

Once swallows returned from wintering grounds, nest boxes were observed two to three times per week to determine if and when breeding pairs of Tree Swallows established nests. Tree Swallow reproductive success was measured using several metrics: clutch initiation date day of year, clutch size (number of eggs), number of eggs successfully hatched, number of nestlings successfully fledged, and mean nestling mass (mg). Nestling mass is considered an important metric of reproductive success; songbird fledgling mass has been strongly linked to post-fledging avoidance of predation (Naef-Daenzer and Gruebler 2016), so the diminished condition of smaller swallows may impair their odds of post-fledging survival. Fledging success (i.e., no. fledglings) has been identified by Cox et al. (2018) as crucial to determining population growth among Tree Swallows. Tree Swallow females lay one egg per day (Hussell and Quinney 1987, Nooker et al. 2005); clutch initiation date was determined based on this rate (i.e., observing a nest with two eggs indicated that laying began the day prior). Any disturbance of nesting or laying, such as predation or destruction of eggs by competing cavity-nesters (typically the House Sparrow [Passer domesticus] or the House Wren [Troglodytes aedon]) was recorded, though such events were very infrequent. Tree Swallows occasionally produce second clutches if their first broods fledge sufficiently early (Monroe et al. 2008). However, second clutches, which were rare in our study, were

FIG. 1. Study sites and land use/land cover in the greater Columbus, Ohio, USA area. Sources: Homer et al. (2015) and QGIS Development Team (2017).
identified but not considered in our analyses due to difficulty in ascertaining if the second clutch was of the same breeding pair. Clutches or nestlings that were destroyed or reduced due to factors outside of the scope of this project (e.g., predation, interspecific competition, flooding) were also identified but excluded from subsequent analyses.

Morphological and individual health measurements were performed on all captured swallows. We weighed all adults (mg; using an OHAUS Scout Pro SP601 portable balance; Parsippany, New Jersey, USA) and measured tarsus length (mm) using handheld calipers. These measurements, in conjunction with body-mass measurements, may be used to estimate individual body fat and general condition (Labocha and Hayes 2012). Scaled mass index (SMI) was used as an estimate of body fat percentage in passerine birds and served as the primary metric of individual body condition for adult birds. SMI was calculated using the method developed by Peig and Green (2009) as follows:

$$\hat{M}_i = M_i \left( \frac{L_0}{L_i} \right)^{b_{\text{SMA}}}$$  (1)

where $M_i$ is the body mass of the individual bird, and $L_i$ is the appropriate linear body measurement (in the case of passerine birds, tarsus length). $L_0$ is the mean linear body measurement of the study sample, and $b_{\text{SMA}}$ is the scaling exponent determined by dividing the slope from an ordinary least-squares regression by the Pearson’s correlation coefficient. Due to sex differences in morphology and mass, male and female swallows were modeled separately in subsequent analysis. Nestling birds were weighed at ~13 d, but morphological measurements were not taken; consequently, SMI was not calculated for nestlings.

Blood samples were drawn from the jugular vein of adults and from nestlings (Sullivan and Vierling 2012) on day 13 after hatching for Hg, blood glucose, and stable-isotope analysis (see Tree swallow diet and trophic position). Concentrations of Hg were calculated for these blood samples by applying a small amount of blood to a dried blood spot (DBS) card, considered a suitable method for measuring contaminant concentrations in wild birds (Shlosberg et al. 2011). DBS cards were sent to Michigan State University’s Diagnostic Center for Population and Animal Health (Lansing, Michigan, USA) to determine concentrations of Hg, measured in parts per billion (μg/g). Although we measured total Hg vs. methylmercury (MeHg; the bioavailable form), concentrations of Hg in blood of insectivorous birds have been found to be primarily MeHg (>95%; Evers et al. 2005, Rimmer et al. 2005). Further, MeHg in fish from the same study system (in some cases, at overlapping sites with those of the current study) constituted 80% (SD = 0.17%) of the total Hg load (Davis et al. 2017).

Blood plasma glucose was also estimated from blood samples, as blood glucose levels are a commonly used indicator of avian body condition. For instance, hyperglycemia or hypoglycemia in birds may indicate septicemia or stress, respectively (Tully et al. 2009, Lill 2011). A droplet of blood was collected on a plastic cuvette and placed inside a HemoCue Glucose 201 Analyzer (Brea, California, USA) for analysis. Two to three nestlings within each nest were sampled for each of the above measurements, thus allowing for internal (i.e., nest-level) replication and ensuring that an excessive volume of blood was not drawn from any one individual bird. Both adults (per nest) were sampled whenever possible, but two blood draws were necessary, spaced out over several weeks to allow time for recovery, to obtain a sufficient quantity of blood.

**Emergent (aquatic) and terrestrial insects**

Tree Swallow food resources, in the form of flying insect prey, were sampled yearly for 10 d in mid-late May and again for 10 d in mid-late July at each of the study sites, aligning with climatic and water-chemistry measurements. For emergent insects, two floating, 1-m² pyramid-style emergent traps (Kautza and Sullivan 2015) were deployed at each study site (one trap at each upstream and downstream section) for two 10-d periods. Likewise, two cloth mesh 1 × 1 × 0.6 m Malaise traps (MegaView Science, Taichung, Taiwan; Townes 1972) were deployed in nearshore vegetation at upstream and downstream locations at each site, suspended from trees at a height of 1 m for two 10-d periods per breeding season. Based on extensive prior work in the study system quantifying ecological linkages between land and water (Rowse et al. 2014, Kautza and Sullivan 2015, Sullivan et al. 2018), we considered our sampling effort sufficient to capture heterogeneity in both emergent and terrestrial flying insects through careful selection of representative habitats in which traps were placed. Moreover, our sampling methodology and effort were generally consistent with other studies that have measured riparian arthropods (Malison et al. 2010, Bellmore and Baxter 2014, Kautza and Sullivan 2015).

Any insects from families of aquatic origin (e.g., Chironomidae) were excluded so that only terrestrial families of flying insects were considered from Malaise traps. All invertebrates collected from traps were stored in 70% ethanol before being enumerated and identified to family using Johnson and Triplehorn (2005) and Merritt et al. (2008). Insects were dried in a 60°C oven and weighed by family, site, and collection period. Insect capture rate (i.e., number of insects m⁻² 10⁻¹ d⁻¹), family richness, and average body size (g, dry mass) were calculated. Due to the presence of a few very large insects in some of the samples (in some instances, two to three orders of magnitude larger than the typical insect), median insect body size (i.e., dry mass) was used for subsequent analysis (Data S2: Inverts.cvs).
Tree swallow diet and trophic position

Analysis of naturally abundant stable isotopes of carbon ($^{13}\text{C}$) and nitrogen ($^{15}\text{N}$) is a powerful tool for investigating trophic relationships and food-web structure (Peterson and Fry 1987, Vander Zanden and Rasmussen 2001, Post 2002, Layman et al. 2012). Enrichment of $^{15}\text{N}$ relative to $^{14}\text{N}$ occurs in consumers with increases in trophic level (Minagawa and Wada 1984). In contrast, ratios of carbon isotopes can reflect dietary sources, including sources of primary production (Finlay 2001, Layman et al. 2012). By examining the ratios of these isotopes, the dietary contributions of terrestrial vs. aquatic insects to consumers can be estimated (Bearhop et al. 1999, Kautza and Sullivan 2016b), as can trophic position (Cabana and Rasmussen 1996, Sullivan et al. 2015, Kautza and Sullivan 2016a).

Beginning in 2015, samples of stream detritus (i.e., coarse benthic organic matter, or CBOM) and periphyton were collected along three transects running perpendicular at upstream, middle, and downstream sections of each 500-m study site. Detritus and periphyton represented terrestrial and aquatic primary producer basal resources, respectively, for subsequent stable-isotope analysis. Multiple (two to three) samples of detritus and periphyton were collected early (late-May) and late (late-July) in the breeding season of each year to capture annual and seasonal variability (Post 2002). Detritus samples were hand collected from the streambed. Periphyton samples were collected by scrubbing the surface of cobble from each transect following Reavie et al. (2010), followed by washing the periphyton into an opaque plastic container using deionized water to remove debris.

We selected the two numerically dominant families from the terrestrial and emergent aquatic insects for each site (i.e., four families per reach) per season, per year (see Emergent (aquatic) and terrestrial insects) to represent terrestrial and aquatic insect for subsequent stable-isotope analysis. In a few instances, one or more numerically dominant insect families had insufficient mass to constitute an isotopic sample. In that event, the next most numerous family was chosen or, failing that, a composite was created from two or more insect families. All samples were dried in a 60°C oven for 48 h and then pulverized and homogenized, either with a ball-mill grinder (for detritus samples) or a mortar and pestle (for insects, blood, and periphyton samples). Insects were weighed by family, time (early or late) in the breeding season, and reach (Iwata et al. 2003). Samples were then packed in 4 × 6 mm tin capsules (Sullivan and Vierling 2012).

