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Differences in urban arthropod communities may not limit the nestling diet of a generalist songbird☆

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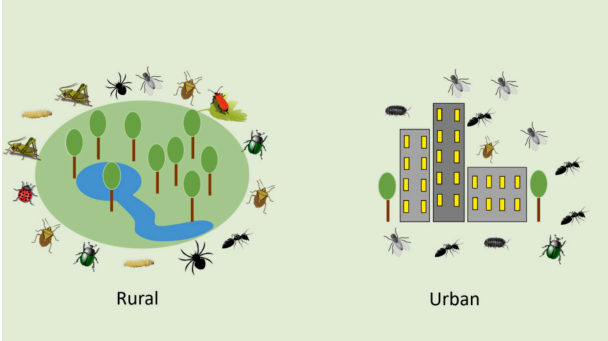
HIGHLIGHTS

- Urbanization alters predator-prey interactions.
- Average arthropod biomass, abundance, and diversity were lower in urban habitats.
- High-trophic level arthropods were less abundant in urban habitats on average.
- Nestlings in urban and rural habitats were fed the same average mass of arthropods.
- Rural nestlings were fed more spiders than urban nestlings.

GRAPHICAL ABSTRACT



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ABSTRACT

Anthropogenic land use, including urbanization, has caused population declines across diverse taxa including arthropods and songbirds. Declines in one taxa can impact other groups based on its role in a community. In particular, declines in lower trophic level taxa, such as arthropods, could have negative impacts on higher trophic level species. Here, we examined how urban arthropod communities compare to rural ones and how these differences may impact song sparrow (*Melospiza melodia*) nestlings living in urban and rural habitats. We quantified differences in the abundance, biomass, and diversity of arthropod communities between replicate urban and rural sites. At the same sites, we also compared the stomach contents of nestlings because song sparrows rely upon arthropod prey during development. We found that the arthropod community in urban habitats had lower average abundance, average biomass, and Simpson's diversity compared to rural habitats. The arthropod communities also significantly differed in the relative abundance of some higher trophic level taxa, such as spiders. However, we found no difference in the total stomach content mass, nor the mass of invertebrate food items in the stomachs of urban and rural nestlings. Thus, though urban habitats had lower availability of

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arthropods, possibly driven by the simplification of urban habitats, there was no evidence of a negative impact on the quantity of food provided to urban song sparrow nestlings.

1. Introduction

Anthropogenic environmental change is the leading cause of wildlife population declines worldwide (Tilman et al., 2017). Land use change or altered disturbance regimes from human activities can result in local extinctions of some species. When taxa are lost, community diversity is reduced, which can make other species within the community more vulnerable to disturbance (Elmqvist et al., 2003). The loss of taxa is often evident when charismatic species such as higher trophic level vertebrates decline. However, the loss of lower trophic level taxa, such as arthropods, can drive the decline of these charismatic species (Tallamy and Shriver, 2021). Recent studies show precipitous declines in arthropod abundance worldwide. Across 10 years of sampling, a 67 % decrease in arthropod biomass was observed in Germany (Seibold et al., 2019). Over 34 years of sampling in Puerto Rico, arthropod biomass declined ten to sixty-fold (Lister and Garcia, 2018). A 10-year period in Denmark saw a >80 % decline in arthropod abundance (Møller, 2019). These declines are often inferred to result from anthropogenic causes such as climate change and pesticide use, but additional factors such as land use changes can reduce arthropod populations (Attwood et al., 2008). The consequences of such declines in arthropod communities have yet to be fully realized (McIntyre, 2000; Butchart et al., 2010).

Urbanization has been predicted to increase by 1.2 million km^2 from 2012 to 2030 with dramatic consequences for wildlife (Seto et al., 2012). Studies have shown that urbanization not only reduces the abundance of many arthropod taxa, but also decreases the diversity of arthropod communities (Gossner et al., 2016; Fenoglio et al., 2020). Specifically, urbanization is associated with a reduced abundance of arthropods such as spiders, ground-dwelling beetles, and caterpillars (Martinson and Raupp, 2013; Seress et al., 2018; Delgado de la flor et al., 2020). Changes in the arthropod community can have consequences for higher trophic level organisms. For example, the loss of pollinators or predators can reduce ecosystem services in urban habitats (Bates et al., 2011; Bennett and Lovell, 2014; Dale and Frank, 2018). The loss of high trophic level arthropod taxa can also increase the abundance of herbivorous arthropods with consequences for the entire food web (McIntyre et al., 2001), in addition to the loss of ecosystem services (Losey and Vaughan, 2006). This loss of arthropod abundance and diversity can also have negative consequences for vertebrate predators such as insectivorous songbirds (Lister and Garcia, 2018; Møller, 2019; Planillo et al., 2020).

