

Mechanistic regulation of begging behavior due to experimental food supplementation across an urbanization gradient

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ABSTRACT

Parent-offspring communication is fundamental to reproductive success, yet how ecological variation shapes nestling begging behavior, physiology, and parental provisioning remain understudied in free-living systems. We investigated these relationships in free-living northern house wrens (*Troglodytes aedon*) breeding across an urbanization gradient differing in food availability. Within each population, we experimentally supplemented half of the nests with mealworms while the remaining nests served as non-supplemented controls to determine whether food availability alters offspring begging behavior, parental provisioning, and baseline corticosterone concentrations. Parent-offspring communication changed markedly with nestling age. At 5–6 days, begging intensity primarily reflected the interaction between parental provisioning and seasonal timing, whereas by 11 days it reflected local food availability and nestling body mass. This developmental shift was accompanied by changes in parental provisioning: as nestlings aged, parents relied increasingly on offspring behavior when allocating food. Nestlings with higher begging scores were more likely to receive food, but successful food acquisition depended primarily on the timing of begging relative to parental feeding decisions rather than on begging duration alone. Food supplementation weakened population differences in parent-offspring communication, indicating that variation in food availability underlies much of the observed behavioral variation. Baseline corticosterone concentrations decreased with increasing food intake only in the population with the lowest food availability. Furthermore, larger nestlings exhibited higher baseline corticosterone concentrations under conditions of high begging intensity and low parental provisioning. In contrast, natural variation in baseline corticosterone did not predict begging behavior, suggesting that baseline corticosterone reflects the energetic and ecological context in which begging occurs rather than acting as its direct driver. Our findings demonstrate that parent-offspring communication is highly context dependent and changes substantially during development, highlighting the importance of considering both offspring behavior and ecological context when studying the evolution of parent-offspring interactions.

1. Introduction

In organisms that provide parental care, successful reproduction depends on effective parent-offspring communication, with both parties adjusting their behaviors according to internal and external conditions. One of the clearest examples of such communication occurs in altricial birds, whose offspring depend entirely on parental care for growth and survival (Loiseau et al., 2008; Brode et al., 2021). Nestlings communicate their nutritional state through a combination of visual and auditory

signals collectively known as begging behavior (Caro et al., 2016, 2025). Parents evaluate both the intensity and duration of these begging displays to adjust their provisioning decisions (Godfray and Charles, 1991; Kilner, 1995). Consequently, begging behavior has been quantified using a variety of approaches, including posture-based scores of increasing intensity (Leonard et al., 2003; Pilz et al., 2004; Grodzinski et al., 2008; Dor and Lotem, 2009), begging duration (Redondo and Castro, 1992; Leonard et al., 2003; Pilz et al., 2004), combinations of posture and duration (Leonard et al., 2003; Lucass et al., 2016; Fresneau

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and Müller, 2019), and vocalizations (Bowers et al., 2016, 2019).

Begging is a highly flexible behavior that nestlings display according to their nutritional needs and condition (Ghalambor et al., 2010). This variation is shaped by two complementary sources of information. First, begging is shaped by the nestling's immediate social and nutritional environment, including sibling competition, short-term hunger (time since the last feeding), and long-term nutritional state (overall nestling body condition; Price and Ydenberg, 1996; Ghalambor et al., 2010). Parents, in turn, integrate the social information conveyed by begging with their own physiological state and assessment of ecological conditions and resource availability to determine how much food to allocate to each offspring (Mock et al., 2011; Royle et al., 2014; Caro et al., 2016, 2025; Koykka and Wild, 2018). Resource quantity and quality are therefore thought to be among the primary selective pressures shaping parental provisioning decisions and, consequently, offspring begging behavior (Caro et al., 2016). When food is abundant, parents can successfully provision all offspring, and nestlings in poorer condition typically beg more intensely and receive preferential feeding (Godfray and Charles, 1991; Cotton et al., 1996; Mock et al., 2011). In contrast, when resources are limited, parents must allocate food more selectively, often investing preferentially in offspring in better condition (Davis et al., 1999; Caro et al., 2016), which may also exhibit more intense competitive signaling (Koykka and Wild, 2018).

Secondly, begging behavior also reflects the physiological state of the offspring, as mediated by underlying physiological mechanisms. Among these, the hypothalamus plays a central role by regulating hunger expression in vertebrates (Clark, 2002; Lees et al., 2017). During periods of food deprivation, vertebrates increase glucocorticoid secretion (corticosterone in birds) through activation of the hypothalamic-pituitary-adrenal (HPA) axis (Kitaysky, 2001; Lendvai et al., 2014). In many vertebrates, baseline glucocorticoid concentrations are positively associated with food intake, with individuals exhibiting their highest daily food intake rates when glucocorticoid concentrations peak (Landys et al., 2006). Consistent with this relationship, experimental studies in several bird species have shown that experimentally elevating plasma corticosterone concentrations increases nestling begging behavior (Loiseau et al., 2008; Bowers et al., 2019). However, the relationship between glucocorticoids and behavior is bidirectional. Glucocorticoid concentrations are not only capable of influencing behavior, but can themselves be shaped by behavioral state, energetic expenditure, and recent foraging success (Horton and Holberton, 2009; Myers et al., 2014; Haller, 2022). Together, these studies suggest that offspring begging integrates information from both the external environment and internal physiological state, while baseline corticosterone can reflect the combined effects of food availability, physiology, and behavior (Benowitz-Fredericks et al., 2026).

Because food availability is one of the principal environmental factors influencing both parental provisioning decisions and offspring physiological state, environmental variation is expected to have key consequences for parent-offspring communication. For many passerines, folivorous caterpillars constitute a key food resource during the nestling stage and are typically abundant in natural habitats (Noordwijk et al., 1995; Visser et al., 1998; Cholewa and Wesolowski, 2011). Due to use of pesticides, land-use change, and increased environmental pollutants, anthropogenic environments usually have reduced availability and diversity of insectivorous prey (Attwood et al., 2008; VanDiest et al., 2024), including those in the arthropod and Lepidoptera taxa (McIntyre, 2000; Cholewa and Wesolowski, 2011; Jones and Leather, 2012; Seress et al., 2018, 2019; Baldan and Ouyang, 2020). In addition to changes in prey abundance, urbanization may also decrease prey quality because insects in anthropogenic landscapes are smaller than those found in natural areas (Eggenberger et al., 2019; Sinkovics et al., 2021, Ferrari et al., 2024). Thus, urban parents deliver smaller prey items to their nestlings (Schwagmeyer and Mock, 2008; Sinkovics et al., 2021). These reductions in food quantity and quality have important fitness consequences, as nestlings raised in resource-poor environments

commonly exhibit poorer body condition (Liker et al., 2008; Ouyang et al., 2019; Baldan and Ouyang, 2020; Seress et al., 2020), which can reduce offspring development, fledging success, and subsequent recruitment (Schwagmeyer and Mock, 2008). Indeed, comparative studies across species inhabiting habitats that differ in resource availability have documented substantial variation in parental and begging behavior (see review Caro et al., 2016) and fitness (Seress and Liker, 2015; Isaksson, 2018). Yet, it remains unknown whether this variation extends to populations within the same species that live in habitats of different resource availability. Therefore, comparing populations of a single species can provide a powerful framework for understanding how local ecological conditions shape flexibility in behavior and physiology.

