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Camera traps at nest boxes reveal consistent importance of Lepidoptera in Eastern Bluebird (*Sialia sialis*) nestling diets

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ABSTRACT

North American insectivorous bird populations have declined precipitously in recent decades. A more robust understanding of their nutritional needs, particularly during the breeding season, can help guide conservation and habitat restoration efforts. We monitored 38 Eastern Bluebird (*Sialia sialis*) broods in New Castle County, Delaware, USA, with camera traps over four breeding seasons to assess the composition of the nestling diet and examine how food provisioning varies over the season and between adult sexes. From the photos, we identified the prey adult bluebirds brought to nestlings to the lowest possible taxonomic level. Based on a review of 8,128 provisioning visits, caterpillars (i.e., larval Lepidoptera and Symphyta) were the predominant prey brought to the nest by both males and females in all years of the study and in both the first and second broods of each season. Most caterpillars are host-plant specialists, and native plants host a much greater number of caterpillar species than do non-native plants. The importance of caterpillars in the diet of Eastern Bluebirds and perhaps many other insectivorous birds highlights the urgent need to conserve native plants already present and make them a central component of habitat restoration.

Las cámaras trampa instaladas en cajas nido revelan la importancia constante de los lepidópteros en la dieta de los polluelos del azulejo garganta canela, *Sialia sialis*

RESUMEN

Las poblaciones de aves insectívoras de América del Norte han disminuido drásticamente en las últimas décadas. Una comprensión más sólida de sus necesidades nutricionales, especialmente durante la temporada de cría, puede ayudar a orientar los esfuerzos de conservación y restauración del hábitat. Hemos monitoreado 38 nidadas de azulejo garganta canela (*Sialia sialis*) en New Castle, Delaware, EEUU, con cámaras trampa, durante cuatro temporadas de cría, para evaluar la composición de la dieta de los polluelos y examinar cómo varía el aprovisionamiento de alimento a lo largo de la temporada

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y entre los sexos de los adultos. A partir de las fotos, identificamos las presas que los adultos llevaban a los polluelos hasta el nivel taxonómico más bajo posible. Basándonos en un análisis de 8128 visitas de aprovisionamiento, las orugas (es decir, larvas de lepidópteros y simfitas) fueron la presa predominante que tanto los machos como las hembras llevaron al nido en todos los años del estudio y en la primera y segunda nidada de cada temporada. La mayoría de las orugas son especialistas en plantas hospedadoras, y las plantas autóctonas albergan un número mucho mayor de especies de orugas que las plantas no autóctonas. La importancia de las orugas en la dieta de *Sialia sialis* y quizás de muchas otras aves insectívoras destaca la urgente necesidad de conservar las plantas autóctonas ya presentes y convertirlas en un componente central de la restauración del hábitat.

Recent analyses suggest that populations of breeding birds have declined in North America by nearly three billion individuals since 1970 (Rosenberg et al. 2019). When data are filtered for terrestrial insectivores and granivores, birds that rely on insects, particularly during the breeding season, have declined on average 10 million individuals per species, while populations of birds that do not rear their young on insects show no significant changes over the past 50 years (Tallamy and Shriver 2021). This detail, coupled with numerous reports of temperate zone insect declines (Harris et al. 2019; Bell et al. 2020; Wagner, Grames, et al. 2021; Edwards et al. 2025), implies a link between the quantity of insect prey available for breeding birds and reproductive output. Indeed, the link between insect availability and brood size, fledging success, and nestling weight has been empirically demonstrated numerous times (Narango et al. 2018; Seress et al. 2018; Bowler et al. 2019; Evans et al. 2024). It follows, then, that successful conservation of insectivorous bird species must include conservation of insect prey essential to their breeding success.

Although the nestling diets of some bird species have been investigated through direct observation and neck ligatures over the last century (e.g., Judd 1901; Pinkowski 1978), food items of most species were typically described in general terms (e.g., “invertebrates”) and were rarely quantified. Recent advances in molecular scatology and stable isotope analyses have provided powerful tools for more taxonomically specific qualitative measures of nestling diets (Jedlicka et al. 2013, 2017; White and Dawson 2021) but more complete measures of diurnal and seasonal diet changes over time are logistically challenging with these techniques.

Reviews suggest that critical macronutrients for nestlings are derived chiefly from invertebrates, even in species that are frugivorous, nectarivorous, or granivorous as adults. For example, nutrient-rich Lepidoptera (butterflies and moths), Coleoptera (beetles), Orthoptera (grasshoppers and crickets), and Araneae (spiders) are consumed more frequently than Diptera (flies), Hemiptera (true bugs), Odonata (dragonflies and damselflies), and aculeate Hymenoptera (wasps) (Razeng and Watson 2015; reviewed by Kennedy 2019). Dietary studies with finer resolution (i.e., to family) are rare and even fewer studies have explored how prey species brought to the nest vary with time of season and parental sex (but see Evans et al. 2024 and references therein for review).

Perhaps the most consistent result from existing studies of nestling diets is the importance of caterpillars (Cooper 1988; Janzen 1988; Kennedy 2019). Redford and Dorea (1984) credit this dietary bias to caterpillars' low percentage of undigestible chitinous exoskeleton as well as their high lipid and protein content. Relative to other groups such as Diptera, Coleoptera, and Hemiptera, caterpillars are also an excellent source of potassium and zinc (Razeng and Watson 2015). Robel et al. (1995) found that Lepidoptera contained higher calcium content than Orthoptera, Hemiptera, Diptera, and spiders. Most notable, however, are the unique contributions of carotenoids to nestling diets. Caterpillars provide far more essential carotenoids for birds than other invertebrate prey do, particularly during the nesting season when alternative plant sources of carotenoids, such as berries, are less common or absent (Eeva et al. 2010; Kennedy 2019). Carotenoids play important roles in immune system function, color vision, and DNA repair (in addition to their role in plumage coloration in some birds) (Biard et al. 2006; Sillanpää et al. 2008).