Songbirds might be especially vulnerable to arthropod declines because many species time breeding to coincide with insect emergence, allowing them to provide nestlings with high-protein diets critical to rapid development and fledging (Gray, 1993; Davis et al., 2005). Indeed, across a gradient of urbanization intensity arthropod and bird abundance are positively correlated, suggesting that urban bird populations are limited by the availability of arthropod prey (Planillo et al., 2020). Further evidence that declining arthropod abundance has negative consequences for songbirds is that lower arthropod abundance is linked to lower nestling body mass (yellow hammers, *Colaptes auratus,* Hart et al., 2006) and compromised fledging success (winchats, *Saxicola rubetra*, Britschgi et al., 2006). Understanding how variation in arthropod abundance in urban areas impacts songbirds requires determining how arthropod communities relate to nestling diet.

In this study we compared arthropod abundance, biomass, and community diversity across replicate urban ($n = 3$) and rural (n = 3) sites in Southwestern Virginia, USA. We expected to see lower arthropod abundance and biomass in urban areas. We especially expected lower abundance and biomass of high trophic level orders such as spiders (Lindeman, 1942). We also expected arthropod community diversity to be lower in urban areas (Chiari et al., 2010). To begin to explore the consequences of variation in arthropod communities for predators we also compared the stomach contents of nestling song sparrows (*Melospiza melodia*) from those same sites to determine how their diet differed. We expected urban nestlings to have a lower mass of stomach contents compared to rural nestlings. Additionally, we expected urban nestlings to have fewer higher trophic level taxa in their stomachs than rural birds.

2. Methods

2.1. Study area

We sampled arthropods and song sparrow nestlings from 3 urban and 3 rural sites near Blacksburg, Virginia, a temperate location in the Appalachian Mountains. These established study sites (Goodchild et al., 2022; Lane et al., 2021; Davies et al., 2018; Davies and Sewall, 2016), are characterized as the most urban or rural sites along an urbanization gradient, based on the quantification of urbanization described in Seress et al. (2014). Briefly, mean building density, number of cells with high building density, number of cells with paved surface, mean vegetation density, and number of cells with high vegetation density were calculated over 1 km^2 grids broken into 100 m × 100 m cells (Davies and Sewall, 2016). Principal component (PC) analyses were then used to select the most urban and most rural sites. We used ArcGIS Online to estimate the sizes of our study sites (Esri, 2024). Our urban sites are local university campuses (1.05 km^2, 0.51 km^2, and 0.33 km^2), while our rural sites include an experimental farm (0.80 km^2), a community park (0.49 km^2), and a riparian restoration site (0.25 km^2; Appendix Table A8). All sites included grassland or managed lawn appropriate for vacuum sampling of arthropods. The density of song sparrow adults at our rural sites was 117.53 per km^2, while urban habitat had 95.77 adults per km^2. We found 85.06 nests per km^2 in rural habitat, and 96.3 nests per km^2 in urban habitat (likely because urban parents were more likely to have multiple nests per year; Appendix Tables A9 and A10; Lane et al., 2023).

2.2. Arthropod sampling

We collected arthropods along transects using vacuum sampling. Four, fifty-meter transects were selected at each site, for a total of twelve rural and twelve urban transects (see Fig. 1 for examples). Each transect was sampled three times per year during the spring and summer in 2020 and 2021. In 2021 these transects were sampled once at the start of each month from May–July (Bennett and Lovell, 2014), but due to disruptions caused by COVID-19 sampling in 2020 occurred mid-May, early June, and early July. Starting locations for each transect were based on randomly selected song sparrow nests found in 2019. If the starting location was within 100 m of another transect, we randomly selected a different nest. Headings were then created using a random number generator which were reselected if they met one or both of the following criteria: 1) part of the transect would be impassable (e.g., it would go through a building), or 2) >50 % of the transect was impermeable surface (e.g., pavement). Any hazards along the transect were skipped, and this distance was added to the end of the transect. For example, a transect with 8 m of road would be 58 m long, although only 50 m would be sampled. Transects were subdivided into five 10 m long sections to prevent the vacuum from becoming blocked by debris.