To investigate whether parent-offspring interactions vary among populations breeding under different ecological conditions, we studied free-living northern house wrens (*Troglodytes aedon*) across an urbanization gradient differing in food availability (Fig. 1A). We experimentally increased food availability through mealworm supplementation to a subset of nests at each site to determine whether increased food resources altered offspring begging behavior and parental provisioning. To characterize ecological differences among populations, we quantified prey composition and prey size delivered to nestlings (Fig. 1B–D; Figs. S4–S5). We hypothesized that food availability shapes both offspring begging behavior and parental provisioning. To test this hypothesis, we quantified three complementary components of begging behavior: begging score, begging duration, and begging intensity (the product of score and duration). Because begging score reflects the intensity of offspring solicitation whereas begging duration reflects its persistence, analyzing both metrics allowed us to determine whether food availability influenced different components of begging behavior and parental decision-making. We predicted that nestlings with higher begging scores would receive more food and have shorter delays to receive the food item, and that the strength of these relationships would depend on food availability. Specifically, we expected parents to allocate food more equally when food was abundant (either naturally or through supplementation), whereas under lower food availability they would allocate food more selectively, preferentially toward individuals in better condition that, ultimately, have a higher chance of survival. Following this same idea, we predicted that the relationship between nestling body mass and begging intensity (representing the total begging effort of a given nestling) would depend on food availability. Particularly, we expected heavier nestlings to beg more intensely under low-resource conditions, where parents preferentially invest in offspring in better condition, whereas lighter, needier nestlings would beg more intensely when food was abundant. Finally, because previous work in some of these populations showed higher baseline corticosterone concentrations under lower food availability (Heppner et al., 2023), we hypothesized that corticosterone mediates begging behavior. If corticosterone mediates begging behavior, then nestlings from lower-resource populations should exhibit higher baseline corticosterone concentrations and more intense begging, and food supplementation should reduce these behavioral and physiological differences among populations.

2. Materials and methods

2.1. Field sites and standard protocols

This study was conducted during three consecutive breeding seasons (April–August 2023–2025) at four study sites located in Washoe and Storey counties, Nevada, USA. Based on seasonal caterpillar biomass (Fig. 1A) and differences in prey composition and prey size delivered to nestlings (Figs. 1B–D; S4–S5), the sites represented a gradient in food availability as well as urbanization (Seress et al., 2014). The McCarran Ranch Preserve (natural; 39.55°N, 119.55°W, urbanization score –2.72) exhibited the highest food availability, the University of Nevada, Reno Agricultural Experiment Station (rural; 39.51°N, 119.74°W,

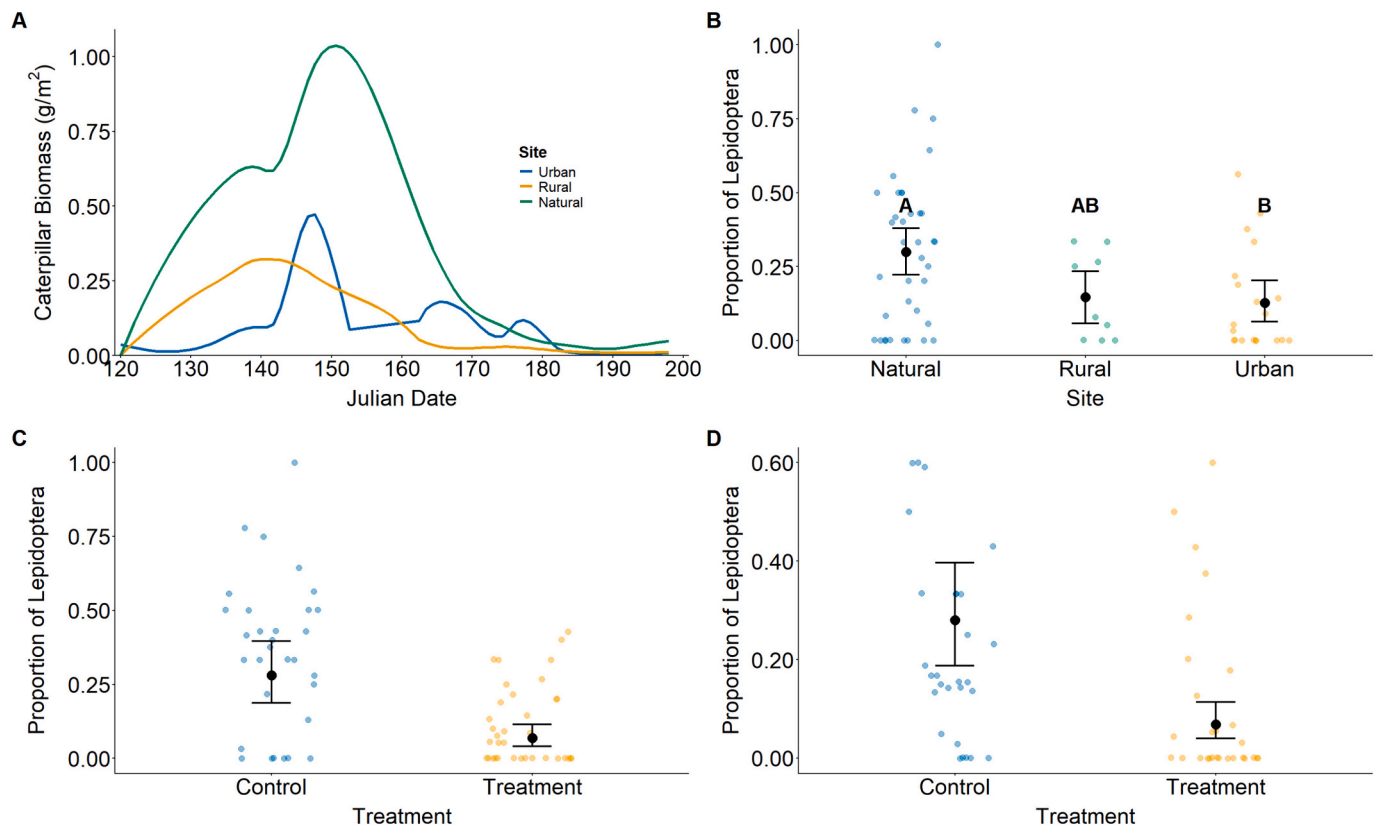


Fig. 1. A) Seasonal variation in mean caterpillar biomass (g/m²) across urban, rural, and natural sites. Solid lines represent LOESS-smoothed relationships between Julian date and mean caterpillar biomass. B) Proportion of lepidoptera ($\pm 95\%$ confidence intervals) fed to 5–6 days old individuals from each site. Different letters denote statistically significant differences among sites based on post-hoc pairwise comparisons from the fitted model. C) Proportion of lepidoptera ($\pm 95\%$ confidence intervals) fed to 5–6 days old individuals with (Treatment) and without (Control) mealworm supplementation. D) Proportion of lepidoptera ($\pm 95\%$ confidence intervals) fed to 11 days old individuals with (Treatment) and without (Control) mealworm supplementation.

urbanization score -1.19) the lowest, and two city parks in Reno, Nevada (urban; 39.50°N , 119.89°W and 39.49°N , 119.85°W , urbanization scores 0.70 and 3.22 , respectively) intermediate food availability.

Northern house wrens are second-cavity nesters that readily use nest boxes to breed in areas with different levels of urbanization (Ouyang et al., 2019; Heppner and Ouyang, 2021). Females lay between 5 and 8 eggs and incubate them for 12–15 days (Johnson, 2014; Heppner et al., 2023). Nestlings fledge when they are around 17 days old (Johnson, 2014). We monitored nest boxes (25–35 per site) two to three times per week at the beginning of the breeding season for nest-building activity. Females lay one egg per day (Heppner et al., 2023) and once egg-laying began, we checked nests every day to determine the start of incubation. Starting on the 11th day of incubation, we monitored nests daily to identify the first day eggs hatched. When at least one egg had hatched, we designated that date as day 0 for the nest. All subsequent references to nestling age (e.g., day 5 and day 11) are therefore based on the age of the “nest.” Hatching was highly synchronous: in more than 90% of nests across all study sites, all eggs hatched within 24 h of the first offspring (Johnson, 2014), minimizing age differences among siblings.

On day 0, we installed a food tray inside the nest box and supplemented half of the nests per site with live mealworms (Fig. 2A). Mealworms are a good source of protein for birds and have been used in multiple avian food supplementation experiments (Finke, 2002; Bañbura et al., 2011; Skwarska, 2018; Seress et al., 2020). Experimental nests received 1.5 g of mealworms per offspring per day until day 12 (modified from Seress et al., 2020). Mealworms were almost entirely consumed throughout the experiment, with leftovers observed in fewer than 1% of supplemented nests across all study sites. Our goal was not to fully satisfy the daily energy requirements of the whole brood but rather

to partially supplement their energy requirements. We measured nestling's body mass (nearest 0.1 g), tarsus, and wing length (nearest 0.01 mm) on days 1, 4, 8 and 12 to monitor growth rate. On days 1 to 4, we marked each nestling by clipping a distinct toenail; then, on day 8, each offspring received a metal band. On day 12, we collected blood samples ($<60\ \mu\text{L}$) from the brachial vein of each nestling between 06:00 and 10:30 to measure baseline plasma corticosterone concentrations. All nestlings within a brood were sampled simultaneously by multiple field personnel to minimize handling time and disturbance, and sampling time had no effect on corticosterone concentrations ($p > 0.05$, mean = $164\ \text{s}$, SD = $52\ \text{s}$). Blood samples were stored on ice and centrifuged at $\sim 10,000\text{g}$ for three minutes. Plasma was stored at -80°C until analysis. After day 12, we monitored nestlings until they fledged ($\sim$ day 17–20).