Given the important roles caterpillars play in the reproduction of insectivorous birds, we sought to measure the frequency with which caterpillars are supplied to nestlings relative to other prey taxa and how that frequency may change as nestlings age, across nesting attempts, and between male and female parental providers. Caterpillar abundance changes throughout the season, with a great flush of palatable geometrids in the spring, followed by more diverse but less abundant erebids, noctuids, and notodontids (Wagner 2025). We used Eastern Bluebirds (*Sialia sialis*; hereafter "bluebird") as a model species to quantify the food items provisioned to nestlings over four breeding seasons using cameras at nest boxes of breeding pairs in Delaware, USA. Bluebirds are ideal candidates for such studies because they readily occupy artificial nest boxes, they can be sexed by plumage, both sexes provision nests, they can produce up to three broods per breeding season, and they are relatively undisturbed by human visits to the nest (Hatch and Parlanti 2009). They also have been the subject of previous foraging studies that found, among other things, that females deliver more prey items than males (Pinkowski 1978), although the taxonomy of these prey has not been established.

We hypothesized that Eastern Bluebird nestling diets would be determined by extrinsic and intrinsic factors related to insect availability and parental sex. We predicted that (1) nestling diets would contain a high proportion of caterpillars relative to other taxa throughout the breeding season because of their high nutritional value, (2) prey composition would be different during the second brood when caterpillar abundance is balanced by maturing Orthoptera and other invertebrates, and (3) female bluebirds would provision nestlings more often than males would.

Methods

Study site and nest boxes

We conducted this study during the bluebird breeding season (Apr–Aug) from 2015 to 2018 at Mt. Cuba Center in Hockessin, Delaware, USA, a 4 km^2 private estate consisting of a mosaic of Piedmont, mid-Atlantic, deciduous forest, and meadows. Dominant trees at the study site comprise black cherry (*Prunus serotina*), white oak (*Quercus alba*), northern red oak (*Quercus rubra*), black tupelo (*Nyssa sylvatica*), black willow (*Salix nigra*), dogwood (*Cornus* spp.), hickory (*Carya* spp.), eastern American black walnut (*Juglans nigra*), red maple (*Acer rubrum*), and tulip poplar (*Liriodendron tulipifera*). Dominant meadow species include bluestem (*Andropogon virginicus*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), mountain-mint (*Pycnanthemum* spp.), milkweed (*Asclepias* spp.), goldenrod (*Solidago* spp.), switchgrass (*Panicum virgatum*), and American asters (*Symphyotrichum* spp.). More than 70 nest boxes are installed in the native meadows and woodland edges and are regularly occupied by cavity-nesting birds, including bluebirds, Tree Swallows (*Tachycineta bicolor*), and House Wrens (*Troglodytes aedon*). Volunteers monitored the nest boxes each week from April to August and collected data on the number of eggs and the number and approximate ages of nestlings. We used 24 nest boxes in this study (Fig. 1) and identified the species using the box based on nest characteristics or by observing the parents.

Camera deployment

We mounted GoPro® HERO cameras (GoPro Hero 3+ and GoPro® Hero Original) on the roofs of nest boxes with bluebird occupants to provide color images of bluebird prey items brought to nestlings. Bluebirds had a tendency to alight on the roof of the nest box with prey in their bills before entering the box to feed their young, which facilitated the capture of clear images (A. Kennedy, personal observation; Fig. 2). We chose these cameras instead of