We conducted vacuum sampling (Buffington and Redak, 1998; Perner et al., 2005) using a Black and Decker leaf blower with the included vacuum attachment on its highest power setting (120 MPH 90

CFM 40 V MAX Lithium-Ion Cordless Handheld Leaf Sweeper/Vacuum). Paint strainer bags (1 gal) were fastened to the opening of the vacuum using an elastic band. One site was sampled per day starting at 10 am, although start times were pushed back until any visible dew evaporated, or pushed to the next day in the event of rain. Date, ambient temperature, start time, and transect duration (to control for observer effort) were all recorded. All transects were sampled by the same observer. Each step by the observer was accompanied by a 180° sweep of the vacuum, keeping the tip against the substrate, whether that was ground, grass, or shrub. Samples were stored at $—20^{C}$ within three hours of collection until processing. An important caveat with vacuum sampling is that while it samples ground and shrub dwelling arthropods well (Cooper and Whitmore, 1990), it undercounts arboreal arthropods.

To quantify arthropods, samples were removed from their bags, and arthropods were manually separated from any debris (grass, mulch, trash, etc) and then sorted into order (Araneae, Diptera, Lepidoptera, Coleoptera, Isopoda, Orthoptera, Hymenoptera, Hemiptera, and 'other'). Each order was then individually counted and weighed (Fisher Science Education ALF64 balance) to the nearest ten-thousandth to determine wet mass.

2.3. Stomach contents assessment

In the summer of 2022, we collected 20 song sparrow nestlings from rural nests and 40 nestlings from urban nests for another study that required terminal collection. Briefly, we located nests using behavioral observation and systematic searching (Lane et al., 2023), and collected nestlings between 5 and 10 days old (average of 6.9 days old). Two nestlings were collected from each nest when possible (16 rural and 30 urban nestlings); in some nests, only a single nestling was collected (1 rural, 7 urban nestlings), and others had three individuals collected (3 rural and 3 urban nestlings). Within 5 min of parents visiting the nest with food, nestlings were euthanized via a lethal dose of inhaled isoflurane and stored at 4 °C for approximately 24 h. To maximize the use of collected specimens, we then dissected out the proventriculus and gizzard and stored their contents in Eppendorf tubes at −80 °C. We then massed stomach contents to the nearest ten-thousandth of a gram and invertebrate food items were separated from debris and vegetation using a dissecting microscope (Leica MZ7). We sorted invertebrates into taxonomic order (Araneae, Diptera, Lepidoptera, Coleoptera, Hymenoptera, Hemiptera, Gastropoda, and 'unidentifiable') and counted individuals conservatively (e.g. eight separate spider legs, a cephalothorax, and an abdomen would be counted as a single spider, while eight cephalothoraxes would be counted as eight individuals). Invertebrates outside of the listed orders and parts that could only be identified as invertebrates due to damage were categorized as 'unidentifiable.' We measured the total wet mass of all invertebrate food items to the nearest ten-thousandths of a gram.

2.4. Data analysis

2.4.1. Arthropod analysis

We conducted all analysis using the program R (R version 4.2.2; R Core Team, 2023). We analyzed the arthropod data with linear mixed effects models (LMMs) using the 'lme4' package (version 1.1.31; Bates et al., 2014). In each model site ID and/or transect ID were the random effects, while habitat type, Julian date as a continuous variable, and year were fixed effects. We ran two separate LMMs to test for habitat differences in arthropod abundance and arthropod biomass, respectively. The residuals from initial models were not normally distributed, so we applied a square root transformation to both datasets. Additionally, we ran multiple LMMs to test for habitat differences in the biomass of specific taxa, and negative binomial generalized linear mixed models (GLMMs) to test for habitat differences in the abundance of specific taxa. Model assumptions were checked using the 'performance' package (version 0.10.5; Lüdecke et al., 2021).

We calculated Simpson's diversity at the taxonomic level of order using the package 'phyloseq' (version 1.42.0; Ferraro and Cole, 1990; McMurdie and Holmes, 2013). While it is unusual to use Simpson's diversity above the level of family, we had only identified the arthropods to order. Simpson's diversity between habitat types was then compared using Kruskal-Wallis chi square testing. We performed PERMANOVA testing of Bray-Curtis matrices using the function 'adonis2' from the package 'vegan' (version 2.6–4) to determine differences in relative abundance of arthropod orders by habitat type, with site as a fixed effect (Dixon, 2003). Each PERMANOVA had 999 permutations.