2.2. Nest recording and video analysis

We recorded begging behavior and parental provisioning at two different time points: on day 5 or 6 and day 11 (see Table S1 for sample sizes). We utilized a camera (WiFi Bird Box Camera, Green Backyard) to record parental feeding behavior and offspring begging behavior for 1.25 h. On the day of recording, we marked each offspring's head with a unique symbol using a black eyeliner (E.L.F. eyeliner) to identify individual nestlings in video recordings.

For the video analysis, we quantified parental provisioning and nestling begging behavior by recording the number of feeding events delivered by each parent to each offspring. Begging posture (or score) reflects the intensity of the display at a given moment, whereas begging duration quantifies how long nestlings sustain that display. Because these two components may vary independently, studies commonly quantify one or both measures, and some combine them into a

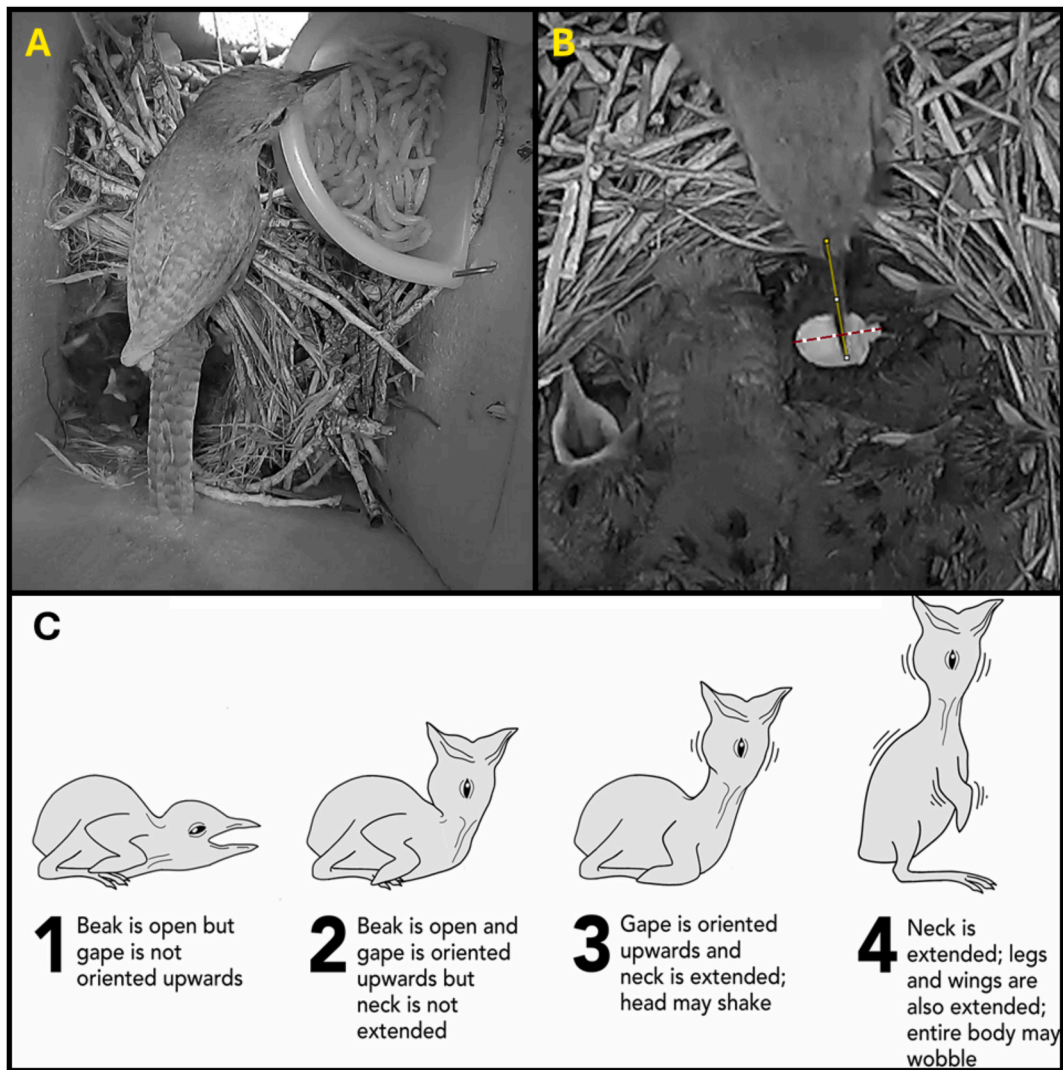


Fig. 2. A) Nest with a food tray supplemented with mealworms. B) Yellow solid line: bill size measure as a unit reference; red dashed line: prey measurement. C) Based on different postures and the intensity of begging, a different begging score was assigned for each begging attempt. Illustration: Ava Ciaccia. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

composite measure of begging intensity to capture the overall energy investment (Redondo and Castro, 1992; Kedar et al., 2000; Leonard et al., 2003; Pilz et al., 2004; Lucass et al., 2016). Therefore, we utilized three complementary metrics of begging behavior: begging score, begging duration, and begging intensity. Begging score was based on the posture adopted by a nestling during a begging event, following an established ordinal scale (Fig. 2C; adapted from Pilz et al., 2004). A begging event was defined as the period from the initiation of begging until the nestling ceased begging. If a nestling stopped begging but resumed within 1 s, the behavior was considered part of the same begging event; longer interruptions were classified as separate events. Begging duration (ss.000) was defined as the duration of a begging event, measured from the moment a nestling began begging until it either received a food item or stopped begging, whichever occurred first. If another nestling was fed during the same parental visit, we continued recording the begging time of the remaining nestlings until they either received food or ceased begging. Finally, begging intensity was calculated as the product of begging score $\times$ begging time, providing an integrated measure of total begging effort displayed by a given nestling.

2.3. Prey type, size and food availability estimation

Using the videos, we identified whether parents were feeding their offspring with lepidoptera (caterpillar, butterfly, and moths), mealworms (for treatment groups), or other types of prey. To estimate the prey size, we modified the method utilized by Barron et al., 2024. We used the program ImageJ (rsb.info.nih.gov/ij/) and considered the parent's bill as one unit of measure. Then, we calculated the size of the prey relative to the parent's bill size (Fig. 2B). We also collected caterpillar frass weekly from May–July under deciduous trees at each site for the entire breeding season using 1×1 m cheesecloths ($n = 2$ per site; Verboven et al., 2003; Rønning et al., 2009). We weighed frass to the nearest 0.001 g and averaged masses per week. Caterpillar biomass was estimated after correcting for temperature (Fig. 1A; Tinbergen and Dietz, 1994).

2.4. Nestling plasma corticosterone assay

To measure corticosterone hormone concentrations from plasma, we used an enzyme-linked immunosorbent assay kit (Enzo Life Sciences; Farmingdale, NY, USA) previously validated for northern house wrens (Davies et al., 2017). Plasma samples were diluted 1:40 in assay buffer

containing 0.5% steroid displacement reagent. Samples were randomized across 10 assay plates with respect to site, year, and nest to minimize potential confounding between biological variables and plate effects. To estimate assay precision, a standard sample was assayed in triplicate on each plate. The intra-assay coefficient of variation was 7.95%, and the inter-assay coefficient of variation was 19.48%. The relatively high inter-assay coefficient of variation resulted from a change in reagent lot number that affected two assay plates. When those two plates were excluded, the inter-plate CV decreased to 10%. Repeating all analyses after excluding samples from the affected plates did not alter the results.