Tissue and blood samples were analyzed for C and N content and isotope signatures by continuous flow elemental analysis isotope ratio mass spectrometry (Delta PlusXP; ThermoFinnigan, Bremen, Germany) at the Washington State University Stable Isotope Core (Pullman, Washington, USA). Stable-isotope ratios are reported in δ notation as parts per thousand (‰) deviation from an established standard (e.g., Pee Dee belemnite limestone for δ$^{13}\text{C}$; atmospheric N for δ$^{15}\text{N}$)

\[
\delta^{13}\text{C}_{\text{sample}} = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1,000 \tag{2}
\]

where $R = 13\text{C}/12\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Typical analytical precision was 0.08‰ for δ$^{15}\text{N}$ and 0.19‰ for δ$^{13}\text{C}$ determination.

Dietary/nutritional sources and trophic position

Based on previous research in the study system (Kautza and Sullivan 2016a, b, Sullivan et al. 2016), mixed-model approaches were expected to be effective due to adequate discrimination between primary producer basal resources in the Scioto River basin. Thus, we used the SIAR package version 4.2 (Parnell and Jackson 2013) to fit Bayesian mixing models in R (R Core Team 2018) (see Metadata S1). SIAR uses Markov chain Monte Carlo (MCMC) methods to calculate posterior distributions of variables of interest, and fits a model with a Gaussian likelihood and Dirichlet prior distribution for the probability of the mixture mean to model dietary proportions (Parnell et al. 2010, 2013). Apart from the implementation of a Dirichlet prior distribution, the methods used by SIAR are analogous to that employed by MixSIAR (Moore and Semmens 2008), which uses a Hilborn sampling-importance-resampling (SIR) algorithm to establish threshold acceptance values for resampling, facilitating larger model runs (Rubin 1988).

Prior to fitting models, t tests were conducted on Tree Swallow blood isotope data to detect potential differences in δ$^{13}\text{C}$ and δ$^{15}\text{N}$ signatures between nestlings and adults and to determine if adult and nestling isotopes should be analyzed separately. We found no significant differences in δ$^{15}\text{N}$ signatures by Tree Swallow age ($t = -0.867, P = 0.388$). However, δ$^{13}\text{C}$ values were significantly higher among adult Tree Swallows ($t = -2.015, P = 0.047$), so adult and nestlings were analyzed separately in all our models. Next, we estimated the dietary contribution of aquatic and terrestrial insects to Tree Swallows by fitting a four-source food-web model using δ$^{13}\text{C}$ and δ$^{15}\text{N}$ signatures from the numerically dominant aquatic and terrestrial insect families at each study site. Separate models were developed for early-season and late-season insect samples (Data S1: 2source_DP_SIAR_output.csv, Data S1_inverts_SIAR_output.csv).

We also calculated Tree Swallow trophic position (TP) using δ$^{13}\text{C}$ and δ$^{15}\text{N}$ values (Cabana and Rasmussen 1996, Sullivan et al. 2018; see Metadata S1). We used standard fractionation values (2‰ ± 0.5‰ for δ$^{13}\text{C}$, 6‰ ± 1‰ for δ$^{15}\text{N}$) as were applied in Kautza and Sullivan (2016b) for riparian swallows.
where $\alpha_1$ is the proportion of $N$ acquired from baseline 1 (detritus); $\alpha_2$ is the proportion of $N$ acquired from baseline 2 (periphyton; note that $\alpha_1$ and $\alpha_2$ were derived from mixing model output, above); $\Delta_n$ is the fractionation rate of $N$, and $\rho$ is the TP of the baseline ($TP = 1$ for the primary producers used as the baselines). Potential temporal shifts were also an area of interest, so we ran separate models for each year of data (for both diet and trophic position) to investigate interannual variability. See Data S1: TRES_SIAR.csv, Data S1: TRES_SIAR_inverts.csv, Data S1: 2source_&_TP_SIAR_output.csv, Data S1: invertSIAR_output.csv, and Data S1: isotopes.R for data, mixed models, and trophic position analysis.

### Climate, chemical water quality, and nutrients

Climate variables included temperature and humidity measurements, collected using deployable Thermocron and Hygrochron iButton (Baulkham Hills, New South Wales, Australia) passive temperature and humidity sensors, respectively, installed inside the nest boxes. One temperature sensor was installed inside each nest box at each study site. In addition, one humidity sensor was installed at one representative nest box (usually the most centrally located) per site. All sensors were set to record temperature and humidity at 6-h intervals. These data were downloaded from the sensors at close of each field season.

For temperature and humidity data, means were calculated for each nest box (Data S2: temp_times). Since temperature and humidity varied by nest box within each study site (e.g., owing to the presence of shading vegetation near some boxes), a site-wide temperature mean was also calculated for each site and year. Separate means were calculated for 30-d periods: one for the earlier part of the breeding season from 30 April to 29 May (inclusive), and one for the latter part of the season, 30 May–29 June (inclusive). Most clutch initiations were expected to fall within the designated early 30-d period from late April through May, while most nesting growth and fledging was expected to occur within the 30-d period from late May through June.

Extreme temperatures were evaluated by counting the number of days during the May–June breeding season in which the temperature passed a designated limit, following methodology developed by Pipoly et al. (2013). Extreme heat days were those in which the highest recorded daily temperature exceeded the 90th percentile of all high temperatures measured for the time period (May–June) in all nest boxes across all five years of data. Similarly, extreme cold days were those in which the lowest recorded daily temperature fell below the 10th percentile of all low temperatures in the same timeframe.

A suite of chemical water-quality variables was measured at each study site twice per year (mid-late May and mid-late July, representing early and late periods in the breeding season). Water samples were collected at the thalweg and toward both banks at upstream, middle, and downstream sections of the stream reach, for a total of nine 250-mg water samples per site. All water-quality measurements were made concurrently at each site between 08:00 and 12:00. These samples were then sent to The Ohio State University’s Service Testing and Research Laboratory (Wooster, Ohio, USA) for analysis of total phosphorus (P; mg/L), total nitrogen (N; mg/L), phosphate (PO₄; mg/L), nitrate (NO₃; mg/L), ammonia (NH₃; mg/L), total dissolved solids (TDS; mg/L), and total Hg (ppt). At the same nine locations per site, water temperature, pH, conductivity, and dissolved oxygen (DO) were also measured using a handheld Hach sensION + Portable Meter (Loveland, Colorado, USA). In addition, water samples were collected in 60-mg plastic bottles in the stream thalweg at the upstream, middle, and downstream of each stream and analyzed in a Hach 2100N Turbidimeter (Loveland, Colorado, USA) to measure the Nephelometric Turbidity Units (NTUs) of each sample.

### Statistical analyses

All statistical analyses were performed using the R statistical package version 3.4.4 (R Core Team 2018) and the R Studio package version 1.1.453 (RStudio Team 2016; see Metadata S2). Site-wide means were calculated for each water-quality/nutrient parameter for each year and collection period (e.g., May or July). We used Welch’s $t$ test (Ruxton 2006) to explore potential differences in emergent and terrestrial insect measures including family richness, density, body size between protected and urban sites and between early and later in the breeding season (Data S2: Inverts.R). Principal component analysis (PCA) was then run on the water-chemistry/nutrient data and land-use data (Data S2: pca_WQ_and_lulc_CSV.csv, Data S2: PCA.R). We retained axes with eigenvalues >1 (Rencher 1995), from which we selected PC1 to represent an Urban Stream Index (USI) similar to Alberts et al. (2013; see Results for details), which was used as a predictor variable in subsequent multiple regression models.

We used linear mixed-effects models (LMMs) as our main statistical tool in order to test for the potential effects of urbanization on Tree Swallow reproductive responses (Data S2: Reproductive_Response.csv) and measures of individual body condition (Data S2: Individual_TRES.csv; Bolker et al. 2009, Harrison et al. 2018). The following variables were modeled: clutch initiation date, clutch size, number successfully fledged, nesting mass, male SMI, female SMI, adult Hg blood concentration, nesting Hg blood concentration, and nesting blood glucose. For individual body condition models, response
variables were log_{10}-transformed to meet assumptions of normality. Year, urbanization (i.e., a categorical variable indicating the site’s land use: urban or protected) and an urbanization × year interaction term were included as fixed effects, with study site included as a random effect. Nest box nested within study site was also included as a random effect in the models in which nesting responses were included. Hg blood concentration data were available for the years 2014–2016 only, while blood glucose data were only collected from 2017 to 2018. LMMs were developed using lmerTest version 3.0 (Kuznetsova et al. 2017) in R. The lmerTest package was used to evaluate random and fixed effects from the models, including the coefficients and P values for fixed effects. The overall effect of each variable (i.e., the sum-to-zero contrast) was also assessed via P values and F statistics calculated with the lmerTest, which employs Satterthwaite’s approximation for degrees of freedom values. R^2 values, both marginal (fixed effects) and conditional (fixed + random effects), were determined for each model with the MuMIn package (Bartoň 2018), which calculates a pseudo-R^2 for mixed-effects models (Data S2: TRES_models.R).