2.4.2. Stomach content analysis

We used three separate models to test for habitat differences in (1) average nestling stomach content mass, (2) average invertebrate food item mass, and (3) average abundance of all invertebrate food items. Nestling age was included as a fixed variable, and nest of origin was included as a random effect to account for possible correlations among nestlings from the same nest. Differences in stomach content mass (square root transformed), invertebrate food mass (square root transformed), and both total abundance and individual order abundance (both square root transformed) were tested using LMMs. Finally, we tested for habitat differences in the presence of invertebrate orders in nestling stomach contents using multiple generalized linear mixed-effects models (GLMMs) with a binomial distribution to indicate the presence or absence of a given order. Once again we included nest origin as a random effect in these models.

Fig. 1. Satellite Imagery of Different Habitat Types. Examples of 50 m transects shown in yellow in both urban (left) and rural (right) habitats. Satellite imagery obtained from Google Earth (version 10.38.0.0).

3. Results

3.1. Arthropod community results

Rural and urban arthropod communities differed significantly in abundance, biomass, and diversity. We found that average arthropod abundance was higher in rural habitats than urban (Fig. 2) (SE = 0.16, df = 22, t value = −5.415, Pr(>|t|) <0.001). There was no effect of Julian date or year on the average arthropod abundance.

Rural habitats also had significantly higher average biomass (Fig. 2) (SE = 0.103, t value = −4.298, Pr(>|t|) = 0.013) than urban habitats. There was a significant positive effect of Julian date (SE = 0.006, df = 4, t value = 3.804, Pr(>|t|) <0.001) but no effect of year (Appendix Tables A4 and A5).

When we compared specific orders across habitat types we found that abundance and biomass were significantly higher in rural habitats for Araneae, Coleoptera, Lepidoptera, Orthoptera, and Hemiptera. The exceptions to this trend were Diptera, Hymenoptera, and 'Others,' which did not differ significantly in abundance between habitat types, and Isopoda, which did not differ significantly in biomass or abundance between habitat types (Table A1 in Appendix).

Simpson's diversity at the taxonomic level of order was significantly higher in rural habitats compared to urban ($p < 0.001$). We also found relative abundance of arthropods differed significantly between habitat types ($R^2 = 0.22$, F = 40.97, Pr(>F) = 0.001) and among sites ($R^2 = 0.055$, F = 2.60, Pr(>F) = 0.002), which is shown in Fig. 3.

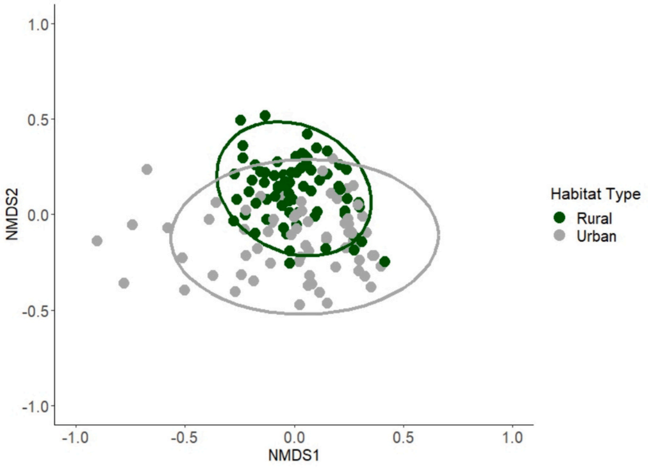

Fig. 3. Arthropod Community Differs by Habitat Type. Non-metric Multidimensional Scaling (NMDS) plot of rural and urban arthropod communities. The composition of arthropod communities differed between habitat types as measured through a Bray-Curtis dissimilarity matrix, which describes differences in the relative abundances of taxa within the community.