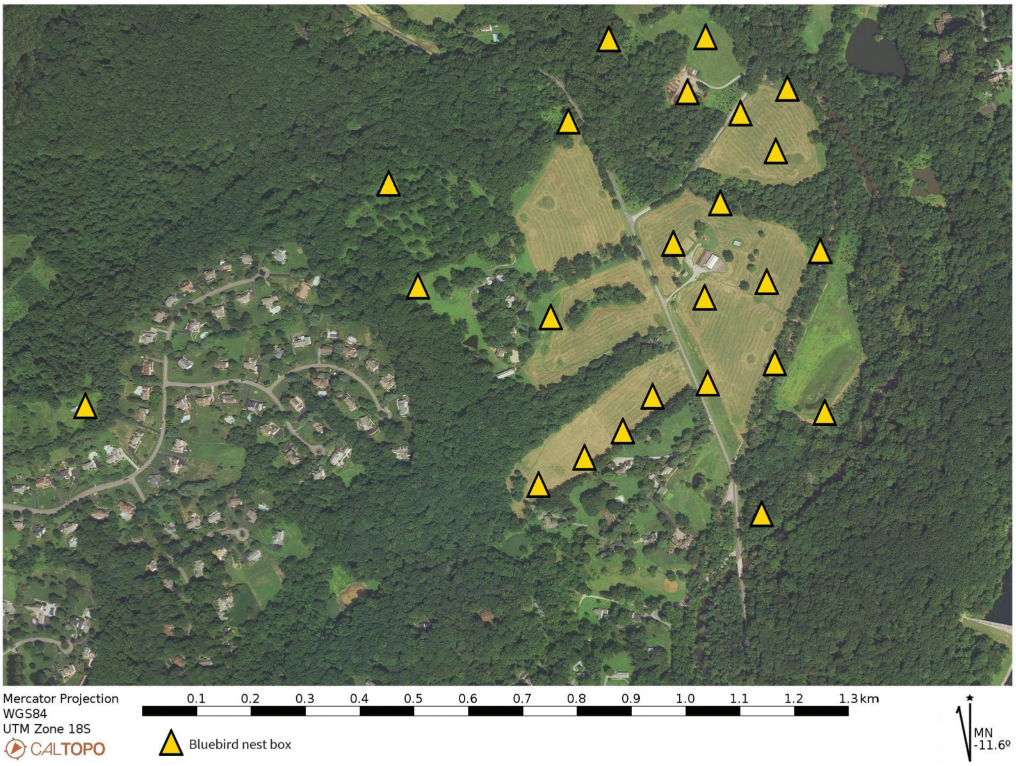

Figure 1. Satellite image of Mt. Cuba Center and environs, New Castle County, Delaware. Yellow triangles indicate nest boxes used in this study.

Figure 2. A female Eastern Bluebird on the roof of a nest box, before provisioning nestlings with prey (*Amphipyra pyramidea* caterpillar) at Mt. Cuba Center, New Castle County, Delaware, June 2016. Photo taken with a GoPro® HERO 3+.

traditional trail cameras because of their affordability, small size (61 mm × 41 mm × 30 mm), and ability to withstand high temperatures, precipitation, and field conditions. Although not motion- or light-activated, these GoPro® HERO models can be set to take images at a predetermined time interval. We used the 1 s interval setting on GoPro® HERO 3+ cameras and the 0.5 s interval on the GoPro® HERO Original, which does not have an option for 1 s intervals.

After we mounted each camera, we monitored bluebird pairs to ensure that the presence of the camera did not disrupt their ability or willingness to land on the box or provision their young. Without exception, all bluebird pairs acclimated and resumed their usual behaviors within minutes. We placed cameras at occupied nest boxes each morning during the breeding season between 0500 h and 0800 h (Eastern Standard Time) and again on weekdays between 0900 h and 1200 h after the first battery ran out. On Saturdays and Sundays, only one recording session took place (because of logistical constraints). Battery life typically lasted 3–4 h (mean ± SD = 3.34 ± 0.71 h). Thus, we did not record every bluebird visit to each nest box during the breeding season.

Data processing

We first filtered all photos visually for samples that included bluebird activity for each camera deployment. We then conducted a second review to identify prey items and the adult sex in each observation. We identified prey items from the photos to the lowest possible taxonomic rank, with assistance from several other insect taxonomists, using references such as Borror et al. (2005) and Wagner (2005). Similar to other studies using visual diet identification, we organized the prey items by order (Fig. 3), with the exception

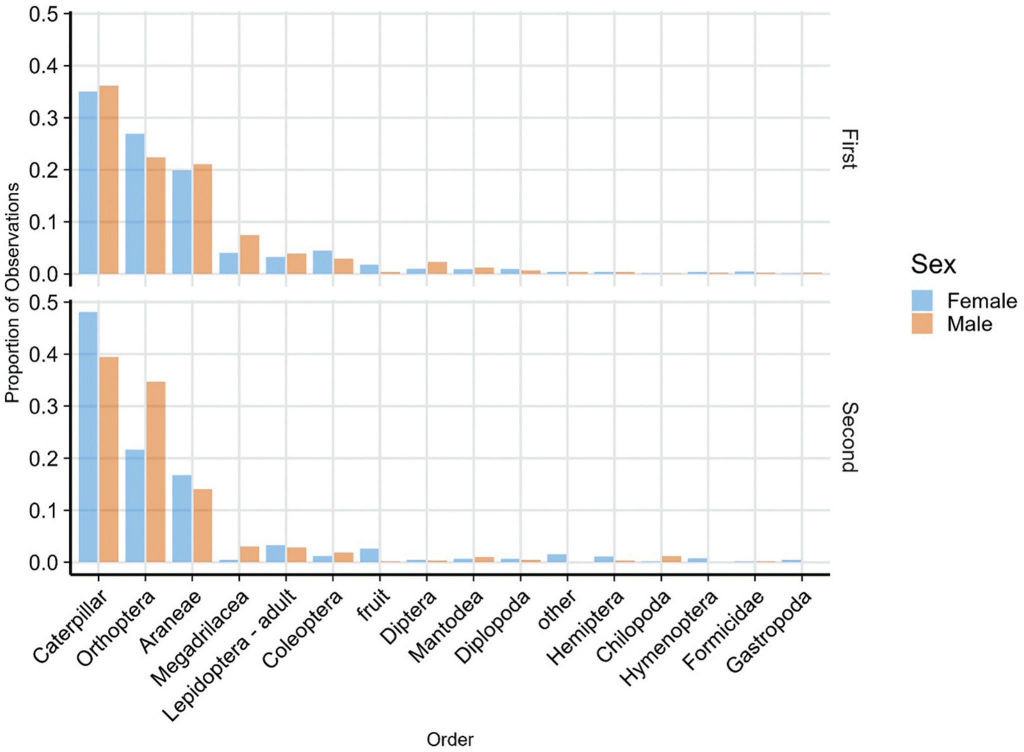

Figure 3. Diet proportions of prey deliveries by Eastern Bluebirds comparing first (top) and second (bottom) broods by adult sex. Both male and female bluebirds consistently delivered caterpillars at higher proportions than other taxa. "Other" represents taxa for which total prey deliveries were <10, which included Isopoda, Opiliones, Odonata, Megaloptera, and Vertebrata.

of ants (Formicidae), which we treated separately from Hymenoptera because of their ecological importance. We recorded the provisioning adult as male, female, or unknown. In a few photos we could not identify prey or adult sex, primarily because of poor photo quality or lighting ($n = 117$ visits). We estimated prey size by measuring prey length compared to bill length in photos, assuming an Eastern Bluebird bill length of 13 mm (Goldman 1975).