Two sets of linear mixed-effects models were also developed for swallow diet and trophic position (as potential mechanisms linking water quality with swallow Hg blood concentrations) with separate models for adult and nestling Tree Swallows. The overall effect of each variable (i.e., the sum-to-zero contrast) was also assessed via P values and F statistics from lmerTest (Kuznetsova et al. 2017) (Data S1: isotopes.R).

In addition to diet and trophic position, we explored additional potential mechanisms (i.e., USI as well as individual measures of water chemistry, nutrient concentrations, air temperature, flying insect prey) potentially driving Tree Swallow reproductive success and body condition with post-hoc multiple regression. Multiple regression models incorporated year as a categorical variable, as many of our predictor variables (particularly the measures of local climate) had considerable interannual variability. For all models, an alpha level of α ≤ 0.05 was used as the threshold of statistical significance, while α ≤ 0.10 was considered evidence of a trend (Data S2: TRES_models.R).

### RESULTS

**Physicochemical and climatic variability between urban and protected sites**

Descriptive statistics showed that concentrations of all nutrients, with the exception of total N, were slightly higher, on average, at the protected sites (Table 2). However, Hg concentrations were ~1.6x greater at urban sites than at protected sites. Mean turbidity of the water column at urban sites was ~32% lower than at protected sites, while water temperature at urban sites was 0.6°C higher. On average, air temperature at urban sites was significantly warmer than at protected sites through the breeding season (urban, 21.9°C; protected, 20.2°C; Welch’s t test, P = 0.001; Fig. 2a). Humidity was not different between land-use types (urban, 70.9%; protected, 73.6%; Welch’s t test, P = 0.224; Fig. 2b), but urban sites were characterized by fewer days of extreme cold (Welch’s t test, P = 0.040; Fig. 2c) and more days of extreme heat (Welch’s t test, P = 0.002; Fig. 2d). Urban sites experienced an average of 3 d of extreme cold and 12 d of extreme heat between 30 April and 28 June, compared to 5 d of extreme cold and 7 d of extreme heat at protected sites.

Principal component analysis was performed using three LULC variables and nine water-chemistry and nutrient variables (Table 3). PC1, with an eigenvalue of 5.57 and accounting for 61.9% of the variance, served as our USI. This axis was primarily influenced by human population density, canopy cover, Hg, impervious surface, and DO. The results of the USI closely correspond with the urban–natural dichotomy established by classifying sites based on impervious surface coverage (Table 1), with some variability given the inclusion of other urban characteristics (e.g., “Mussel” USI was driven mostly by human population density and water chemistry).

**Invertebrate prey assemblages between urban and protected sites**

For emergent aquatic insects, there was little distinction in family richness (Welch’s t test, t = 0.407, df = 90.4, P = 0.686; see Appendix S2: Fig. S1a) or density (Welch’s t test, t = 0.736, df = 97.70, P = 0.464;
Appendix S2: Fig. S1b; estimated via rate of capture) between urban and protected sites. Median emergent aquatic insect body size was similar at protected and urban sites over the course of the study (Welch’s t test, \( t = -0.019, \) df = 99.0, \( P = 0.985; \) Appendix S2: Fig. S1c). We also did not observe a difference between emergent insect body size (Welch’s t test, \( t = -1.116, \) df = 116.7, \( P = 0.267; \) data not shown) or density (Welch’s t test, \( t = -1.141, \) df = 214.0, \( P = 0.255; \) data not shown) between early and later periods in the breeding season. For terrestrial flying insects, median insect body size at the protected sites was \( >3 \times \) that of urban sites (Welch’s t test, \( t = -1.773, \) df = 57.9, \( P = 0.081; \) Appendix S2: Fig. S1c). Neither terrestrial insect family richness (Welch’s t test, \( t = -0.631, \) df = 86.3, \( P = 0.523; \) Appendix S2: Fig. S1a) nor density (Welch’s t test, \( t = -1.385, \) df = 50.3, \( P = 0.172; \) Appendix S2: Fig. S1b) was different between urban and protected sites.

**Tree Swallow reproductive success**

We observed little variability in clutch size, either across years (LMM, \( P = 0.186; \) Table 4, Fig. 3a) or between urban and protected sites (LMM, \( P = 0.362).\) Significantly earlier clutch initiation at urban sites (LMM, \( P = 0.018; \) Table 4, Fig. 3b) was observed. Number of successfully fledged young was significantly higher at the urban nesting sites than at protected sites (LMM, \( P = 0.003; \) Table 4, Fig. 3c), with urban nests yielding, on average, \(~1.5~\) fledglings each year than their protected counterparts. Nestling mass at 13 d showed no significant difference by land use (LMM, \( P = 0.510; \) Table 4, Fig. 3d); but there was a trend of interannual differences (LMM, \( P = 0.060; \) Table 4); average nestling mass ranged from 21.1 g in 2014 to

![Figure 2](image-url)
Table 4. Results from linear mixed-effects models with fixed (year, land use [urban or protected], and year × land use) and random (site, nestbox, site × nestbox) effects.

| Linear mixed models | Fixed effects | Random effects | $R^2$ |
|---------------------|---------------|----------------|-------|
|                     | df | F   | P    | Variance | SD | Marginal | Conditional | n   |
| No. fledged         |    |     |     |          |    |          |             |     |
| Year                | 4, 107.00 | 3.20 | 0.017** |          |    |          |             | 117  |
| Land use            | 1, 107.00 | 9.51 | 0.003** | 0.000    | 0.007 | 0.163    | 0.163      |      |
| Year × land use     | 4, 107.00 | 0.13 | 0.972  | 3.002    | 1.733 |          |             |      |
| Site                |    |     |     |          |    |          |             |      |
| Residuals           |    |     |     |          |    |          |             |      |
| Nestling mass       |    |     |     |          |    |          |             |      |
| Year                | 4, 95.03 | 2.34 | 0.060* |          |    |          |             | 108  |
| Land use            | 1, 5.48  | 0.50 | 0.510  | 1.215    | 1.102 | 0.101    | 0.240      |      |
| Year × land use     | 4, 95.03 | 1.31 | 0.271  | 6.646    | 2.578 |          |             |      |
| Site                |    |     |     |          |    |          |             |      |
| Residuals           |    |     |     |          |    |          |             |      |
| No. eggs            |    |     |     |          |    |          |             |      |
| Year                | 4, 115.90 | 1.57 | 0.186  |          |    |          |             | 128  |
| Land use            | 1, 5.80  | 0.98 | 0.362  | 0.014    | 0.118 | 0.121    | 0.140      |      |
| Year × land use     | 4, 115.90 | 1.70 | 0.154  | 0.626    | 0.791 |          |             |      |
| Site                |    |     |     |          |    |          |             |      |
| Residuals           |    |     |     |          |    |          |             |      |
| Clutch initiation date |  |     |     |          |    |          |             |      |
| Year                | 4, 122.83 | 1.33 | 0.264  |          |    |          |             | 136  |
| Land use            | 1, 5.65  | 0.77 | 0.018** |          |    |          |             |      |
| Year × land use     | 4, 122.83 | 0.53 | 0.713  | 2.918    | 1.708 | 0.187    | 0.229      |      |
| Site                |    |     |     |          |    |          |             |      |
| Residuals           |    |     |     |          |    |          |             |      |
| Adult diet: early emergent insects |  |     |     |          |    |          |             |      |
| Year                | 3, 50.63  | 4.23 | 0.010** |          |    |          |             | 62   |
| Land use            | 1, 5.48  | 0.90 | 0.380  | 0.012    | 0.110 | 0.15     | 0.56       |      |
| Year × land use     | 2, 50.46  | 1.50 |        | 0.013    | 0.114 |          |             |      |
| Site                |    |     |     |          |    |          |             |      |
| Residuals           |    |     |     |          |    |          |             |      |
| Nestling diet: early emergent insects |  |     |     |          |    |          |             |      |
| Year                | 3, 292.47 | 16.26 | <0.001** |          |    |          |             | 306  |
| Land use            | 1, 5.12  | 1.29 | 0.310  | 0.010    | 0.099 | 0.23     | 0.69       |      |
| Year × land use     | 2, 293.01 | 18.35 | <0.001** |          |    |          |             |      |
| Site                |    |     |     |          |    |          |             |      |
| Site × box          |    |     |     |          |    |          |             |      |
| Residuals           |    |     |     |          |    |          |             |      |
| Adult diet: late emergent insects |  |     |     |          |    |          |             |      |
| Year                | 2, 49.38  | 0.20 | 0.820  |          |    |          |             | 60   |
| Land use            | 1, 5.31  | 0.09 | 0.770  | 0.015    | 0.121 | 0.06     | 0.60       |      |
| Year × land use     | 2, 49.38  | 0.24 | 0.120  | 0.011    | 0.105 |          |             |      |
| Site                |    |     |     |          |    |          |             |      |
| Residuals           |    |     |     |          |    |          |             |      |
| Nestling diet: late emergent insects |  |     |     |          |    |          |             |      |
| Year                | 2, 272.11 | 2.06 | 0.130  |          |    |          |             | 282  |
| Land use            | 1, 5.29  | 0.25 | 0.640  | 0.006    | 0.078 | 0.04     | 0.56       |      |
| Year × land use     | 2, 272.11 | 1.47 | 0.230  | 0.003    | 0.056 |          |             |      |
| Site                |    |     |     |          |    |          |             |      |
| Site × box          |    |     |     |          |    |          |             |      |
| Residuals           |    |     |     |          |    |          |             |      |
| Trophic position: adult |  |     |     |          |    |          |             |      |
| Year                | 2, 41.57  | 0.18 | 0.830  |          |    |          |             | 60   |
| Land use            | 1, 5.95  | 10.64 | 0.020** |          |    |          |             |      |
| Year × land use     | 2, 41.57  | 1.89 | 0.160  | 0.008    | 0.089 |          |             |      |
21.9 g in 2015 (P = 0.159), 21.7 g in 2016 (P = 0.023), 20.4 g in 2017 (P = 0.253), and 20.2 g in 2018 (P = 0.133). Site emerged as an influential factor for nestling mass, where the inclusion of random effects increased the R² from 0.10 to 0.24. Double-brooding (i.e., a second brood in the same season by one or both of the same adult birds) occurred infrequently: one double-brood was observed each year in 2015, 2017, and 2018, while two were observed in 2016. Double-broods were observed only at urban sites.