3.2. Stomach content results

We found no significant difference in total stomach content mass (SE = 0.054, t value = 0.261, Pr(>|t|) = 0.796), or invertebrate food item mass (SE = 0.03, t value = 0.987, (Pr(>|t|) = 0.332) between urban and rural song sparrow nestlings. However, the abundance of invertebrate food items, and the abundance of specific invertebrate orders differed by habitat (Tables A6-A7 in Appendix). Specifically, urban nestlings had a higher average abundance of invertebrate food items in their stomachs compared to rural nestlings (SE = 0.426, t value = 2.044, Pr(>|t| = 0.050). However, rural nestlings had a greater abundance of Araneae (SE = 0.153, t value = −2.121, Pr(>|t|) = 0.042) and a non-significant trend for Lepidoptera (SE = 0.205, t value = −1.722, Pr(>|t|) = 0.095), while urban nestlings had a higher abundance of Coleoptera (SE = 0.226, t value = 2.398, Pr(>|t|) = 0.024), and a non-significant trend for Hymenoptera (SE = 0.516, t value = 1.757, Pr(>|t|) = 0.089). There were no significant differences between urban and rural nestlings in the abundance of Hemiptera (SE = 0.172, t value = 0.012, Pr(>|t|) = 0.990), Gastropoda (SE = 0.232, t value = 1.587, (Pr(>|t|) = 0.130) or 'unidentifiable' arthropods (SE = 0.225, t value = 0.663, Pr(>|t|) = 0.513), (Table A2 in Appendix). Finally, we found no significant differences in the presence or absence of individual invertebrate orders by habitat type (Table A3 in Appendix).

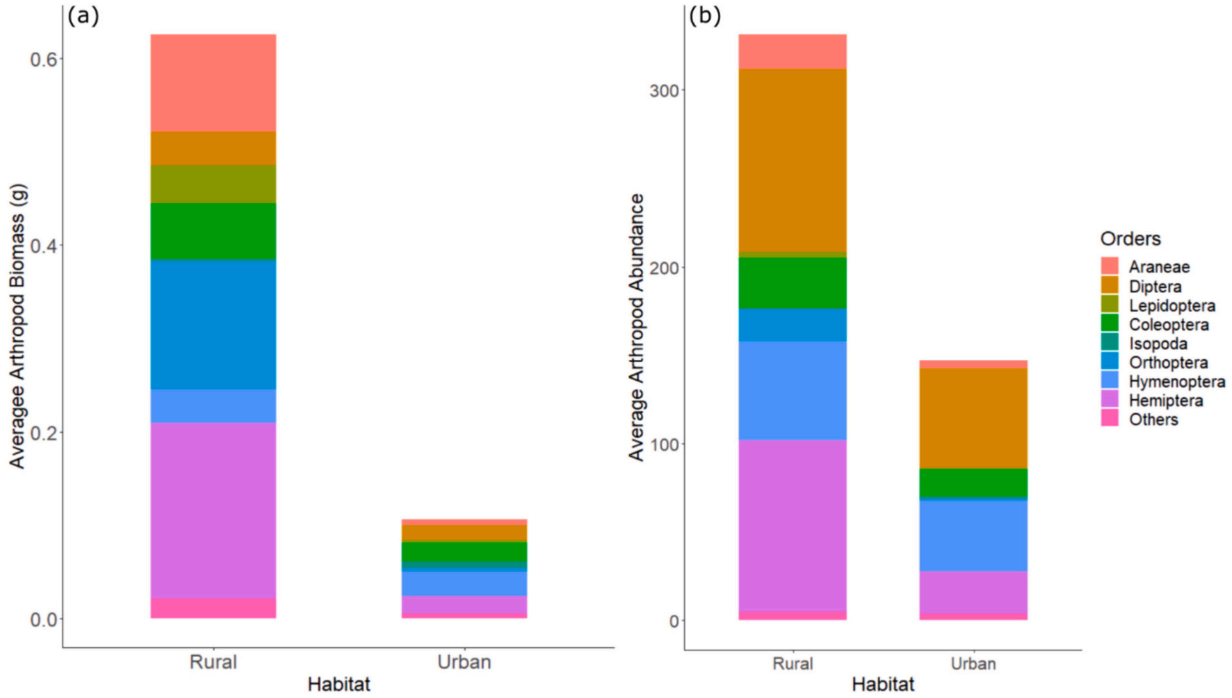

Fig. 2. Differences in Average Arthropod Abundance and Biomass by Habitat Type. Average arthropod biomass in grams (a) and abundance quantified as the average number of arthropods per transect (b) was lower in rural habitats than urban habitats. Stacked bars indicate the biomass and abundance of each taxa.