We determined the following about each nest: (1) brood size at the time of recording, (2) nestling age from hatch day, where hatch day = day 0, (3) Julian date, (4) year, and (5) brood number (i.e., first or second brood of the season, or early versus late breeding attempts). Bluebirds regularly reuse nest boxes within a season, so we assumed all nesting attempts made in the same box following a successful nest represented the second brood of the same pair. We removed nests that did not have complete nest information ($n = 11$) from analyses that included nest variables.

Statistical analyses

We performed all analyses in Program R version 4.2.2 using the R Studio environment version 2022.72.576 (R Core Team 2022; RStudio Team 2022).

Prey size, provisioning frequency, and caterpillar prey delivery

We modeled three response variables: prey size (i.e., length in mm), provisioning frequency per hour (i.e., number of visits per camera deployment, divided by the total length of camera deployment, rounded to whole numbers), and caterpillar prey delivery (probability of delivered prey being a caterpillar). We modeled these responses and their relationships with several variables related to intrinsic and extrinsic characteristics of the nest using generalized linear mixed models. For our models of prey size and caterpillar prey delivery, each visit was a replicate, whereas for provisioning frequency, we used the camera deployment as the replicate. For all models, we included fixed effects of sex (male, female), brood number (first or second), brood size (range: 2–5), and nestling age (range: 0–24 days). We removed all observations where sex could not be identified ($n = 117$ visits). We used generalized linear mixed models with two random intercepts: nest box ID and year. A random intercept of box ID accounts for variation from repeated observations of the same pair. The random intercept of year accounts for inter-yearly variation. We included random intercepts as crossed effects because nest boxes were monitored for multiple years. Because prey size was a continuous variable bounded by zero, we modeled it using a Gamma distribution with a log link in our mixed-effect model using the function “glmmTMB” from the glmmTMB package (Brooks et al. 2017). For provisioning frequency, an overdispersed count bounded by zero, we used a negative binomial distribution. For our caterpillar prey delivery response, we first coded all provisioning visits as delivering a caterpillar (mostly Lepidoptera, but also including larvae of Symphyta) or not, where 1 = caterpillar and 0 = not a caterpillar. We then used a binomial distribution to model the proportion of prey deliveries that were caterpillars.

For prey size, provisioning frequency, and caterpillar prey delivery models, we first considered a full model that included biologically plausible two-way interactions among the four fixed effects: sex, brood number, brood size, and nestling age. We included these interactions to account for potential context-dependent effects such that the relationship with nestling age might be dependent on brood size. We then removed interaction terms that were not significant ($P < 0.05$) to simplify model structure. Before running the model, we standardized our fixed effect for nestling age to have a mean of zero and standard deviation of one to aid in model convergence. We assessed model fit by evaluating the distribution of residuals. We ran these models using the functions “glmer” and “glmer.nb” from the package lme4.

Community composition

To model the relationship between prey composition and fixed effects of sex, brood number, brood size, and nestling age, we used a permutational ANOVA test (PERMANOVA), which evaluates differences in multivariate centroids among groups. Our response variable was the multivariate response of number of each prey item for all invertebrate groups. For this analysis, we converted nestling age into the categorical variable nestling state where nestlings <8 days old (half of the nestling cycle) were considered early, and nestlings >8 days old were considered late nestlings. We also removed the following prey items that were provisioned by <10 individuals, so that they would not overly influence our results: Megaloptera, Odonata, Gastropoda, Isopoda, and Opiliones. We ran the PERMANOVA model for 9999 permutations using the function “adonis2” from package vegan. We used the “simper” function (from the vegan package) to identify which prey taxa contributed most to the compositional differences between groups, based on Bray–Curtis dissimilarities. This analysis decomposes overall dissimilarity between groups into the contribution of each taxon, helping identify which prey items are most influential in driving observed differences in composition. Lastly, we used a constrained correspondence analysis (CCA) biplot to visualize how cumulative prey composition (aggregated across multiple feeding visits) varied in relation to our four nest-level fixed effects.

Results

Over the 4 years of the study, we observed provisioning behavior and prey delivery at 63 nests located in 24 nest boxes for a total of 138 adult-nest combinations across 639 observation days. We observed 8,128 prey items provisioned to nests, where 7,014 (86%) could be identified at least to order. For identifiable prey items, 86% were composed of only three orders. Lepidoptera (both adults and larvae) were the most common food items bluebirds provisioned to nestlings (41% of deliveries), followed by Orthoptera (26%) and Araneae (19%; Fig. 3). There was a tendency for spiders and earthworms to comprise a higher proportion of the diet during the first brood compared to the second (0.21 vs. 0.15 and 0.06 vs. 0.02 of all deliveries), and there was a tendency for caterpillars and Orthoptera to comprise a lower proportion of the diet in the first brood compared to the second (0.36 vs. 0.44 and 0.25 vs. 0.28 respectively). There were few differences between sexes except that, in second broods, females fed more caterpillars and males more Orthopterans and earthworms (Fig. 3).