2.5. Statistical analysis

All statistical analyses were conducted in R version 4.5.1 (R Core Team, 2023). We used the glmmTMB package (McGillucuddy et al., 2025) to fit generalized linear mixed-effects models (GLMMs) and generalized linear models (GLMs) and the emmeans package (Lenth, 2021) to report *p*-values. Prior to model fitting, we evaluated multicollinearity among explanatory variables using variance inflation factors (VIFs); all predictors had VIF values below 2, indicating that multicollinearity was not a concern. Candidate models initially included biologically relevant main effects and their interactions based on our *a priori* hypothesis. We modeled three-way interactions among variables that we expected to covary biologically due to site and/or treatment effects. Whenever three-way interactions were not significant, we removed the interactions in a step-wise manner to examine two-way interactions and fixed effects. Models were simplified using Akaike's Information Criterion (AIC), and interaction terms were retained only when they improved model fit and were statistically significant. Non-significant interactions that did not improve model fit were removed to obtain more parsimonious final models. Significance was assessed at $\alpha = 0.05$, and model diagnostics were evaluated using the DHARMA package (Hartig, 2021). We inspected residual uniformity, dispersion, and outliers using formal tests and graphical diagnostics. Across models, residuals showed no evidence of over- or under-dispersion and no excess of outliers.

To test whether begging intensity would differ among different sites, we fitted separate models for early (5–6 days) and late (11 days) nestling stages. In both, the response variable (begging intensity—amount of time an offspring begged multiplied by the begging score) was continuous and right-skewed; thus, we used a Gamma distribution. For both models we utilized a log link. Fixed effects for both models included site, nestling's total body mass, parental provisioning/brood size (PP/BS), Julian date, year, and treatment (mealworm supplemented or control). For the late-stage model, we also included corticosterone concentration. Nest ID was included as a random factor to account for nest-specific variation in both models. In both models, we tested the interaction between site $\times$ total body mass $\times$ treatment, treatment $\times$ corticosterone concentration, and PP/BS $\times$ Julian date as we expected these variables to covary.

To test the hypothesis that baseline corticosterone reflects the interaction between offspring energetic state and ecological context, we modeled corticosterone concentration as the response variable using a Gamma distribution with a log link. Fixed effects included site, begging intensity, nestling's total body mass, total food received, PP/BS, Julian date, year, and treatment. Nest ID was included as a random effect to account for non-independence among nestlings within the same nest.

To test the hypothesis that parental provisioning changes with ecological conditions and offspring begging, we fitted separate models for early (5–6 days) and late (11 days) nestling stages. In both, the response variable, food received (1 - yes, 0 - no), had a binomial distribution and we utilized a logit link. Continuous predictors were mean-centered and scaled to unit variance prior to analysis to improve model convergence, reduce collinearity among interaction terms, and facilitate interpretation of model coefficients. Fixed effects for both models

included site, begging score, begging duration, total body mass, Julian date, year and treatment. We included nest and offspring ID (nested within nest) as random intercepts to account for the non-independence of repeated observations within nestlings and nests.

To analyze prey size delivered by parents, we ran separate models for early and late nestling stages, with log-transformed prey size as the response variable. Fixed effects included the interaction of site and treatment, Julian Date, total nestling body mass, and year, with nest ID as a random factor. To analyze the amount of lepidoptera (caterpillars, butterflies, and moths) in the nestling's diet, we ran separate models for early and late nestling stages. We modeled the probability of a parent bringing lepidopteran prey in a given visit using a binomial distribution and logit link. Fixed effects included site and mealworm supplementation.

We additionally tested whether nestling growth and survival differed among sites. To assess growth, we fitted nonlinear mixed-effects models with a logistic growth function to nestling body mass measured at 1, 4, 8, and 12 days post-hatching. Because residual variance increased with nestling age, we incorporated a power variance structure as a function of age. We tested whether growth rates differed among sites by comparing models in which the logistic growth-rate constant (*k*) was either shared among or allowed to vary among sites using a likelihood-ratio test. Finally, to assess nestling survival, we used a binomial generalized linear model with the numbers of nestlings surviving and lost between day 4 and day 12 specified as the binomial response and site as the predictor.

3. Results

3.1. Begging intensity 5–6 days old

There was no effect of site on begging intensity ($\chi^2 = 4.40$, *df* = 2, *p* = 0.11; Table 1), but the response variable was significantly related to parental provisioning/brood size (PP/BS) and its interaction with Julian date ($\chi^2 = 13.49$, *df* = 1, *p* = 0.0002; Table 1; Fig. 3A). This interaction indicates that the relationship between parental provisioning rate and begging intensity changed over the course of the breeding season. When parental provisioning was low, individuals early in the breeding season showed higher begging intensity than those raised later in the season. In contrast, when parental provisioning was high, individuals raised later

Table 1

Results of Type II Wald chi-square tests from generalized linear mixed-effects models examining the effects of site, body mass, treatment (mealworm supplementation), Julian date, year, corticosterone concentration, and parental provisioning per brood size (PP/BS) on offspring begging intensity at 5–6 days and 11 days of age. Rows in bold indicate statistically significant effects (*p* < 0.05).

	Wald chi-square (χ^2)	Df	p
Begging intensity (5–6 days)			
Site	4.40	2	0.11
Body Mass	1.13	1	0.29
Treatment	0.01	1	0.90
Julian Date	0.42	1	0.52
Year	0.82	1	0.37
Parental Provisioning/Brood Size (PP/BS)	15.43	1	<0.0001
PP/BS * Julian Date	13.49	1	0.0002
Begging Intensity (11 days)			
Site	8.04	2	0.01
Body Mass	5.26	1	0.02
Treatment	9.79	1	<0.0001
Julian Date	2.76	1	0.09
Year	5.77	1	0.06
Corticosterone concentration	0.01	1	0.91
Parental Provisioning/Brood Size (PP/BS)	14.59	1	0.0001
Site * Body Mass	14.04	2	0.0008