4. Discussion

Urbanization often lowers the abundance and biomass of some taxa, which can reduce community diversity (Fenoglio et al., 2020). Here, we examined how urbanization impacts the arthropod community and the diet of nestling song sparrows, which rely on arthropods, by comparing replicate urban and rural sites in Southwestern Virginia. We found lower average abundance, biomass, and diversity of arthropods in urban habitats. Despite this lower biomass and abundance of arthropod prey in urban areas, we found no difference in stomach content mass between urban and rural nestlings. Thus, in our study system we found no evidence that developing songbirds are negatively impacted by lower arthropod abundance or biomass. The effects of urbanization we measured on arthropod abundance and biomass may not be of sufficient magnitude to negatively impact nestling song sparrows. Additionally, our study species of song sparrows are generalists and may have shifted their diet in urban areas to cope with lower availability of arthropod prey.

4.1. Lower arthropod abundance and biomass in urban areas

We found that urban habitats had lower average arthropod abundance and average biomass than rural habitats (Fig. 2; Appendix Figs. A3 and A4). Of note, the biomass and abundance of Araneae, Coleoptera, Lepidoptera, Orthoptera, and Hemiptera were all lower in urban habitats compared to rural. It is important to note that while vacuum sampling performs well collecting both ground and shrub dwelling arthropods, arboreal arthropods, which have been found to make up portions of song sparrow diet (Smith, 1978), are often underrepresented. Lower abundance and biomass of arthropods could result from differences in resource availability, habitat simplification, or disturbance. Urban areas often have fragmented habitat and less greenspace (Liu et al., 2016), which can reduce available resources and limit which arthropod taxa are present (McIntyre, 2000; Shochat et al., 2004; Philpott et al., 2014). In contrast, rural communities often have access to extensive green space and are typically not as limited by resource availability, except for some desert habitats (Faeth et al., 2005; Miles et al., 2019). Urban habitats are also often characterized by more frequent human disturbance, such as lawn mowing or pesticide use, which has been shown to reduce arthropod abundance (Sattler et al., 2010; Siviter et al., 2023) or, in some cases, to increase the prevalence of herbivorous arthropod species while reducing the prevalence of higher trophic level arthropod predators (Raupp et al., 2010; Szczepaniec et al., 2011). Our findings therefore contribute to growing evidence that urbanization negatively impacts arthropod abundance and biomass.

Our finding of lower abundance and biomass of Araneae is of particular interest because lower abundance of such predator taxa suggests there is less prey available to support arthropods at higher trophic levels (Shochat et al., 2004). Additionally, a lower abundance of high trophic level arthropods could, in turn, limit resources for vertebrate predators. High trophic level arthropods are often high in protein, which could be especially important to vertebrate predators (Kohl et al., 2015). This is true for songbirds, as many species rely upon not only high trophic level arthropods such as Araneae, but other preferred protein rich herbivorous orders, such as Lepidoptera, to feed their young (Cowie and Hinsley, 1988; Kaspari and Joern, 1993; Seress et al., 2018). Loss of this preferred protein rich arthropod prey has detrimental effects on songbirds ranging from reduced breeding success to worsened offspring body condition and reduced population sizes (Illera and Díaz, 2006; Planillo et al., 2020; Grames et al., 2023). Though prior studies in our system have found higher nest success in urban areas due to reduced nest predation (Lane et al., 2023), it is not yet clear if altered arthropod abundance by habitat type, particularly Araneae and Lepidoptera, could impact nestling condition, future survival, and reproduction.

4.2. Arthropod diversity differs by habitat

Our urban arthropod community has lower Simpson's diversity than our rural community. This is consistent with a recent meta-analysis concluding that urban areas have less diverse arthropod communities than rural ones (Fenoglio et al., 2020), although there are often taxon specific exceptions (Jones and Leather, 2012; Chatelain et al., 2023). A limitation to our approach is that we sorted arthropods by order, which underestimates diversity that could exist within orders. However, other studies characterizing arthropods by family or genus also found lower arthropod diversity in urban habitats (Bang and Faeth, 2011; Chatelain et al., 2023). Lower community diversity is associated with lower community resilience due to less redundancy of functional niches (Elmqvist et al., 2003; Mori et al., 2013). This in turn has the potential for cascading effects throughout the entire community from producers to vertebrate predators, as arthropod diversity often influences the success of other taxa (Bennett and Gratton, 2013; Bowler et al., 2019).