Using regression models, we investigated possible mechanisms driving variability in reproductive responses. For number fledged, the USI was positively related to fledging success (P < 0.001; Fig. 4a). Nestling mass was negatively related to the number of extreme heat days during the breeding season (P = 0.027; see Table 4. Continued.

| Linear mixed models | Fixed effects | Random effects | R²  | n |
|---------------------|--------------|----------------|-----|---|
|                     |   df       |   F          |   P   | Variance | SD | Marginal | Conditional |
| Site                |             |              |      | 0.034 | 0.185 | 0.48 | 0.61 | 51 |
| Residuals           |             |              |      | 0.097 | 0.311 |       |       |    |
| Trophic position:  |             |              |      |       |       |       |       |    |
| nestling           |             |              |      |       |       |       |       |    |
| Year                | 2, 231.36   | 134.04       | <0.001** | 0.435 | 0.660 | 0.14 | 0.93 | 253 |
| Land use            | 1, 4.378    | 0.72         | 0.430 | 0.056 | 0.237 |       |       |    |
| Year × land use     | 1, 242.67   | 2.85         | 0.092* | 0.043 | 0.207 |       |       |    |
| Site                |             |              |      |       |       |       |       |    |
| Site × box          |             |              |      |       |       |       |       |    |
| Residuals           |             |              |      |       |       |       |       |    |
| Adult Hg            |             |              |      |       |       |       |       |    |
| Year                | 2, 18.00    | 2.58         | 0.103 |       |       |       |       |    |
| Land use            | 1, 18.00    | 7.13         | 0.016** | 0.000 | 0.000 | 0.603 | 0.603 | 24 |
| Year × land use     | 2, 18.00    | 2.73         | 0.09*  | 0.758 | 0.870 |       |       |    |
| Site                |             |              |      |       |       |       |       |    |
| Site × box          |             |              |      |       |       |       |       |    |
| Residuals           |             |              |      |       |       |       |       |    |
| Nestling Hg         |             |              |      |       |       |       |       |    |
| Year                | 2, 61.36    | 115.79       | <0.001** | 0.284 | 0.533 | 0.808 | 0.959 | 167 |
| Land use            | 1, 4.13     | 0.37         | 0.573 | 0.347 | 0.589 |       |       |    |
| Year × land use     | 2, 61.36    | 8.96         | <0.001** | 0.173 | 0.416 |       |       |    |
| Site                |             |              |      |       |       |       |       |    |
| Site × box          |             |              |      |       |       |       |       |    |
| Residuals           |             |              |      |       |       |       |       |    |
| Male SMI            |             |              |      |       |       |       |       |    |
| Year                | 4, 33.00    | 4.23         | 0.007** | 0.000 | 0.021 | 0.273 | 0.305 | 42 |
| Land use            | 1, 33.00    | 0.23         | 0.633 | 0.009 | 0.097 |       |       |    |
| Year × land use     | 3, 33.00    | 0.08         | 0.969 |       |       |       |       |    |
| Site                |             |              |      |       |       |       |       |    |
| Site × box          |             |              |      |       |       |       |       |    |
| Residuals           |             |              |      |       |       |       |       |    |
| Female SMI          |             |              |      |       |       |       |       |    |
| Year                | 4, 59.00    | 10.14        | <0.001** | 0.000 | 0.000 | 0.293 | 0.293 | 69 |
| Land use            | 1, 59.00    | 0.26         | 0.872 | 0.015 | 0.124 |       |       |    |
| Year × land use     | 4, 59.00    | 0.70         | 0.593 |       |       |       |       |    |
| Site                |             |              |      |       |       |       |       |    |
| Site × box          |             |              |      |       |       |       |       |    |
| Residuals           |             |              |      |       |       |       |       |    |
| Nestling glucose    |             |              |      |       |       |       |       |    |
| Year                | 1, 74.64    | 2.99         | 0.088* | 107.7 | 10.38 | 0.070 | 0.425 | 167 |
| Land use            | 1, 5.44     | 1.99         | 0.213 |       |       |       |       |    |
| Year × land use     | 1, 74.64    | 0.31         | 0.581 | 1,003.5 | 31.68 |       |       |    |
| Site                |             |              |      |       |       |       |       |    |
| Site × box          |             |              |      |       |       |       |       |    |
| Residuals           |             |              |      | 1,800.7 | 42.43 |       |       |    |

Note: Marginal R² is variation explained by fixed effects alone; conditional R² is variation explained by both fixed and random effects. Early and late emergent insects for diet/nutritional subsidy models refer to early and late periods in the breeding season.

*Evidence of a trend; i.e., 0.5 ≥ P < 0.10.

**Significant (P < 0.05) effect.
Appendix S2: Clutch initiation date was also related to temperature, with evidence of a trend for earlier laying associated with higher average temperatures in the early part of the season ($P = 0.053$; Appendix S2: Fig. S2b). At the site level, number of days of extreme cold was negatively associated with fledgling success ($P = 0.010$; Fig. 4b). However, by nest (i.e., the temperatures recorded at each individual nest from clutch initiation through fledging), no significant relationships or trends emerged between temperature and fledging success or nestling mass ($P > 0.10$, data not shown).

**Tree swallow nutritional subsidies/diet and trophic position**

Mixing models indicated that from 2014 to 2017, nutritional subsidies from early-season emergent aquatic insects contributed ~27% and 41% to adult swallow diet.
at protected and urban sites, respectively, but these differences were not significant (LMM, $P = 0.380$; Table 4, Fig. 5a; also see Appendix S2: Table S1 for credible intervals). Land use was also not implicated as a significant factor driving the 44% (protected) vs. ~33% (urban) adult reliance on emergent insects during the latter part of the breeding season (LMM, $P = 0.770$; Table 4, Fig. 5b). Among adult swallows, there was significant interannual variability in the reliance on terrestrial vs. aquatic flying insect nutritional subsidies; however, this pattern was observed for early-season insects only (LMM, $P = 0.010$; Table 4), with 2014 and 2016 associated with slightly higher consumption of aquatic prey. The random effect of site was considerable: $R^2$ increased for adult swallows and early-season insects from 0.15 (marginal) to 0.56 (conditional), and from 0.06 to 0.60 for late-season insects.

Although land use alone was not implicated as a significant driver behind nestling emergent-insect reliance (Table 4, Fig. 5a, b), the interaction of land use × year (LMM, $P < 0.001$; Table 4) was a significant influence on the ~24% (protected) and 48% (urban) reliance on nutritional subsidies from early-season emergent insects (Fig. 5a). This relationship was related to increased consumption of aquatic insect prey in 2016 and 2017 by nestlings (Table 4). As with adult swallows, random effects were also important for nestling reliance on emergent insects: $R^2$ increased from 0.23 (marginal) to 0.69 (conditional) in the early-season insect model, and 0.04 to 0.56 in the late-season model.