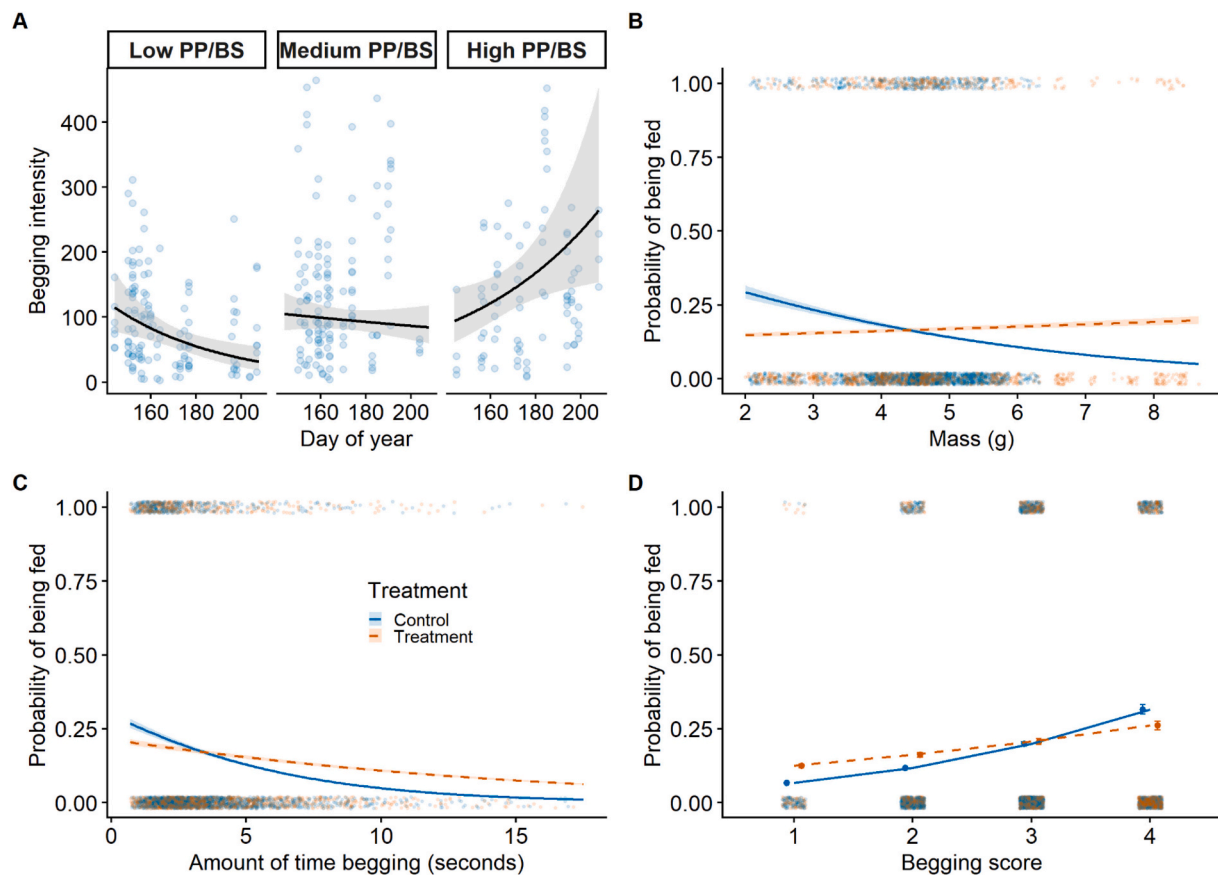


Fig. 3. (A) Relationship between day of year and nestling begging intensity for 5–6 days old nestlings across three levels of parental provisioning/brood size (PP/BS: Panels show model predictions at representative values of PP/BS corresponding to the mean (Medium) and ± 1 SD (Low and High); note that PP/BS was modeled as a continuous variable in all analyses). Points represent observed begging intensity values. Solid black lines show fitted values from the Gamma mixed-effects model, and shaded areas indicate 95% confidence intervals; Predicted probability of a nestling receiving food (5–6 days old) as a function of (B) total body mass, (B) begging duration and (C) begging score. Points represent observed feeding events (0/1). Lines show fitted values from the binomial mixed-effects model, and shaded bands represent 95% confidence intervals. Colors indicate treatment (mealworm supplementation). In panels B–D, predictions are shown at representative values of the focal predictor (mass, begging duration, or begging score, respectively), averaged over site and year. These results indicate that parent-offspring communication is context-dependent: begging intensity vary with season and parental provisioning; furthermore, feeding probability is higher for smaller nestlings and nestlings that beg less (begging duration) and show a higher motivation (begging score). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

in the breeding season begged more than those raised early in the season.

3.2. Parent's response to begging - 5–6 days old

There was no direct effect of site on the probability of a given nestling being fed ($\chi^2 = 3.21$, $p = 0.20$, Table 3). However, when considering the interaction between food supplementation and site, ($\chi^2 = 6.18$, $p = 0.045$), offsprings being raised at the rural site, under supplementation, showed a higher probability of being fed compared to other sites and treatments (Fig. S2).

The probability of a nestling being fed was strongly associated with both begging behavior and offspring body condition, and several of these relationships differed between treatments. Nestlings that begged for longer durations were less likely to have received food during a begging event ($\chi^2 = 28.24$, $p < 0.0001$) while the ones with higher begging scores were more likely to be fed during a begging event ($\chi^2 = 57.94$, $p < 0.0001$). There was no overall main effect of treatment, site, or Julian date (Table 3).

Food supplementation significantly modified the relationships between feeding probability and body mass ($\chi^2 = 14.71$, $p < 0.001$), begging duration ($\chi^2 = 10.04$, $p = 0.001$), and begging score ($\chi^2 = 7.13$, $p = 0.008$), indicating that experimental conditions altered how parents

responded to their offspring traits and behavior regardless of the site (Fig. 3B–D; Table 3). Under control conditions, feeding probability declined with increased mass, while it increased with higher body mass in the treatment group (Fig. 3B). Although the longer begging durations were associated with a lower probability of receiving food for both treatment groups, the decrease for control individuals was steeper (Fig. 3C). Post hoc contrasts confirmed that offsprings raised with food supplementation had significantly higher probabilities of being fed at intermediate and high body mass and at intermediate and long begging durations compared to the control ones (all Tukey-adjusted $p < 0.05$, Fig. 3B–C).

Begging score was a strong positive predictor of feeding probability in supplemented and control nestlings (Fig. 3D). However, treatment effects were most pronounced at low to intermediate begging scores (1–2), where treatment young were substantially more likely to be fed than control ones (all Tukey-adjusted $p < 0.05$). This difference diminished at high begging scores, where feeding probabilities converged between treatments (begging score 3–4, Tukey-adjusted $p > 0.05$).

In addition, there was a significant interaction between begging duration and begging score to predict feeding probability ($\chi^2 = 15.98$, $p < 0.001$, Table 3), indicating that the effect of begging duration depended on visual cues (Fig. S1). Although begging duration was negatively associated with the probability of receiving food, this

relationship became progressively stronger as begging score increased. Thus, individuals exhibiting higher begging scores experienced a steeper decline in feeding probability with increasing begging duration.

3.3. Begging intensity - 11 days old

The effect of nestling mass on begging intensity depended on site (site $\times$ mass: $\chi^2 = 7.28$, $df = 2$, $p = 0.026$; Fig. 4A). At the natural site (high-food availability), nestlings with a higher body mass had a lower begging intensity, whereas at the rural site (low-food availability) individuals with a higher body mass had a higher begging intensity. In the urban site (intermediate-food availability), the relationship between mass and begging intensity was weakly positive and intermediate between the other two environments.

Begging intensity was significantly associated with site, PP/BS, Julian date, food supplementation, and the interaction between site and nestling mass (Table 1). There was a strong positive effect of PP/BS ($\chi^2 = 18.52$, $df = 1$, $p < 0.0001$) and a positive effect of Julian date ($\chi^2 = 8.32$, $df = 1$, $p = 0.004$), indicating that offsprings begged more intensely when PP/BS was higher later in the breeding season. Food supplementation had a strong negative effect on begging intensity ($\chi^2 = 22.61$, $df = 1$, $p < 0.0001$), with supplemented nestlings showing

substantially lower begging levels than control ones in all sites (Fig. S3).

3.4. Parents' response to begging - 11 days old

The probability of a nestling receiving food was strongly associated with both begging score and begging duration, and these relationships depended on environmental context and food supplementation (Table 3). Nestlings with higher begging scores were more likely to receive food ($\chi^2 = 301.79$, $df = 1$, $P < 0.0001$). In contrast, longer begging durations were associated with a lower probability of receiving food ($\chi^2 = 49.06$, $df = 1$, $P < 0.0001$), consistent with nestlings typically ceasing to beg once they received a food item. There was also an overall effect of site ($\chi^2 = 9.23$, $df = 2$, $p = 0.01$) and treatment ($\chi^2 = 7.61$, $df = 1$, $p = 0.006$).

Begging score did not have a uniform effect across environments or treatments. Instead, there was a significant three-way interaction between begging score, treatment, and site ($\chi^2 = 7.49$, $df = 2$, $p = 0.024$; Fig. 4B). Feeding probability increased with begging score in all sites, but this increase was strongest under food supplementation and at the site with lowest ambient food availability (rural). Post hoc comparisons showed that treatment significantly increased feeding probability. In the site with naturally high food availability, when food supplemented,