We also found differences between urban and rural arthropod communities based on the relative abundances of taxa present (Fig. 3), which is not surprising given the other documented differences. Differences in relative abundance could be driven by factors outside of the scope of this project such as microsite diversity, producer biomass, or interspecies interactions (Greenberg and McGrane, 1996; Perner et al., 2005; Philpott et al., 2014; Miles et al., 2019). Another potential driver for differences in the arthropod community is habitat simplification (Scott et al., 2024). Urbanization increasing the amount of impermeable surfaces is often accompanied by habitats becoming more simplified (McKinney, 2008). Future work could disentangle whether differences in the arthropod community are due to urbanization specifically, or if habitat simplification in any form drives community change. These differences in diversity suggest that the urban arthropod community could be at greater risk of further disturbance (Tilman, 1996), which could in turn put vertebrate predators in urban areas at greater risk of population decline.

4.3. Nestling stomach content, but not mass of food items, differs by habitat

There were no significant differences in urban and rural nestling stomach content mass, nor was there a difference in the mass of invertebrate food items. Urban nestlings did have a significantly higher average abundance of invertebrate prey items in their stomachs, suggesting that more items were required to reach stomach mass equal to that of rural birds. However, prior work in this system found no significant difference in the visitation rate of urban versus rural song sparrow parents, suggesting that urban parents were either not limited by arthropod abundance or were able to compensate for lower prey availability (Lane et al., 2023). The lower density of adult song sparrows in urban habitats could reduce competition for prey, but many other species rely on arthropods in urban areas and we have no data on interspecific competition. The finding that the mass of stomach contents did not differ between habitat types suggests that song sparrow parents provide similar amounts of food to their offspring in both habitats, though the types and nutritional quality of arthropods may differ. Prior studies of nestling diets have reported that songbirds rely upon spiders and caterpillars as a rich source of protein and fat (Ramsay and Houston, 2003; Wiesenborn, 2011; Razeng and Watson, 2015). We found that the stomachs of rural nestlings had significantly more spiders and a non-significant trend of more caterpillars than those of urban nestlings (Appendix Table A2), suggesting rural nestlings have access to more protein and fat-rich food sources. The stomachs of urban nestlings contained significantly more beetles, however, which have also been shown to have high concentrations of fats and protein (Ramsay and Houston, 2003; Razeng and Watson, 2015). Urban nestlings also had a non-significant trend of more ants in their stomachs than rural birds, though ants are lower in protein and fats than prey such as spiders, caterpillars, or beetles (Razeng and Watson, 2015). Thus, though we found lower abundance and biomass of arthropods in urban habitats, our analysis of song sparrow nestling stomach contents shows that birds in both habitats have equal masses of invertebrate prey. It is important to note that, though songbird nestlings rely upon high-protein invertebrate foods during development (Birkhead et al., 1999), song sparrows are a generalist species that may more readily adjust its diet to different invertebrate taxa (Stofberg et al., 2019). Studies of specialist species may yield very different findings, and the consequences of any adjustments in the diet of urban nestlings for reproduction and survival remain unknown.

5. Conclusion

Urbanization threatens a wide variety of wildlife. Understanding the consequences of urbanization for wildlife requires research across levels of biological organization from individual condition and fitness to impacts on population size and community structure. Measuring the impacts of urbanization on lower trophic level taxa such as arthropods is crucial, as the loss of lower trophic level organisms can have consequences for both their predators and entire communities (Tallamy and Shriver, 2021). However, changes in lower trophic levels may need to reach a tipping point before consequences are seen for higher trophic level predators. In this study, we did not find any differences in the mass of stomach contents of nestling song sparrows despite a lower abundance of arthropods in urban habitats relative to rural ones. Though we find no evidence of negative consequences of altered arthropod communities for the diet of song sparrow nestlings, future work on diverse predator species and community dynamics is critical to understanding the consequences of urbanization across trophic levels.

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CRediT authorship contribution statement

Isaac J. VanDiest: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Korin R. Jones:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Taylor E. Fossett:** Writing – review & editing, Project administration, Investigation. **Samuel J. Lane:** Writing – review & editing, Project administration, Investigation, Conceptualization. **Kendra B. Sewall:** Writing – review & editing, Writing – original draft, Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data underlying this manuscript are made accessible through the Virginia Tech Data Repository at https://doi.org/10.7294/24773736

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Ethics statement

All animals were collected under the relevant federal and state permits from USDS, USFWS, VA DGIF, and Institutional Care and Use Committee at Virginia Tech.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.176518.

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