Regarding trophic position, which ranged from 1.28 to 4.20 across all sites for adult swallows, we observed considerable variability by land use for adult swallows, with swallows at urban sites feeding at significantly higher trophic positions than those at protected sites (LMM, $P = 0.020$; Table 4, Fig. 6a). Among nestlings, our results did not show variability by land use alone (LMM, $P = 0.430$; Table 4, Fig. 6b). However, nesting trophic position was 35% and 25% higher in 2016 and 2017, respectively, relative to 2015 (LMM, $P < 0.001$; Table 4). The interaction of land use × year revealed a trend toward higher trophic position at urban sites in 2016 as well (LMM, $P = 0.092$; Table 4). Site, included as a random effect in our models, accounted for 0.13 additional variation among adult swallows (Table 4). The random effect of site, however, was far more pronounced (0.79) among nestlings (Table 4).

**Tree Swallow individual body condition**

Adults at urban sites had significantly higher Hg blood concentrations than those at protected sites...
(LMM, \(P = 0.016\)), while no difference was observed in nestlings (LMM, \(P = 0.573; \text{Table 4, Fig. 7a}\)). However, nestling Hg had an interaction effect with year (LMM, \(P < 0.001; \text{Table 4}\)), related to lower Hg among nestlings at urban sites in 2015 and 2016. Nestlings with the lowest average blood concentrations of Hg were observed in 2016 (\(P < 0.001\)), a year that coincided with very low observed Hg concentrations in the water column. Both adults and nestling Hg concentrations were heavily influenced by site or site \(\times\) nest box, suggesting that local-scale variability among sites was important. For instance, the USI emerged as a strong predictor of elevated Hg in adult swallows (LMM, \(P = 0.001; \text{see Appendix S2: Fig. S3}\)).

Nestling blood glucose showed no significant difference between land-use types (LMM, \(P = 0.213; \text{Table 4, Fig. 7b}\)), although random effects (site, site \(\times\) nest box) were very influential (\(R^2\) marginal = 0.07, \(R^2\) conditional = 0.43; Table 4). Neither male (LMM, \(P = 0.633\)) nor female (LMM, \(P = 0.872\)) SMI varied by land use alone (Table 4; Fig. 7c). However, male swallows exhibited significant annual variability (LMM, \(P = 0.007; \text{Table 4}\), with the highest SMI in 2018 (LMM, \(P = 0.002; \text{note that no adult male Tree Swallows were captured in 2015}\)).

**DISCUSSION**

Urbanization can exert strong impacts on both avian communities and ecosystem functioning (Schlesinger et al. 2008). For instance, a meta-analysis by Chamberlain et al. (2009) of 10 North American and European passerine bird species showed a general trend toward smaller clutches, fewer successfully fledged young, earlier clutch initiation dates, and lower nestling mass among urban breeders. In the Columbus-area system of our current study, Rodewald et al. (2013) observed that the aerial insectivorous Acadian Flycatcher (Empidonax virescens) exhibited diminished reproductive output in urban settings, implicating increased brood parasitism in urbanized landscapes as a likely factor. Given the reliance of riparian swallows and other aerial insectivores on emergent aquatic insect nutritional subsidies (Nakano and Murakami 2001, Kautza and Sullivan 2016b), we expected that losses in water quality and altered temperature regimes in urban areas would be reflected in urban-breeding Tree Swallows, both through impaired reproductive success and compromised body condition of nestlings and adults.

Our results challenged some of our expectations. We observed limited differences in nestling mass or clutch...
size between urban Tree Swallows and their counterparts nesting in protected areas. There was also little variability in clutch size by land use, although nesting mass exhibited strong interannual differences: we observed significantly lower mean nesting mass over all study sites in 2015, a result we also observed across the study system in 2017. High variability in nesting mass also implies that local, site-specific effects such as microclimatic differences may exert a greater influence on nesting mass than urbanization alone. Extreme heat, for example, which was significantly more pronounced at our urban sites (Fig. 2d), has been related to thermal stress, inhibited growth, and even increased mortality in nesting passerine birds of various species (Cunningham et al. 2013, Rodriguez and Barba 2016, Andrew et al. 2017). The link between water quality and Tree Swallows in our study system was evidenced by the important nutritional reliance on emergent insects (Fig. 5). In turn, water quality, via its influence on emergent insects (e.g., Hg contamination), was also implicated as an urban-related factor linked to swallow responses. For example, urbanization as estimated via our Urban Stream Index was positively related to blood Hg concentrations in adult Tree Swallows (Appendix S2: Fig. S3).

In a notable divergence from our hypothesis, the number of successfully fledged young was higher for urban broods than at protected sites. As clutch size did not vary substantially with land use (Table 4, Fig. 3a), lower nest productivity at protected sites must be attributed to higher mortality of eggs or nestlings. Since nests experiencing losses from predation, interspecific competition, floods, and similar events were excluded from our analyses, this mortality is due to starvation, exposure, disease, or other indeterminate causes, some of which can be related to the environmental conditions measured, including local climate and food availability. Fledging success, more than other factors, may play a leading role in driving population growth. Population models developed by Cox et al. (2018), based on 42-yr study of a Tree Swallow population in Ontario, Canada, indicated that fledging success and overwinter survival were the two most influential drivers of population change, while clutch size was of limited importance.

Urbanization, as quantified by the USI, was related to increased fledging success (Fig. 4a). Variability in the quantity and quality (Appendix S2: Fig. S1a–c) of insect prey among sites and land-use types was likely a factor related to the influence of land use on Tree Swallow fledging success. Previous studies of insectivorous birds including for Barn Swallows (Teghløj 2017) and House Wrens (Newhouse et al. 2008) have reported lower nesting mass among birds breeding in developed areas, results that are thought to be related to reduced prey quality or abundance. Yet, we found no difference in emergent insect or flying insect richness or abundance between our urban and protected sites (Appendix S2: Fig. S1a, b).

Median body size of emergent insects was not significantly different between our protected and urban sites. However, small-bodied Chironomidae dominated the emergent insect assemblages across our study sites and may have masked potential shifts in body size driven by other insect taxa. Anecdotally, we noted the presence of more-large-bodied taxa (e.g., Odonata) at urban reaches, likely driving the slightly greater variability in body size observed at urban sites (Appendix S2: Fig. S1c). Supporting this observation, working in the same study system, Alberts et al. (2013) found that the biomass of emergent insects in boluses of adult swallows provisioning nestlings was greater at urban than protected reaches. Other evidence also indicates that Tree Swallows selectively catch larger-bodied prey when provisioning nestlings (Quinney and Ankney 1985, McCarty and Winkler 1999), underscoring the importance of prey body size as a potential determinant of fledging success and post-fledging survival and suggesting that both availability of emergent insects as well as swallow foraging tactics are important factors mediating water-quality effects on aerial insectivores. Although terrestrial insect body size was greater at the protected sites, experimental work by Twining et al. (2016) suggests that the nutritional benefits of aquatic insects, which are relatively rich in omega-3 long-chain polyunsaturated fatty acids, may be more important than terrestrial insect prey availability.

Although our study design captured emergence events both early and later in the swallow breeding season, aquatic insect emergence can be highly variable spatially and temporally (Malison et al. 2010, Kautza and Sullivan 2015). Increased frequency of sampling may have captured increased variability in emergence dynamics and could have refined models linking Tree Swallows with water quality via emergent insects.

**Temperature**

Among our four reproductive response metrics, only responses of clutch initiation date conformed to our hypotheses, with urban birds laying eggs significantly earlier than their protected counterparts (Fig. 3b). There were significant differences in both air temperatures (Fig. 2a) and frequency of extreme temperatures (Fig. 2c, d) between urban and protected sites, implicating the urban heat-island effect as a likely driver of air temperature variability among sites (Oke 1982). The early temperature period (30 April–29 May) captured most of the clutch initiations (93.0%). In our investigation of potential drivers of reproductive response, air temperature during this period emerged as the strongest predictor of clutch initiation date, a finding that was consistent across all years of data (Appendix S2: Fig. S2b). Urban sites were both markedly warmer and associated with significantly earlier clutch initiation (Fig. 3b), suggesting local-scale climate conditions as a key mechanism driving these differences. The availability of insect prey has
been identified as a breeding cue in Tree Swallows (Nooker et al. 2005), pointing to temperature-driven insect activity or emergence as the link between temperature and clutch initiation (Eeva et al. 2000). Our results echo findings by Russell (2003), who observed strong and consistent correlations between laying date and local-scale air temperature in early May among Tree Swallows from 1969 to 2001. More recently, Bournet et al. (2015) not only revealed similar correlations between regional-scale temperatures and Tree Swallow clutch initiation date, but also strong evidence that the rise in interannual spring temperature is associated with earlier Tree Swallow clutch initiation dates. Dunn and Winkler (1999) showed advances in laying dates across the breeding range linked to climate change, including a more pronounced rate of change at the southern edge of the range (as in southern Ohio).