Prey size and provisioning frequency

For prey size, our model showed that males brought larger prey than females and prey size increased as nestlings aged, approximately 1 mm per day (Table 1, Fig. 4A). The increase in prey size with nestling age and brood size was weaker in second broods (Table 1).

For provisioning frequency, our model showed that males delivered prey at higher frequencies than females, but only when nestlings were young (Table 1, Fig. 4B); females provisioned more frequently than males when nestlings were older. There was a modest difference in this relationship between first and second broods; increases in provisioning rates with nestling age were steeper in second broods (Table 1).

Caterpillar prey delivery

The probability of a prey item being a caterpillar was primarily related to brood number, nestling age, and brood size (Fig. 5); it was unrelated to sex. There was a strong interaction between brood size and brood number (Table 1) such that caterpillar probabilities were higher for small broods in the first brood than in the second brood, but in the second brood they strongly declined with brood size to levels similar to the first brood. There was a negative relationship between nestling age and caterpillar probability, such that probability declined from a predicted 0.37 on day 1 to 0.23 on day 22.

Table 1. Results from generalized linear mixed models examining prey size, provisioning frequency, and the probability that a prey item was a caterpillar. Prey size (length in mm) and provisioning frequency (visits per hour) were modeled using a negative binomial error distribution, and caterpillar probability was modeled using a binomial distribution. Significant effects (determined as a P-value < 0.05) are indicated in bold. P-values and confidence intervals based on asymptotic Wald tests per the function "glmer".

Response variables	Fixed effects and interactions	b ± SE	95% CI	Z	P
Prey size (mm, $n = 8{,}011$)	**Intercept**	**3.03 ± 0.04**	**2.95, 3.10**	**78.66**	**<0.001**
	Sex (male)	**0.09 ± 0.01**	**0.06, 0.11**	**6.34**	**<0.001**
	Brood number (second)	−0.01 ± 0.02	−0.06, 0.04	−0.49	0.622
	Brood size	0.00 ± 0.01	−0.02, 0.02	0.09	0.925
	Nestling age	**0.09 ± 0.01**	**0.07, 0.11**	**7.99**	**<0.001**
	Sex × nestling age	**0.05 ± 0.01**	**0.02, 0.08**	**3.75**	**<0.001**
	Brood number × nestling age	**−0.09 ± 0.02**	**−0.12, −0.06**	**−6.03**	**<0.001**
	Brood number × brood size	**−0.08 ± 0.02**	**−0.12, −0.03**	**−3.22**	**0.001**
Provisioning frequency (visits/hour, $n = 1{,}086$)	**Intercept**	**0.69 ± 0.23**	**0.25, 1.13**	**3.07**	**0.002**
	Sex (male)	**0.30 ± 0.05**	**0.21, 0.39**	**6.52**	**<0.001**
	Brood number (second)	−0.09 ± 0.08	−0.25, 0.07	−1.08	0.282
	Brood size	0.07 ± 0.04	−0.01, 0.15	1.82	0.068
	Nestling age	**0.18 ± 0.03**	**0.11, 0.15**	**5.17**	**<0.001**
	Sex × nestling age	**−0.32 ± 0.04**	**−0.40, −0.23**	**−7.56**	**<0.001**
	Brood number × nestling age	**0.11 ± 0.05**	**0.02, 0.21**	**2.29**	**0.02**
Caterpillar (yes/no, $n = 8{,}011$)	**Intercept**	**−0.91 ± 0.13**	**−1.16, −0.66**	**−7.06**	**<0.001**
	Sex (male)	−0.05 ± 0.06	−0.17, 0.07	−0.82	0.413
	Brood number (second)	0.21 ± 0.11	−0.01, 0.42	1.89	0.058
	Brood size	−0.00 ± 0.05	−0.11, 0.10	−0.04	0.967
	Nestling age	**−0.14 ± 0.03**	**−0.20, 0.08**	**−4.74**	**<0.001**
	Brood number × brood size	**−0.35 ± 0.11**	**−0.57, −0.13**	**−3.12**	**0.002**

Prey composition

Composition of prey varied somewhat with brood size ($R^2 = 0.01$, $P = 0.001$), brood number ($R^2 = 0.01$, $P = < 0.001$), nestling stage ($R^2 = 0.01$, $P = 0.0001$), and adult sex ($R^2 = 0.004$, $P = 0.006$). However, all variables contributed relatively little to variation in prey composition, as indicated by the small R^2 values, suggesting that prey composition remains relatively stable regardless of adult sex, brood number, or nest status. In all dissimilarity comparisons, caterpillars, Orthoptera, and Araneae contributed the most to dissimilarity results with a cumulative 77–80% influence. The following prey items contributed to compositional differences (Fig. 6) according to the simpr analysis for dissimilarity. Compared to females, males provisioned less fruit ($P = 0.01$). Second broods were provisioned with more caterpillars ($P = 0.002$), Orthoptera ($P = 0.009$), and Chilopoda ($P = 0.05$). Older nestlings were fed fewer caterpillars ($P = 0.004$), orthopterans ($P = 0.007$), and Araneae ($P = 0.02$), and more Megadrilacea ($P = 0.02$), Coleoptera ($P = 0.005$), Hemiptera ($P = 0.01$), and fruit ($P = 0.008$). All prey items were fed at similar frequencies between small and large broods. According to our CCA, the four explanatory variables ordinated into two components (Eigenvalues: 0.04 CCA1 and 0.03 CCA2) that together explained 78% of the variance in prey composition (Fig. 6).