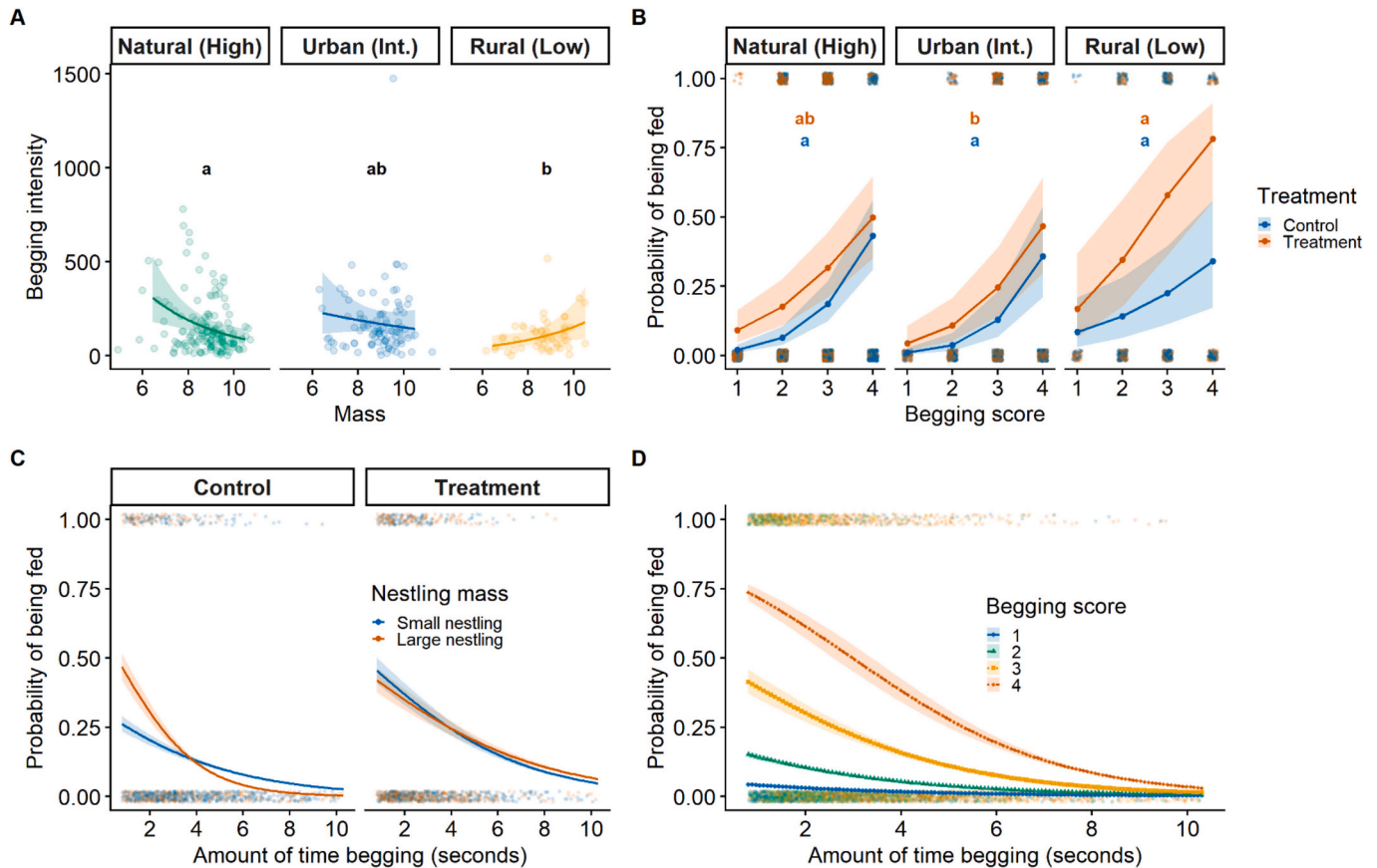


Fig. 4. (A) Relationship between nestling mass and begging intensity across sites with distinct ambient food availability: Natural (High), Urban (Intermediate), and Rural (Low). Points represent observed begging intensity values. Solid lines show fitted values from the Gamma mixed-effects model, and shaded areas indicate 95% confidence intervals. Different letters denote significant differences among sites (post hoc comparisons, $P < 0.05$).

Predicted probability of an 11-day-old nestling receiving food in relation to (B) begging score across sites and treatments, (C) begging duration as a function of nestling mass and treatment, and (D) begging duration at different begging scores. Points represent observed feeding events (0/1). Lines show fitted values from the binomial mixed-effects model, shaded areas indicate 95% confidence intervals, and different letters denote significant differences among sites (post hoc comparisons, $P < 0.05$). In (C), model predictions are shown at representative body masses corresponding to the mean -1 SD ("Small nestling") and mean $+1$ SD ("Large nestling"); body mass was modeled as a continuous variable in all analyses. Feeding probability increased with begging score in all environments, although the magnitude of this increase depended on both site and food supplementation. Feeding probability declined with increasing begging duration, but this relationship depended on nestling mass and treatment (C) and became progressively stronger as begging score increased (D).

Different begging metrics are presented across panels because each analysis used the begging variable retained in the corresponding final model.

nestlings at begging scores 1, 2 and 3 had a higher probability of being fed (all Tukey-adjusted $p < 0.05$), while in the intermediate food availability site the same trend occurred when nestlings were begging at scores 1 and 2 (all Tukey-adjusted $p < 0.05$). At the rural site (low-food availability), nestlings at begging scores 3 and 4 had a higher probability of being fed when food supplemented (all Tukey-adjusted $p < 0.05$), showing a different pattern when compared to the two other sites.

There was a strong three-way interaction between begging duration, nestling body mass, and treatment ($\chi^2 = 51.27$, $df = 1$, $p < 0.001$; Fig. 4C). Under control conditions, larger individuals were more likely to be fed than lighter ones early in begging bouts, but this difference diminished and reversed as begging duration increased. Under food supplementation, feeding probabilities were consistently higher overall, and the effect of nestling mass across begging durations was absent.

Finally, the association between begging duration and feeding probability depended on begging score ($\chi^2 = 4.44$, $df = 1$, $P = 0.035$; Fig. 4D). Nestlings exhibiting higher begging scores were initially much more likely to receive food than those with lower begging scores. However, this advantage declined with increasing begging duration, such that feeding probabilities reduced and became similar across begging scores during prolonged begging bouts.

3.5. Corticosterone concentration - 11 days old

Corticosterone levels depended on interactions between total food received and site, nestling mass and begging intensity, and nestling mass and total food received (Table 2). The effect of total food received on corticosterone differed among sites (site $\times$ total food received: $\chi^2 12.47$, $df = 2$, $p = 0.002$; Fig. 5A), but not by treatment ($\chi^2 0.05$, $df = 1$, $p = 0.81$; Table 2). While there is no visible trend between natural (high-food availability) and urban sites (intermediate-food availability), there is a within-site treatment in rural birds (low-food availability). Rural nestlings that receive less food have a higher corticosterone level compared to well-fed ones. Post hoc contrasts indicated that the food-corticosterone relationship differed significantly between rural and natural sites ($p = 0.007$) and between rural and urban sites ($p = 0.003$), whereas natural and urban sites did not differ.

There was a significant interaction between offspring body mass and begging intensity ($\chi^2 = 7.22$, $df = 1$, $p = 0.007$). At low begging intensity, corticosterone tended to decrease with increasing mass, whereas at higher begging intensities this relationship weakened and became positive (Fig. 5B). Post hoc slope comparisons confirmed that the effect of mass differed significantly across begging levels (all Tukey-adjusted $p < 0.05$), indicating that heavier nestlings only exhibited elevated corticosterone when begging intensity was high.

Finally, corticosterone concentration was also dependent on an interaction between nestling mass and total food received ($\chi^2 = 6.84$, df

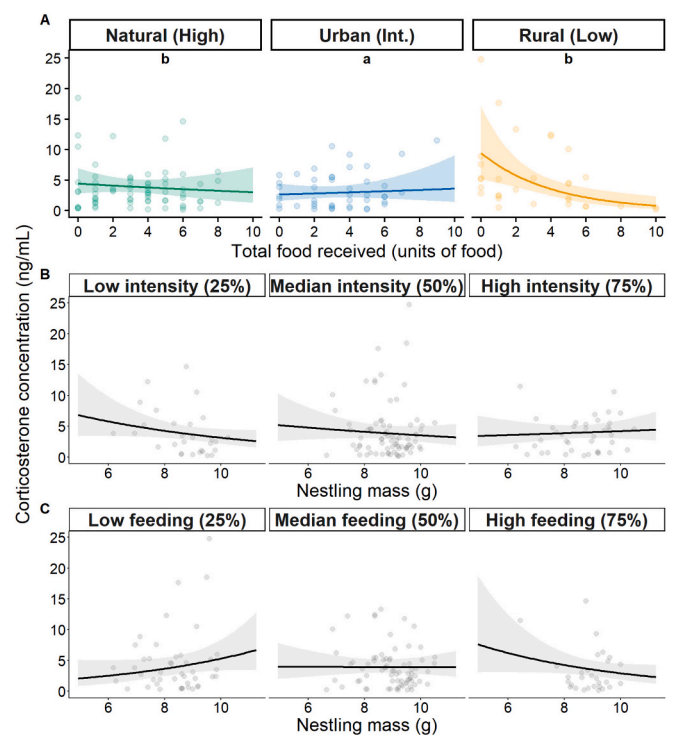


Fig. 5. Relationships between corticosterone concentration and (A) total food received across sites with distinct ambient food availability: Natural (High), Urban (Intermediate), and Rural (Low), (B) nestlings mass at different levels of begging intensity (25th, 50th, and 75th percentiles), and (C) nestlings mass at different levels of total food received (25th, 50th, and 75th percentiles). Please note that in the analyses, these variables were treated as continuous but separated into percentiles here for visualization purposes. Points represent observed corticosterone concentrations. Lines show fitted values from the Gamma mixed-effects model, and shaded areas indicate 95% confidence intervals. At the rural site, individuals that received less food had higher corticosterone concentrations. In addition, at all sites, individuals that received less food always begged more. Whether the ones receiving less were the smallest or the biggest nestlings in a given nest depended on begging intensity and parental provisioning.