Variability in temperatures has also been related to Tree Swallow reproduction. In our study, the frequency of extreme cold days was related to fewer fledged young (Fig. 4b), with protected sites associated with more days of extreme cold (Fig. 2c). Cold snaps are strongly associated with elevated nestling mortality, as they suppress flying insect activity while increasing energetic demands on Tree Swallows (Winkler et al. 2013). Warmer conditions associated with urban heat islands, that is, overall higher temperatures, fewer days of extreme cold, and more stable overnight temperatures (Tan et al. 2015), may mitigate the impact of periods of cold weather while intensifying flying insect activity early in the morning relative to cooler non-urban areas. Tree Swallow nests observed by Ardia (2013) yielded results in line with these expectations, as higher nighttime temperatures in nest boxes were related to higher fledge rates. For context, the 10th and 90th temperature percentiles were 17°C and 31°C (30 April–28 June), respectively, for our data. Climate normals (i.e., three-decade averages of meteorological parameters) for the period 1981–2010 show average daily low temperatures of 10.2°C and 15.4°C for May and June, respectively, and highs of 23.8°C and 28.6°C for the same months (Arguez et al. 2010).

Higher spring temperatures may also provide an additional benefit to Tree Swallows by extending the breeding season, a phenomenon that has been linked to greater fecundity in other passerine species (Townsend et al. 2013). Monroe et al. (2008) observed regular double brooding among a population of Tree Swallows in Virginia, which can dramatically increase swallow reproductive output and may have a positive influence on population growth. Of note, we only observed double brooding at warmer urban sites.

Nonetheless, higher temperatures may have negative implications for aerial insectivore body condition and reproductive success. For instance Ardia (2013) found that extreme heat (≥35°C) in Tree Swallow nests was related to both impaired body condition (including reduced mass) and reduced fledging success. As Ohio lies near the southern end of the Tree Swallow’s breeding range (Winkler et al. 2011), it is likely that extreme heat events will have a greater impact on Ohio Tree Swallow populations than their counterparts breeding farther north. High-resolution data that capture the effects of temperature across both local and broader spatial scales, including potential impacts on nestling and egg mortality (Ardia 2013) or nestling growth (Pipoly et al. 2013), will be critical in understanding impacts of both urbanization and climate change on aerial insectivores.

Overall, temperature variability stemming from urbanization and climate change will have complex and interactive effects on aerial insectivores. However, these interactions are replete with trade-offs, and thus are complicated and difficult to predict. For instance, cold snaps can restrict insect flight activity with grave consequences for daily brood survival rates in Tree Swallows (Winkler et al. 2013). While the heat-island effect of urbanization may buffer against critical cold, the potential synergistic effects of urbanization and climate change can lead to extreme heat events, with consequences ranging from losses in individual condition (as we observed with losses in nestling mass with elevated temperatures) to mortality (Catry et al. 2015). Further, microclimatic features (e.g., vegetation and aspect of the nesting site) can lead to high variability in both mean and extreme temperatures at the nest level, which we suspect contributed to lack of relationships observed between Tree Swallows and temperature at the resolution of the nest box (vs. site). This result implies that the indirect effects of temperature on aerial insectivores (via insect activity) were likely more influential than the direct effect of temperature extremes on nestlings in our study system.

Mercury

In addition to a 482% increase in Hg blood concentrations in adult swallows at urban sites, the results of our mixed-effects model (Table 4) indicate substantial variability among study sites beyond the urban-protected dichotomy. For example, the USI, which reflects a suite of continuous variables of urbanization, strongly predicted Hg concentrations in adult swallows, supporting the premise that emergent insects serve as vectors for aquatic contaminants to terrestrial consumers (Walters et al. 2008, Sullivan and Rodewald 2012). Elevated Hg concentrations found in adult swallows align with previous findings in the same study system by Alberts et al. (2013), who speculated that higher concentrations among adult swallows may be due to nestlings’ rapid growth as Hg is incorporated into feathers (Condon and Cristol 2009). Differences in adult and nestling Hg blood concentrations may also be a consequence of prey selection; i.e., selection of more Hg-rich invertebrates from higher trophic positions or of aquatic origin (Rimmer et al. 2010, Alberts et al. 2013), which could also drive the strong positive relationship between urbanization...
and Hg in adult Tree Swallows relative to the negative relationship we observed in nestlings in 2015 and 2016.

The mean trophic position of 3.09 of adult Tree Swallows in our study is on par with that of riparian swallows and other water-associated passerines reported by Sullivan et al. (2015), and was 22% greater at urban vs. protected sites. In addition to generally elevated concentrations of Hg in stream water at urban sites of our study (Table 2), the greater trophic position of adult swallows was a critical mechanism leading to markedly greater concentrations of Hg in swallow blood at urban sites. Although mixed models suggested no difference in the nutritional contribution of emergent insects between urban and protected sites (Fig. 5), bolus data from prior studies in the Columbus system (Alberts et al. 2013) indicate that swallows tend to target larger-bodied insects such as damselflies and dragonflies, which are predatory taxa that bioconcentrate Hg and thus increase Hg biomagnification in swallows and other predators.

Tree Swallows tend to forage over open fields or water (McCarty and Winkler 1999, Ghilain and Bélisle 2008). Thus, stream channel width or the distribution of riparian vegetation may influence swallow reliance on emergent insects, thereby increasing their exposure to Hg (Alberts et al. 2013). Hg concentrations in both adult and nesting swallows also appeared to track interannual variation in Hg concentrations measured in the water column—for instance, adult swallows across the study system and urban nestlings exhibited significantly lower Hg in 2016 (Table 4), a year with the lowest observed Hg concentrations in the river sites—further supporting a link for the transfer of contaminants between aquatic and terrestrial systems.

Mercury has an array of well-documented harmful health impacts on birds (Boening 2000); among Tree Swallows, weakened immune responses have been identified as a major adverse effect of Hg exposure, with potential long-term consequences for fitness (Hawley et al. 2009). Further, Hg has been linked to impaired reproductive success in Tree Swallows (Brasso and Cristol 2008). Although adult Hg blood concentrations \( (-x = 0.23 \mu g/g, SD = 0.32 \mu g/g) \) in our study system are more on par with reference vs. contaminated sites in other studies (e.g., contaminated 3.56 \( \mu g/g \), reference 0.17 \( \mu g/g \) [Brasso and Cristol 2008]; contaminated 3.03 \( \mu g/g \), reference 0.16 \( \mu g/g \) [Hallinger and Cristol 2011]), even trace levels of contaminants can impair avifauna. For instance, Rowe et al. (2014) reported that mean Hg concentrations of 0.21 \( \mu g/g \) in adult Acadian Flycatcher blood were related to fewer fledged young.

CONCLUSIONS

Cities have transformed landscapes across North America, with far-reaching and persistent ecological consequences. However, our results indicate that some characteristics of the urban environment may confer certain advantages on aerial insectivorous birds in terms of reproductive success. For instance, in our Columbus-area study system, we observed greater fledging success at urban nests, which may be linked to both greater variability in body size of nutritionally beneficial emergent insects and to microclimatic differences. Temperature regimes in urban areas may mitigate the impact of early spring cold snaps, afford a longer breeding season, and spur insect activity. If climate change prompts phenological changes in the timing of spring migration as predicted (Crick 2004), the risks associated with early nesting could be minimized by the availability of warmer urban breeding habitats. However, climate shifts also come with unfavorable ecological consequences. Global climate change is expected to increase the frequency of extreme heat events (Gerald and Tebaldi 2004), the impacts of which will be intensified by the urban heat-island effect (Stone et al. 2010). Cities like Columbus, home to the eighth-most intense summer urban heat island among the 60 largest U.S. cities (Kenward et al. 2014), may experience the most intense impacts. Nestling mass has been identified as a strong indicator of post-fledging survival, itself a key predictor of population growth (Cox et al. 2018). Post-fledging survival was not addressed by our research, but it represents a key line of investigation in understanding aerial insectivore population declines.

Other hazards associated with urbanization are also evident. Among these, perhaps the most notable in our results are the differences in Hg concentrations. The relationship between Hg in the aquatic environment and bioaccumulation of Hg in Tree Swallows indicates not only a danger from Hg toxicity, but also a vulnerability to the transfer of other contaminants from aquatic systems, such as selenium, PCBs, and emerging contaminants. Further describing urbanization at a finer level of resolution than the urban-protected dichotomy will also be an important step in predicting the linked effects of urbanization, climate, and water quality on aerial insectivores. For instance, continued refinement of indices of urbanization, such as the USI we developed for this study, will enable improved quantification of the impacts of both well recognized as well as new urban stressors across land-use gradients.