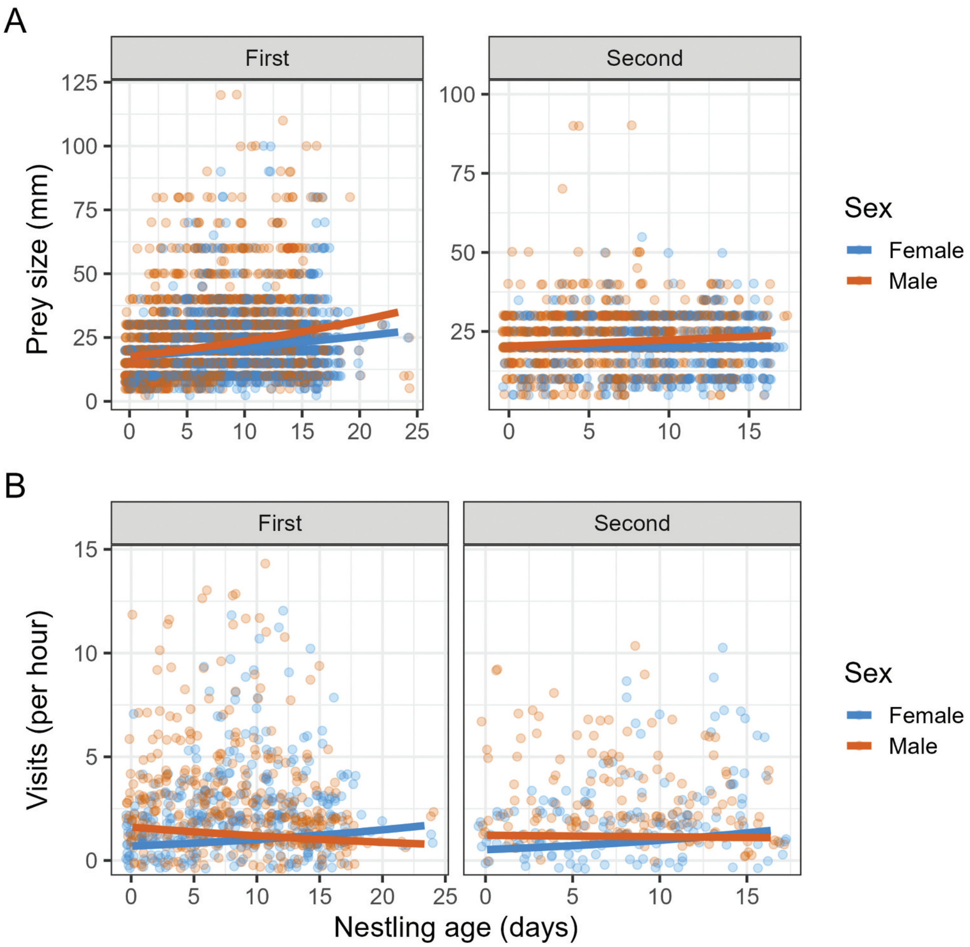

Figure 4. Relationships of (A) prey size (mm) and (B) provisioning rate (visits/h) to nestling age for adult females and males during first and second broods of Eastern Bluebirds. Lines show predicted values from linear mixed models; points represent raw data. Random intercepts of box and year were held constant (set to a single box identity and year). Prey size increased with nestling age in both broods; adult males delivered larger prey than females, and differences between the sexes increased as nestlings aged. Provisioning rates also varied by adult sex, such that females provisioned less frequently than males when nestlings were young, but this relationship reversed as nestlings aged.

Discussion

We mounted GoPro® cameras on the roofs of nest boxes occupied by Eastern Bluebirds to measure the relative abundance and type of prey provisioned to nestlings by parents of both sexes. Data from our camera images generally support the conclusions of bluebird diet studies that employed other methods such as fecal analyses, throat ligatures, gut content, and foraging observations (Pinkowski 1978; Herlugson 1982; Jedlicka et al. 2017; Stalwick 2018). During our study, caterpillars, Orthoptera and Araneae dominated nestling diets, although a diversity of other prey items from 14 taxonomic orders were also provisioned at lower frequencies. Of the three primary prey types, caterpillars (larvae of both Lepidoptera and Symphyta) were most often