$= 1$, $p = 0.009$). When total food received was low, corticosterone increased with nestling mass, whereas at intermediate and high feeding levels this relationship weakened and became negative (Fig. 5C). Thus, heavier individuals showed elevated corticosterone primarily under conditions of low food availability and this trend reversed under high parental provisioning.

3.6. Offspring growth rate and survival

Nestling growth-rate constants did not differ among sites (likelihood-ratio test: $\chi^2 = 2.27$, $df = 2$, $P = 0.322$). Similarly, nestling survival from day 1 to day 12 did not differ among sites (likelihood-ratio test: $\chi^2 = 2.44$, $df = 2$, $P = 0.296$). Overall survival was high across populations, with 153 of 157 nestlings (97.5%) surviving in the urban population, 66 of 71 (93.0%) in the rural population, and 243 of 252 (96.4%) in the natural population.

3.7. Prey size

When nestlings were 5–6 days old, parents at the rural site (low-food availability) fed their offspring smaller prey compared to those at the natural site (high food availability; Fig. S4A; Table S2; Tukey-adjusted $p < 0.05$). In addition, parents in treatment nests consistently delivered larger prey items, a pattern observed both when nestlings were younger (5–6 days old; Fig. S4B) and older (11 days old; Fig. S5B). At 11 days of

Table 2

Results of Type II Wald chi-square tests from generalized linear mixed-effects models examining the effects of site, body mass, treatment (mealworm supplementation), Julian date, year, parental provisioning per brood size, begging intensity and total food received on corticosterone concentration at 11 days of age. Rows in bold indicate statistically significant effects ($p < 0.05$).

	Wald chi-square (χ^2)	Df	p
Corticosterone concentration (11 days)			
Site	4.76	2	0.09
Body mass	0.27	1	0.60
Treatment	0.05	1	0.81
Julian Date	0.26	1	0.61
Year	0.0008	1	0.98
Parental Provisioning/Brood Size	0.11	1	0.74
Begging Intensity	0.12	1	0.73
Total Food Received	0.04	1	0.85
Body Mass * Begging Intensity	7.22	1	0.007
Body Mass * Total food Received	6.84	1	0.009
Site * Total Food Received	12.47	2	0.002

Table 3

Results of Type II Wald chi-square tests from generalized linear mixed-effects models examining the effects of site, body mass, treatment (mealworm supplementation), Julian date, year, begging score, and begging duration on food received at 5–6 days and 11 days of age. Rows in bold indicate statistically significant effects ($p < 0.05$).

	Wald chi-square (χ^2)	Df	p
Food Received (5–6 days)			
Site	3.21	2	0.20
Body Mass	2.00	1	0.16
Treatment	0.72	1	0.40
Julian Date	0.02	1	0.90
Year	4.70	2	0.10
Begging Duration	28.24	1	<0.0001
Begging Score	57.94	1	<0.0001
Treatment * Body Mass	14.71	1	0.0001
Treatment * Begging Duration	10.04	1	0.002
Treatment * Begging Score	7.13	1	0.008
Treatment * Site	6.20	2	0.045
Begging Duration * Begging Score	15.98	1	<0.0001
Food Received (11 days)			
Site	9.23	2	0.01
Body Mass	0.57	1	0.45
Treatment	7.61	1	0.006
Julian Date	2.57	1	0.11
Year	5.15	2	0.08
Begging Duration	49.06	1	<0.0001
Begging Score	301.79	1	<0.0001
Begging Score * Treatment * Site	7.49	2	0.02
Begging Duration * Treatment * Body Mass	51.27	1	<0.0001
Begging Duration * Begging Score	4.44	1	0.03

age, larger nestlings also received larger prey items (Fig. S5C). Finally, while prey size decreased throughout the breeding season at the natural (high-food availability) and rural (low-food availability) sites, the opposite pattern emerged in the urban site (intermediate-food availability), where parents increased the size of the food delivered to their offspring toward the end of the season (Fig. S5A, Tukey-adjusted $p < 0.05$).

3.8. Lepidopterans provisioning

When nestlings were 5–6 days old, the proportion of lepidopterans that parents fed their offspring varied by site and mealworm supplementation (Table S2, Fig. 1B–D). Parents at the urban site (intermediate-food availability) fed nestlings with fewer lepidopteran than the ones at the natural site (high-food availability; $p = 0.006$, Fig. 1B). For 11 days old nestlings, there was no difference in the proportion of lepidopterans fed to offspring by site ($p = 0.35$, Table S2), but it varied whether nests were mealworm-supplemented ($p = 0.0004$, Fig. 1D, Table S2), with nestlings at control nests receiving more lepidopteran prey.

4. Discussion

We present novel experimental data on how variation in food availability influences nestling begging behavior and parental food allocation across free-living populations of a single bird species. Our results demonstrate that parent-offspring interactions are highly context dependent. The relationships among nestling condition, begging behavior, parental food allocation, and corticosterone varied with environmental conditions, developmental stage, and experimental food supplementation. Food supplementation consistently reduced begging intensity in older nestlings, modified how parents allocated food among offspring and the type of prey they delivered, highlighting food availability as a major ecological factor shaping parent-offspring interactions. Variation in local food resources influences offspring

behavior and physiology and parental decision-making, emphasizing the importance of environmental context in understanding parent-offspring behavior.

4.1. Total begging effort varies across development and ecological context

For 5–6-day-old individuals, parental provisioning and Julian date play a major role in shaping begging intensity across all sites. When parents exhibit higher provisioning rates, begging intensity increases throughout the breeding season (Fig. 3A). In contrast, under lower and intermediate provisioning rates, the opposite pattern emerges, with nestlings decreasing their begging intensity as the season progresses (Fig. 3A). Although previous studies have shown that in northern house wrens and other species, such as European starlings (*Sturnus vulgaris*) and tree swallows (*Tachycineta bicolor*), the energetic cost of begging is relatively low compared to total daily nestling expenditure, overt solicitation, particularly when provisioning is limited, still may negatively affect growth and ultimately reduce offspring fitness (Wright and Leonard, 2002; Leonard et al., 2003). Furthermore, phenology is a key factor influencing food (arthropod) availability for nestlings, and insect abundance generally declines toward the end of the breeding season in temperate regions (Verboven et al., 2001). Therefore, when provisioning is already low, begging intensity could become more energetically expensive (and thus reduced) when food becomes less abundant in the environment. However, when provisioning remains high despite limited food availability, competition among siblings may intensify, leading nestlings to increase begging later in the season to outcompete siblings.