Tree Swallows, however, may be unique in their responses to urbanization, and other aerial insectivorous species might fare differently. Foraging and nestling strategies, and dietary preferences likely all figure into individual species’ responses to urbanization. For instance, altered vegetation structure and composition in urban habitats may be detrimental to the foraging efforts of salliers such as flycatchers (Schneider and Miller 2014). Cavity-nesters like Tree Swallows may benefit from the proliferation of artificial nest boxes (Norris et al. 2018) and the open-water environments of...
impounded urban rivers, while nesting sites for otherwise urban-tolerant species, such as Chimney Swifts (COSEWIC 2018) and Common Nighthawks (B Brigham 1989), have declined due to changes in building construction. Overall, the joint effects of urbanization, water quality, and climate change on Tree Swallows and other aerial insectivorous birds are a complex puzzle, yet an important one to solve in order to mitigate continued population losses of this guild.

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Literature Cited

Alberts, J. M., S. M. P. Sullivan, and A. Kautzka. 2013. Riparian swallows as integrators of landscape change in a multiuse river system: implications for aquatic-to-terrestrial transfers of contaminants. Science of the Total Environment 463–464:42–50.

Allan, J. D. 2004. Influence of land use and landscape setting on the ecological status of rivers. Limnietica 23:187–198.

Andrew, S. C., L. L. Hurley, M. M. Mariette, and S. C. Griffith. 2017. Higher temperatures during development reduce body size in the zebra finch in the laboratory and in the wild. Journal of Evolutionary Biology 30:2156–2164.

Ardia, D. R. 2013. The effects of nestbox thermal environment on fledging success and haematocrit in Tree Swallows. Avian Biology Research 6:99–103.

Ardia, D. R., C. B. Cooper, and A. Dhondt. 2006. Warm temperatures lead to early onset of incubation, shorter incubation periods and greater hatching asynchrony in Tree Swallows Tachycineta bicolor at the extremes of their range. Journal of Avian Biology 37:137–142.

Arguez, A., J. Durre, S. Applequist, M. Squires, R. Vose, X. Yin, and R. Bilotta. 2010. NOAA’s U.S. climate normals (1981–2010). Subset: monthly normals, OH Columbus Vly Crossing, NOAA National Centers for Environmental Information. 2019. https://doi.org/10.7289/V5PN93JP

Bartoń, K. 2018. MuMin: Multi-model inference. http://github.com/cran/MuMin

Beare, L. 2018. Temperatures in excess of critical thresholds threaten nestling growth and survival in A rapidly-warming arid savanna: a study of Common Fiscals. PLoS ONE 8:103-114.

Bein, K. 2018. MuMIn: Multi-model inference. http://github.com/cran/MuMin

Bearhop, S., D. R. Thompson, S. Waldron, I. C. Russell, G. Alexander, and R. W. Furness. 1999. Stable isotopes indicate the extent of freshwater feeding by cormorants Phalacrocorax carbo shot at inland fisheries in England. Journal of Applied Ecology 36:75–84.

Becker, M. E., and P. J. Weisberg. 2015. Synergistic effects of spring temperatures and land cover on nest survival of urban birds. Condor 117:18–30.

Bellmore, J. R., and C. V. Baxter. 2014. Effects of geomorphic process domains on river ecosystems: a comparison of floodplain and confined valley segments. River Research and Applications 30:617–630.

Bigelow, D. P., and A. Borchers. 2012. Major uses of land in the United States. EIB-178. U.S. Department of Agriculture, Economic Research Service, Washington, D.C., USA.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506–519.

Boening, D. W. 2000. Ecological effects, transport, and fate of mercury: a general review. Chemosphere 40:1335–1351.

Böhning-Gaese, K., M. L. Taper, and J. H. Brown. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? Conservation Biology 7:76–86.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geagne, J. R. Poulsen, H. Stevens, and S. W. Jada-Simone. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Bourret, A., M. Bélisle, F. Pelletier, and D. Garant. 2015. Multidimensional environmental influences on timing of breeding in a tree swallow population facing climate change. Evolutionary Applications 8:933–944.

Brasso, R. L., and D. A. Cristol. 2008. Effects of mercury exposure on the reproductive success of Tree Swallows (Tachycineta bicolor). Ecotoxicology 17:133–141.

Bigham, R. M. 1989. Roost and nest sites of Common Nighthawks: Are gravel roofs important? Condor 91:122–124.

Brown, D. G., K. M. Johnson, T. R. Loveland, and D. N. Theobald. 2005. Rural land-use trends in the conterminous United States, 1950–2000. Ecological Applications 15:1851–1863.

Caban, G., and J. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Sciences USA 93:10844–10847.

Catry, I., T. Catry, P. Patto, A. M. A. Franco, and F. Moreira. 2015. Differential heat tolerance in nestlings suggests sympatric species may face different climate change risks. Climate Research 66:13–24.

Chamberlain, D., B. Hatchwell, and K. J. Gaston. 2009. Avian productivity in urban landscapes: a review and meta-analysis. Ibis 151:1–18.

Condon, A. M., and D. A. Cristol. 2009. Feather growth influences blood mercury level of young songbirds. Environmental Toxicology and Chemistry 28:395–401.

COSEWIC. 2018. COSEWIC assessment and status report on the Chimney Swift Chauteria pelagica in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada (Species at Risk Public Registry). xii + 63 pp.

Cox, A. R., R. J. Robertson, B. C. Fedy, W. B. Rendell, and F. Bonier. 2018. Demographic drivers of local population decline in Tree Swallows (Tachycineta bicolor). Condor 120:842–851.

Crick, H. Q. P. 2004. The impact of climate change on birds. Ibis 146:48–56.

Crooks, K. R., A. V. Suarez, and D. T. Bolger. 2004. Avian assemblages along a gradient of urbanization in a highly fragmented landscape. Biological Conservation 115:451–462.

Cunningham, S. J., R. O. Martin, C. L. Hojem, and P. A. R. Hockey. 2013. Temperatures in excess of critical thresholds threaten nestling growth and survival in A rapidly-warming arid savanna: a study of Common Fiscals. PLoS ONE 8: e74613.

Davis, B. P., S. M. P. Sullivan, and K. Stefanik. 2017. Reductions in fish-community contamination following lowhead dam removal linked more to shifts in food-web structure than sediment pollution. Environmental Pollution 231:671–680.

Driscoll, C. T., et al. 2007. Mercury contamination in forest and freshwater ecosystems in the Northeastern United States. BioScience 57:17–28.
interspecific concordance inform guild-level population trends for aerial insectivorous birds. Ecography 39:774–786.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of $^{15}$N along food chains: further evidence and the relation between $^{15}$N and animal age. Geochimica et Cosmochimica Acta 48:1135–1140.

Monroe, A. P., K. K. Hallinger, R. L. Brasso, and D. A. Cristol. 2008. Occurrence and implications of double brooding in a southern population of Tree Swallows. Condor 110:382–386.

Moore, J. W., and B. X. Semmens. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters 11:470–480.

Muldal, A., H. L. Gibbs, and R. J. Robertson. 1985. Preferred nest spacing of an obligate cavity-nesting bird, the Tree Swallow. Condor 87:356–363.

Naef-DuenaZer, B., and M. U. Gruetbeler. 2016. Post-fledging survival of altricial birds: ecological determinants and adaptation. Journal of Field Ornithology 87:227–250.

Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Application 3:209–212.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences USA 98:166–170.

Nebel, S. A., Mills, J. D. Mcracker, and P. D. Taylor. 2010. Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation & Ecology 5:1.

Newhouse, M. J., P. P. Marra, and L. S. Johnson. 2008. Reproductive success of House Wrens in suburban and rural landscapes. Wilson Journal of Ornithology 120:99–104.

Nooker, J. K., P. O. Dunn, and L. A. Whittingham. 2005. Effects of food abundance, weather, and female condition on reproduction in Tree Swallows (Tachycineta bicolor). Auk 122:1225–1238.

Norris, A. R., K. E. H. Aitken, K. Martin, and S. Pokorny. 2018. Nest boxes increase reproductive output for Tree Swallows in a forest grassland matrix in central British Columbia. PLoS ONE 13:e0204226.

North American Bird Conservation Initiative Canada. 2012. The state of Canada’s birds, 2012. Environment Canada, Ottawa, Ontario, Canada.

Ohio Environmental Protection Agency. 2014. Scioto River watershed. Columbus, Ohio, USA. https://epa.ohio.gov/dsw/tml/SciotoRiver

Oke, T. R. 1982. The energetic basis of the urban heat island. Quarterly Journal of the Royal Meteorological Society 108:1–24.