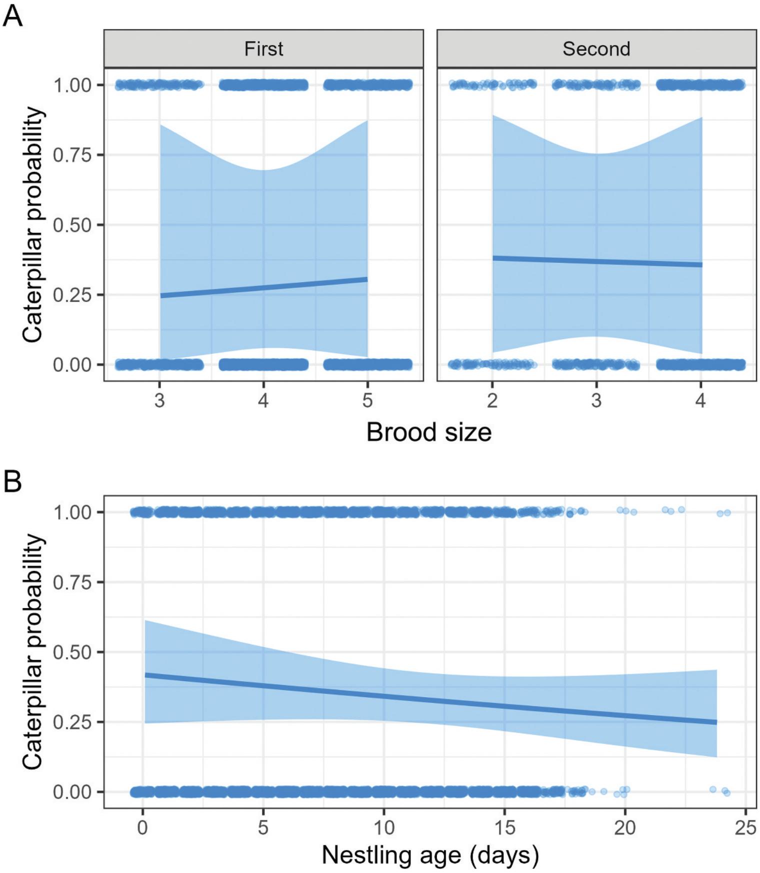

Figure 5. Relationships of caterpillar probability to (A) brood size for first and second broods and (B) nestling age, for Eastern Bluebirds. Lines represent predicted values from a generalized linear mixed model; shading indicates 95% confidence interval; points represent raw data. Random effects of box and year were held constant (set to a single box and year). Caterpillar probability remained stable across brood sizes in first broods but declined with brood size in second broods. Caterpillar probability also declined with nestling age.

provisioned, consistent with the findings of Pinkowski (1978). We found this was true regardless of parent sex, nestling age, brood number, or brood size. In order of prey frequency, caterpillars were followed by Orthoptera (Acrididae, Gryllidae, Tettigoniidae, and Gryllotalpidae) and then various spider taxa. Earthworms, a common feature of some thrush diets (Wheelwright 1986), were taken less frequently than Orthoptera and Araneae, followed by Lepidoptera adults. Most of the Lepidoptera caterpillars provisioned were moths; butterfly caterpillars and adults comprised just a small component of the nestling diet (0.4%). This difference was unsurprising as many butterflies are chemically protected and aposematic prey items, both as caterpillars and as adults (e.g., Dyer 1995; Sime et al. 2000). Prey composition remained relatively stable between first and second broods. While our study did not assess prey availability, we expect that caterpillar abundance would peak earlier in the season than Orthoptera abundance, and both groups would experience stronger seasonal peaks

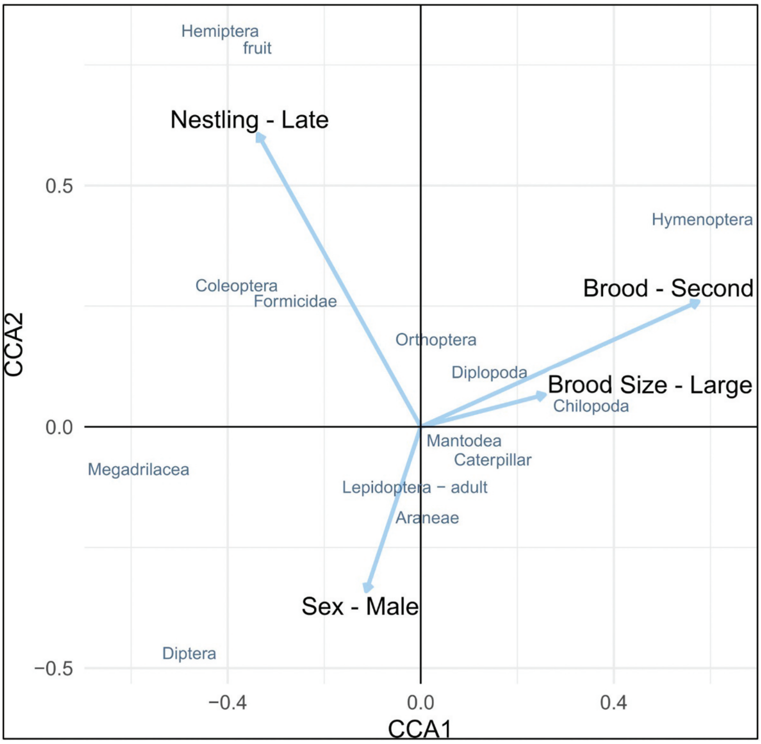

Figure 6. Canonical correlation biplot between adult sex and nest-associated variables (arrows, large text), and prey items (smaller text). Prey items were slightly adjusted and formatted to improve clarity using the program Inkscape.

than Araneae (Hurlbert et al. 2018). Even with an influx of grasshoppers, crickets, and katydids later in the season, caterpillars remained the dominant food for bluebirds.

Our study expanded upon the work of Pinkowski (1978) in the following ways. Pinkowski identified 2,503 samples of food provisioned to nestlings in 45 Eastern Bluebird nests. He used neck ligatures for 1.5–2.5 h each day, and rarely sampled the same nest on two consecutive days. He also noted that smaller food items were underrepresented as they pass through the ligature and are not recorded. Pinkowski supplemented the neck ligature method with observations made through a spotting scope; the sex of the adult bird provisioning the nestling was only known for the observations made with a spotting scope (1,359 food items). Thus, in comparison, our study nearly tripled the number of identified food items, captured a higher percentage of food items provisioned to each brood, and included data on parental sex for a higher percentage of prey. Additionally, our study offers a summary of the bluebird diet in a different part of the bluebird range, approximately 685 km east of Pinkowski's study site.