At 11 days, the relationship between body mass and begging intensity differed among populations, indicating that the association between offspring condition and begging behavior changes over development and depends on ecological context. Although the relationship between body condition and begging intensity differed among populations at 11 days, these differences were not accompanied by corresponding differences in parental food allocation (Fig. 4B–D). This indicates that variation in begging intensity alone does not determine parental feeding decisions. Instead, the distinct begging patterns observed among populations suggest that local ecological conditions influence how offspring express begging behavior. One possible explanation is that differences in food availability alter the energetic costs and benefits of begging (Price and Ydenberg, 1996; Ghalambor et al., 2010). Under conditions of greater food availability, smaller nestlings may be able to sustain higher begging intensity because the energetic costs of solicitation are offset by more frequent food delivery (Godfray and Charles, 1991; Cotton et al., 1996; Mock et al., 2011). Conversely, when food availability is lower, prolonged or intense begging may be more energetically demanding, such that only nestlings in better condition can afford to maintain high levels of begging (Koykka and Wild, 2018). Although this interpretation is consistent with theoretical predictions that the costs of begging depend on offspring energetic state and resource availability (Price and Ydenberg, 1996; Wright and Leonard, 2002), our results also demonstrate that these differences in total begging intensity do not directly translate into differences in parental food allocation, suggesting that parents integrate additional sources of information when making feeding decisions (see below).

4.2. Parental food allocation depends on food availability and offspring behavior

Food supplementation altered the probability that 5–6-day-old nestlings received food (Fig. 3B–D), demonstrating that food availability influences how parents use offspring cues when making feeding decisions. Under natural food conditions (control nests), smaller nestlings had a higher probability of receiving food than larger nestlings (Fig. 3B). In addition, parents responded more strongly to begging score: nestlings exhibiting the highest begging scores had approximately a 20% greater probability of being fed than those with the lowest scores, whereas this

difference was less than 10% in food-supplemented nests (Fig. 3D). These patterns are consistent with life-history theory, which predicts that parents adjust their reproductive decisions according to prevailing environmental conditions, particularly food availability (Perrins, 1965; Lack, 1968; Smith and Fretwell, 1974). Because food supplementation began immediately after hatching, supplemented parents experienced greater food availability and stability throughout the nestling period than they would under control conditions. Under these circumstances, parents appeared to allocate food less selectively to younger nestlings, reducing the influence of offspring body condition and begging score on feeding decisions. Rather than indicating a change in offspring begging behavior itself, these results suggest that improved food availability and predictability relaxed the constraints on parental food allocation. Another important cue that parents use to decide which offspring to feed is whether nestlings are actively begging when food is being allocated. After a nestling receives a food item, it immediately stops begging to swallow the prey, whereas its siblings often continue begging. Consequently, the negative relationship between begging duration and the probability of being fed (Fig. 3C) is likely an inherent consequence of the feeding process rather than evidence that prolonged begging is ineffective. In other words, shorter begging durations may partly reflect successful parental provisioning: nestlings that are fed earlier stop begging earlier, whereas unfed siblings continue begging and consequently accumulate longer begging durations.

For 11-day-old nestlings, parents appeared to rely even more strongly on offspring begging behavior when allocating food. Across all populations, nestlings with higher begging scores had a greater probability of receiving food, and food supplementation consistently increased feeding probability (Fig. 4B). In contrast to younger nestlings, body mass did not directly influence parental food allocation among sites, suggesting that parents relied increasingly on behavioral cues rather than morphological aspects when allocating food later in nestling development. Previous theoretical and empirical studies have suggested that nestlings adjust their begging behavior through experience in order to maximize food rewards (Kacelnik et al., 1995; Cotton et al., 1996; Lotem, 1998), a prediction later supported experimentally under both laboratory and field conditions (Kedar et al., 2000). Our results are consistent with this hypothesis. Older nestlings that synchronized their begging more closely with parental food allocation had a higher probability of obtaining food, particularly when food availability depended solely on ambient resources. Such behavioral adjustment may become increasingly important as nestlings approach fledging, when differences in nutritional state can have lasting consequences for growth, survival, and recruitment (Thompson et al., 1993; Wiebe, 2020; Whitenack et al., 2025). Rather than depending solely on begging intensity, feeding success appears to result from the interaction between the timing of offspring solicitation and parental decision-making under different ecological conditions.

4.3. Corticosterone concentration reflects ecological and nutritional context

Although experimentally elevating corticosterone increases begging behavior in nestlings (Loiseau et al., 2008; Bowers et al., 2019), we found no evidence that natural variation in baseline corticosterone predicted begging intensity in our populations. Instead, corticosterone concentrations are affected by the interaction between begging intensity and body mass, suggesting that baseline corticosterone reflects the energetic context in which begging occurs rather than begging behavior itself. Baseline corticosterone concentrations were also associated with the amount of food nestlings received, although this relationship differed among populations. Specifically, at the low-food availability site, nestlings that received more food exhibited lower baseline corticosterone concentrations (Fig. 5A), whereas no such relationship was detected at the intermediate- or high-food availability sites. This pattern is consistent with previous studies showing that recent or frequent

feeding reduces baseline corticosterone concentrations, presumably by increasing satiety and reducing energetic stress (Landys et al., 2006; Busch and Hayward, 2009; Benowitz-Fredericks et al., 2024, 2026). Conversely, food limitation is known to elevate baseline corticosterone concentrations in developing birds (Kitaysky et al., 1999; Busch and Hayward, 2009), facilitating behavioral and physiological responses that promote food acquisition. Our results are broadly consistent with those of Benowitz-Fredericks et al. (2026), who likewise found little evidence that baseline corticosterone and begging behavior were directly related once food availability was experimentally increased. Together, these studies suggest that food availability modulates the relationship between physiology and behavior, rather than baseline corticosterone acting as a direct determinant of begging intensity.

Differences in prey quality among populations may also contribute to these patterns. Parents at the natural (high-food availability) site delivered a greater proportion of lepidopteran, whereas adults at the urban (intermediate-food availability) site increasingly delivered larger prey later in the breeding season (Fig. S5A). Lepidopteran larvae are highly nutritious and constitute the primary food source for developing passerine nestlings (Cholewa and Wesolowski, 2011), while larger prey may partially compensate for lower prey quality or abundance. Consequently, nestlings at these sites may have experienced less variation in nutritional state despite differences in the number of prey items received. Although speculative, this may help explain why corticosterone concentrations were less closely associated with food intake at the natural and urban sites than at the low-food availability, rural site.

Our results indicate that corticosterone concentrations depend on the interaction between nestling body mass and both begging intensity and parental provisioning. Larger nestlings generally have greater energetic requirements because metabolic rate and growth costs increase with body size (Weathers, 1992; Klaassen, 1994). Under conditions of high begging activity or reduced provisioning, elevated baseline corticosterone may therefore reflect greater energetic demand or nutritional stress in these individuals. Conversely, when begging intensity was low, conditions likely associated with greater satiety, the relationship reversed, with smaller nestlings exhibiting relatively higher corticosterone concentrations. Our findings indicate that baseline corticosterone reflects the interaction between offspring energetic state and ecological context rather than functioning as a simple physiological correlate of begging behavior. Instead, corticosterone appears to integrate information about nutritional state and food availability, with its relationship to begging behavior emerging only within specific ecological contexts.

5. Conclusion

Our study demonstrates that parent-offspring interactions are dynamic and strongly influenced by both developmental stage and ecological context. Experimental food supplementation altered offspring begging behavior and parental food allocation, highlighting food availability as an important factor shaping these interactions. Importantly, the mechanisms underlying food allocation changed as nestlings developed: parental provisioning early in development was more closely associated with offspring body condition, and older nestlings were more successful when they synchronized their begging with parental feeding decisions. These findings suggest that parent-offspring communication can change for different populations, is not static throughout development, and that studies focusing on a single population and nestling age may overlook important shifts in the behavioral mechanisms underlying food allocation. Future work should therefore consider how developmental stage interacts with ecological conditions to shape both offspring behavior and parental decision-making.

CRedit authorship contribution statement

Ivan C.C. Provinciato: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project

administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Amy M. Yanagitsuru:** Writing – review & editing, Project administration, Methodology, Investigation. **Ava Ciacchia:** Writing – review & editing, Project administration, Methodology, Investigation, Data curation. **Olivia Oldham:** Writing – review & editing, Methodology, Investigation, Data curation. **Jenny Q. Ouyang:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Ethics declaration

This study was conducted in accordance with the ARRIVE (Animal Research: Reporting of In Vivo Experiments) guidelines.

This study was approved by the University of Nevada Reno Institutional Animal Care and Use Committee.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jhbeh.2026.106002>.

Data availability

Data and code available at <https://doi.org/10.5061/dryad.pzgmsbd35>.

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