Parnell, A. C., R. Inger, S. Bearhop, and A. L. Jackson. 2010. Source partitioning using stable isotopes: coping with too much variation. PLoS ONE 5:e9672.

Parnell, A., and A. Jackson. 2013. SIAR: stable isotope analysis in R. https://cran.r-project.org/package=siar

Parnell, A. C., D. L. Phillips, S. Bearhop, B. X. Semmens, E. J. Ward, J. W. Moore, A. L. Jackson, G. Grey, D. J. Kelly, and R. Inger. 2013. Bayesian stable isotope mixing models. Environmetrics 24:387–399.

Peig, J., and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118:1883–1891.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293–320.

Pipoly, I., V. Bokony, G. Seress, K. Szabo, and A. Liker. 2013. Effects of extreme weather on reproductive success in a temperate-breeding songbird. PLoS ONE 8:e80033.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

QGIS Development Team. 2017. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org/

Quinney, T. E., and C. D. Ankney. 1985. Prey size selection by Tree Swallows. Auk 102:245–250.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Reavie, E. D., T. M. Jicha, T. R. Angradi, D. W. Bolgrien, and B. H. Hill. 2010. Algal assemblages for large river monitoring: comparison among biovolume, absolute and relative abundance metrics. Ecological Indicators 10:167–177.

Rencher, A. C. 1995. Methods of multivariate analysis. John Wiley and Sons, New York, New York, USA.

Rendell, W. B., and R. J. Robertson. 1993. Cavity size, clutch-size and the breeding ecology of Tree Swallows Tachycineta bicolor. Ibis 135:305–310.

Rimmer, C. C., K. P. Mcfarland, D. C. Evers, E. K. Miller, Y. Aubry, D. Busby, and R. J. Taylor. 2005. Mercury concentrations in Bicknell’s thrush and other insectivorous passerines in Montane forests of northeastern North America. Ecotoxicology 14:223–240.

Rimmer, C. C., E. K. Miller, K. P. McFarland, R. J. Taylor, and S. D. Faccio. 2010. Mercury bioaccumulation and trophic transfer in the terrestrial food web of a montane forest. Ecotoxicology 19:697–709.

Rious-Paquette, S., F. Pelletier, D. Garant, and M. Bélisle. 2014. Severe recent decrease of adult body mass in a declining insectivorous bird population. Proceedings of the Royal Society B 281:20140649.

Rodewald, A. D., and M. H. Bakermans. 2006. What is the appropriate paradigm for riparian forest conservation? Biological Conservation 128:193–200.

Rodewald, A. D., L. J. Kearns, and D. P. Shustack. 2013. Consequences of urbanizing landscapes to reproductive performance of birds in remnant forests. Biological Conservation 160:32–39.

Rodriguez, S., and E. Barba. 2016. Nestling growth is impaired in Bicknell’s thrush and other insectivorous passerines in Montane forests of northeastern North America. Ecological Monographs 76:1–14.

Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11:141–156.

Rotenborn, S. C. 1999. Predicting the impacts of urbanization on riparian bird communities. Biological Conservation 88:289–299.

Rowse, L. M., A. D. Rodewald, and S. M. P. Sullivan. 2014. Pathways and consequences of contaminant flux to Acan- dian flycatchers (Empidonax virescens) in urbanizing land- scapes of Ohio, USA. Science of the Total Environment 485–486:461–467.

Roy, A. H., A. D. Rosemond, M. J. Paul, D. S. Leigh, and J. B. Wallace. 2003. Stream macroinvertebrate response to catchment urbanisation (Georgia, U.S.A.). Freshwater Biology 48:329–346.

RStudio Team. 2016. RStudio: integrated development environment for R. RStudio, Boston, Massachusetts, USA. http://www.rstudio.com/.
Rubin, D. B. 1988. Using the SIR algorithm to simulate posterior distributions. Pages 395–402 In J. M. Bernardo, editor. Bayesian Statistics 3: Proceedings of the Third Valencia International Meeting, June 1–5, 1987. Oxford University Press, Oxford, UK.

Rumbold, S. N., and D. D. 2006. The unequal variance t-test is an underused alternative to Student’s t-test and the Mann-Whitney U test. Behavioral Ecology 17:688–690.

Schlesinger, M. D., P. N. Manley, and M. Holyoak. 2008. Seto, K. C., B. Guneralp, and L. R. Hutyra. 2012. Global forest clearing: identifying opportunities to avoid land use. Nature 488:295–300.

Schneider, S. C., and J. R. Miller. 2014. Response of avian communities to invasive vegetation in an urbanizing environment. Ecology 89: 2302–2314.

Schneider, S. C., and J. R. Miller. 2007. A database of avian blood spot examinations for exposure to environmental contaminants. Journal of Environmental Monitoring 9: 1183–1187.

Schwalm, C. R. 2006. Using the SIR algorithm to simulate posterior distributions. Pages 395–402 In J. M. Bernardo, editor. Bayesian Statistics 3: Proceedings of the Third Valencia International Meeting, June 1–5, 1987. Oxford University Press, Oxford, UK.

Schwalm, C. R. 2006. Using the SIR algorithm to simulate posterior distributions. Pages 395–402 In J. M. Bernardo, editor. Bayesian Statistics 3: Proceedings of the Third Valencia International Meeting, June 1–5, 1987. Oxford University Press, Oxford, UK.

Schulz, C., and A. Gliwicz. 2010. The impact of urbanization and the urban heat island effect on day to day temperature variation. Urban Climate 12:1–10.

Tegelhøj, P. G. 2017. A comparative study of insect abundance and reproductive success of barn swallows Hirundo rustica in two urban habitats. Journal of Avian Biology 48:846–853.

Townes, H. 1972. A weight-light Malaise trap. Entomological News 83:239–247.

Townsend, A. K., T. S. Sillett, N. K. Lany, S. A. Kaiser, N. L. Rodenhouse, M. S. Webster, and R. T. Holmes. 2013. Warm springs, early lay dates, and double brooding in a North American migratory songbird, the Black-throated Blue Warbler. PLoS ONE 8:e59467.

Tully, T., G. Dorrestein, and A. Jones, editors. 2009. Clinical tests. Pages 456. Handbook of avian medicine, T. N. Tully, G. M. Dorrestein, and A. K. Jones. Second edition. Elsevier Limited, New York, New York, USA.

Twining, C. W., J. T. Brenna, P. Lawrence, J. R. Shipley, T. N. Tollefson, and D. W. Winkler. 2016. Omega-3 long-chain polysaturated fatty acids support aerial insectivore performance more than food quantity. Proceedings of the National Academy of Sciences USA 113:10920–10925.

U.S. Census Bureau. 2010. TIGER/Line shapefile, 2010, 2010 state, Ohio, 2010 census block state-based. U.S. Census Bureau, Washington, D.C., USA.

U.S. Environmental Protection Agency (U.S. EPA). 2008. Urban heat island basics. In Reducing urban heat islands: compendium of strategies. Draft. https://www.epa.gov/heat-islands/heat-island-compendium

U.S. Geological Survey. 2014a. NLCD 2011 percent developed imperviousness (2011 edition, amended 2014) – National Geospatial Data Asset (NGDA) land use land cover. U.S. Geological Survey, Sioux Falls, South Dakota, USA.

U.S. Geological Survey. 2014b. NLCD2011 USFS percent tree canopy (cartographic version). U.S. Geological Survey, Sioux Falls, South Dakota, USA.

U.S. Geological Survey. 2018. Bird Banding Laboratory, Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Urban, M. C., D. K. Skelly, D. Burchsted, W. Price, and S. Lowery. 2006. Stream communities across a rural-urban landscape gradient. Diversity and Distributions 12:337–350.

Vander Zanden, M. J., and J. B. Rasmussen. 2001. Variation in 13C and 15N trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography 46:2061–2066.

Viertz, G. J., C. J. Walsh, and T. D. Fletcher. 2015. Urban hydrogeomorphology and the urban stream syndrome: treating the symptoms and causes of geomorphic change. Progress in Physical Geography 40:480–492.

Visser, A. M. E., A. J. Van Noordwijk, J. M. Tinbergen, C. M. Lessells, M. E. Visser, A. J. Van Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1999. Warmer springs lead to mistimed reproduction in Great Tits (Parus major). Proceedings of the Royal Society B 265:1867–1870.

Walsh, C. J., A. H. Roy, J. W. Feninella, P. D. Cottingham, P. M. Groffman, and R. P. Morgan. 2005. The urban stream syndrome: current knowledge and the search for a cure. Journal of the North American Benthological Society 24:706–723.
SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1442/full

DATA AVAILABILITY

Data are available in the Dryad Digital Repository (Sullivan et al. 2020): https://doi.org/10.5061/dryad.xpnvx0kdc