The importance of caterpillars in bluebird nestling diets also reflects their importance for other insectivorous birds for which nestling diets have been studied and quantified. Meunier and Bedard (1983) determined that caterpillars are the most abundant prey types in the diet of Savannah Sparrow (*Passerculus sandwichensis*) nestlings. Metabarcoding of fecal samples from House Wren nestlings indicated that Lepidoptera, specifically moths (Noctuidae, Erebidae, and Geometridae), were among the most frequently provisioned taxa (Grabarczyk et al. 2022). Similar findings have been reported for nestlings of Black-throated Blue Warbler (*Setophaga caerulescens*, Rodenhouse and Holmes 1992), Black-capped Chickadee (*Poecile atricapillus*, Kluyver 1961), Carolina Chickadee (*Poecile carolinensis*, Brewer 1961), Hooded Warbler (*Setophaga citrina*, Nagy and Smith 1997), and many other passerines breeding in the eastern USA (e.g., Best 1977; Auer et al. 2016). Given the impact of food availability on reproductive output (Martin 1987), caterpillars might be disproportionately important to fitness across many insectivorous bird species.

Our comparisons between the sexes found that female bluebirds provisioned less frequently and with smaller food items than males, but there were few differences in prey type or prey composition. Pinkowski (1978), in contrast, found that females provisioned more frequently than males, albeit with high variation across nests. Pinkowski did not consider prey type or availability. Across our analyses, only fruit and earthworm provisioning differed between sexes, with fruit delivered more often by females and earthworms more often by males, but both of these food items made up an inconsequentially small proportion of total provisioned items (<1% and 4% respectively).

Females may provision less than males, particularly in the early stages of a brood, because it is females that brood nestlings until they are better able to thermoregulate. Females may also adjust provisioning effort in response to male provisioning (Pinkowski 1978) or habitat quality, whereby females provision more when food availability is low and unreliable (and males provision less often) and less when food availability is high and reliable (and males provision more often). Pinkowski (1978) noted that male bluebirds remain and forage closer to the nest than females do, and habitat quality influences the distance bluebirds will travel to acquire prey. Although bluebirds are ubiquitous across landscapes that likely vary in habitat quality, most studies of bluebird provisioning behavior (including this one) have used single study sites for comparisons. Needed are evaluations of diet and provisioning variation over multiple habitat types that vary in quality to determine how bluebirds adjust effort in response.

Our study also revealed sex-specific shifts in provisioning effort and caterpillar prey with nestling age; males increased prey size and reduced visits as nestlings grew, whereas females increased visits but did not significantly increase prey size. Both sexes reduced caterpillar provisioning in older nestlings and larger broods. These findings are similar to those of Pinkowski (1978), who found that provisioning increased with nestling age, but the percentage of male observations declined. Foraging is risky; these shifts suggest that more energetically-taxing nests, i.e., those with more or larger nestlings, evoke changes in provisioning behavior indicative of risk-sensitive foraging (Stephens and Krebs 1986). Caterpillars are high-quality prey worth the extra effort when predation risks associated with foraging are low, but when risks are high, bluebirds may instead forage for prey that are lower quality but easier to locate. The difference in effort between females and males, but lack of a difference in prey items delivered to nests, suggests females may be absorbing more of the reproductive costs of energetically-taxing nests, which could have population-level consequences when food availability is low, as in human degraded landscapes (Narango et al. 2018; Richard et al. 2019).

Several lines of evidence suggest that bluebirds prefer caterpillars over other prey when feeding their young. In staged prey choice experiments, Kennedy (2019) found that provisioning bluebirds exhibit preferences for soft-bodied prey such as caterpillars. Indeed, optimal foraging theory predicts that birds should seek prey with the greatest energy and nutritional returns (Royama 1970; Stephens and Krebs 1986); given the carotenoid benefits (Eeva et al. 2010) and ease with which caterpillar prey can be digested (Redford and Dorea 1984), it would be surprising if bluebirds did not preferentially seek caterpillars for provisioning their nestlings, other factors such as prey abundance being equal. We lacked data on prey abundance and availability, which are necessary to determine foraging preferences directly. However, the provisioning patterns we observed, namely that caterpillars were the most frequently delivered prey items in both broods by both sexes (Fig. 3), are consistent with prioritizing caterpillars over other prey types. Moreover, the fact that caterpillars continued to be delivered to nestlings more often than other prey in the second brood, after the great flush of spring caterpillars had ended and the abundance of alternative prey such as grasshoppers and katydids was increasing (Wagner 2025), also suggests that caterpillars are a priority within bluebird nestling diets.

Conservation implications

Given that many Lepidoptera species are experiencing significant decline (Wagner, Fox, et al. 2021), the apparent reliance of bluebird nestlings on caterpillars highlights the need to integrate Lepidoptera conservation into broader bird protection efforts. Most caterpillar species are host-plant specialists (Forister et al. 2015), underscoring the importance of conserving native plant species that support these critical prey populations. Habitat restoration strategies that focus on increasing native plants and reducing invasive species likely have cascading positive impacts on not just Lepidoptera populations, but also insectivorous birds, including bluebirds (Narango et al. 2020). Considering bluebird population declines across urbanized, agricultural, and otherwise developed landscapes (Jackson et al. 2013), it is likely that these human modifications contribute to the loss of key invertebrate food resources through additional mechanisms like pesticides, pollution, and invasive species. Future studies should examine how local and landscape-scale habitat degradation impacts caterpillar availability, and in turn, bluebird reproductive output.

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