Dynamic Changes in Begging Signal Short-Term Information on Hunger and Need

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abstract: Dynamic signals can convey distinct information to a receiver on different timescales, making assessment of how quickly signal strength changes important for understanding signal function. Here, we combine repeated measures of offspring begging behavior of western bluebirds with assessments of fitness as well as quantitative genetic analyses of cross-fostered offspring to investigate whether variation in begging behavior conveys information about hunger, need, or quality or has no signaling function. Begging intensity increased with food deprivation, supporting the signal-of-hunger hypothesis. However, after controlling for this variation, multiple lines of evidence showed that begging also signaled need but not quality. Specifically, begging intensity was repeatable only on short timescales, and nestlings that begged more intensely were in poorer condition. Moreover, variation in mean begging intensity was not strongly related to measures of fitness. In general, we found that begging behavior is a highly flexible trait that appears to be unconstrained by both genetic and early developmental influences, as indicated by the cross-fostering experiment that confirmed that the nest environment, not genetic relatedness, explained variation in begging behavior. Together, these results support the idea that begging dynamically signals shorter-term information: hunger and need. More generally, they show the importance of assessing the timescale of signal change to understand its function.

Keywords: dynamic signals, evolution of behavior, behavioral flexibility, begging.

Introduction

Signaling traits are ubiquitous in biological systems, and the evolution of stable signal-receiver dynamics requires a consistent link between trait variation and information content of the signal (Endler 1992). Information signaled serves to reduce uncertainty about a signaler's state (Dall et al. 2005), and in systems that are evolutionarily stable in the long-term, receivers should respond only to signals that convey accurate information. Thus, knowledge of how such accuracy is maintained is critical to understanding signal function and evolution (Searcy and Nowicki 2005). Central to assessment of a signal's information content are comparisons of signal intensity either among individuals or, for dynamic signaling traits, within the same individual over time. In the latter case, assessing within-individual variation is essential to identifying the causes of variation in signaling (Patricelli and Hebets 2016).

Because signals are often thought to provide information about the status or quality of the signaler (e.g., Bowers et al. 2019), understanding the timescale over which a signal changes can clarify the developmental period over which the signal integrates such information (Hill et al. 1999). For example, signals that remain constant throughout an individual's life, such as bird song that is learned during a finite window of time during the juvenile period, may integrate information about either the quality of an individual's rearing environment or its genetic quality (Nowicki et al. 1998; Pitcher and Neff 2007). On the other hand, signals that change within an individual over time, such as for birds that molt into a new plumage annually or for behavioral displays that change within minutes, hours, or days, may provide more fine-scale information about changes in an individual's current status or condition (e.g., Duckworth et al. 2004; McAuley and Bertram 2016). At the same time, dynamic signals may also be noisy, and some variation may convey no information about current state or quality (Patricelli et al. 2016). For example, consistent individual differences, observed as variation in signal strength, may generate noise. Such differences among individuals, which can be due to a stable environment, early-life developmental effects, or genetic differences, can be consistent even when there is within-individual flexibility in the signal on shorter timescales (Stamps 2016). Accounting for consistent differences among individuals may thus be important to understanding the information

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content of signals and requires accurate assessment of both the timescale and the sources of variation in a signaling behavior.

While recent studies highlight the importance of assessing within-individual variation in dynamic signaling traits (Vitousek et al. 2014; Patricelli and Hebets 2016), few studies have combined repeated measures over multiple timescales with quantitative genetic studies (but see Wetzel et al. 2020). Here, we demonstrate the utility of harnessing information from multiple timescales of signal change—over minutes and days and between generations—to investigate the function of conspicuous begging behavior. Nestling begging behavior provides a unique opportunity to link timescales of signal variation to information content for several reasons. Begging behavior has historically been modeled within a signal-receiver framework (Searcy and Nowicki, 2005), where through begging, offspring signal to parents within a closed arena (the nest) to convey information that influences the behavior of parents. As this signaling interaction occurs dozens of times each day over the course of the nestling period, nestling begging signals provide ample opportunity to quantify variation in the signal across multiple timescales.

Moreover, there is ongoing debate about what state, if any, nestlings are signaling to parents through begging (Grodzinski et al. 2011; Hinde and Godfray 2011; Johnstone and Kilner 2011; Kölliker 2011; Mock et al. 2011a, 2011b; Wright 2011). Begging intensity has been shown to vary widely among offspring and is often risky and energetically expensive (Christe et al. 1996; Briskie et al. 1999; Neuenschwander et al. 2003), yet empirical studies addressing the question of why individuals vary have produced disparate results (see below; Kölliker 2011). Current hypotheses to explain variation in begging behavior make clear predictions about how this behavior should vary within and among individuals and across different timescales. Our aim is to not only demonstrate the power of integrating information across timescales to understand signal function in general but also to better understand the information content of conspicuous begging signals in particular.

Begging has been hypothesized to provide parents with three alternative types of information about nestling state, which have been categorized as hunger, need, or quality (Mock 2011b). Signals of hunger convey information about short-term changes in offspring fullness (fig. 1A; Grodzinski and Lotem 2007; Mock et al. 2011b). Under this hypothesis, the strength of the begging signal indicates to the parents the time since last feeding and whether offspring are ready for another meal. While almost all studies agree that begging intensity signals hunger, there is considerable debate about whether additional information about offspring need or quality is conveyed

after accounting for variation due to hunger. Signals of need provide information about the marginal fitness benefit gained by receiving more food (Godfray 1991, 1995). Offspring that signal their need indicate to parents the value of gaining extra resources. Thus, offspring that are in relatively poor condition should signal at a higher level than nestmates in better condition even after controlling for their current hunger state because they need extra food to increase condition above the current state (Mock et al. 2011b; fig. 1A).

Signals of quality convey information about intrinsic aspects of an individual's health and vigor that may influence their reproductive value (Grafen 1990; Mock et al. 2011b). While typically also assessed by measuring differences in nestling condition, in contrast to the signal-of-need hypothesis, the signal-of-quality hypothesis predicts that higher-quality offspring should beg more intensely than lower-quality offspring, conveying information about individual vigor similar to that signaled by sexual traits under the handicap principle (fig. 1A; Zahavi 1975; Mock et al. 2011b). A key, but rarely tested, assumption of the signal-of-quality hypothesis is that because begging intensity should convey information about intrinsic aspects of an individual's merit, the signal itself should show relatively stable differences among individuals (Dale et al. 2001; Wilson and Nussey 2010). Another and relatively unexamined idea is that variation among offspring begging behavior could also reflect consistent individual differences, particularly if offspring and adult expressions of certain traits, such as boldness or aggression, are difficult to decouple across life stages (McCowan and Griffith 2014; Moore and Martin 2019). In this case, stable differences among nestlings in begging behavior would not necessarily reflect offspring quality during the nestling period but may contribute to noise in the signal (Patricelli et al. 2016).

These hypotheses make alternative predictions about sources of variation in begging behavior, its repeatability, and how it relates to variation in individual condition and fitness (fig. 1). Therefore, we use a quantitative genetic framework to test these predictions. This framework allows us to assess repeatability of begging behavior over different timescales and also to determine whether variation is underlain by genetic, permanent-environment (e.g., early maternal effects), or common-nest-environment effects. Specifically, signals of hunger should change on an extremely short timescale on the order of minutes to hours, reflecting an individual's current digestive tract state (from empty to full) and its readiness for another meal. In this case, we expect to see very low or no repeatability in begging and expect that variation is due solely to current environmental variation (fig. 1A, 1B). Signals of need should change on a moderate timescale on the order of days, reflecting slower changes in condition based on the accumulation
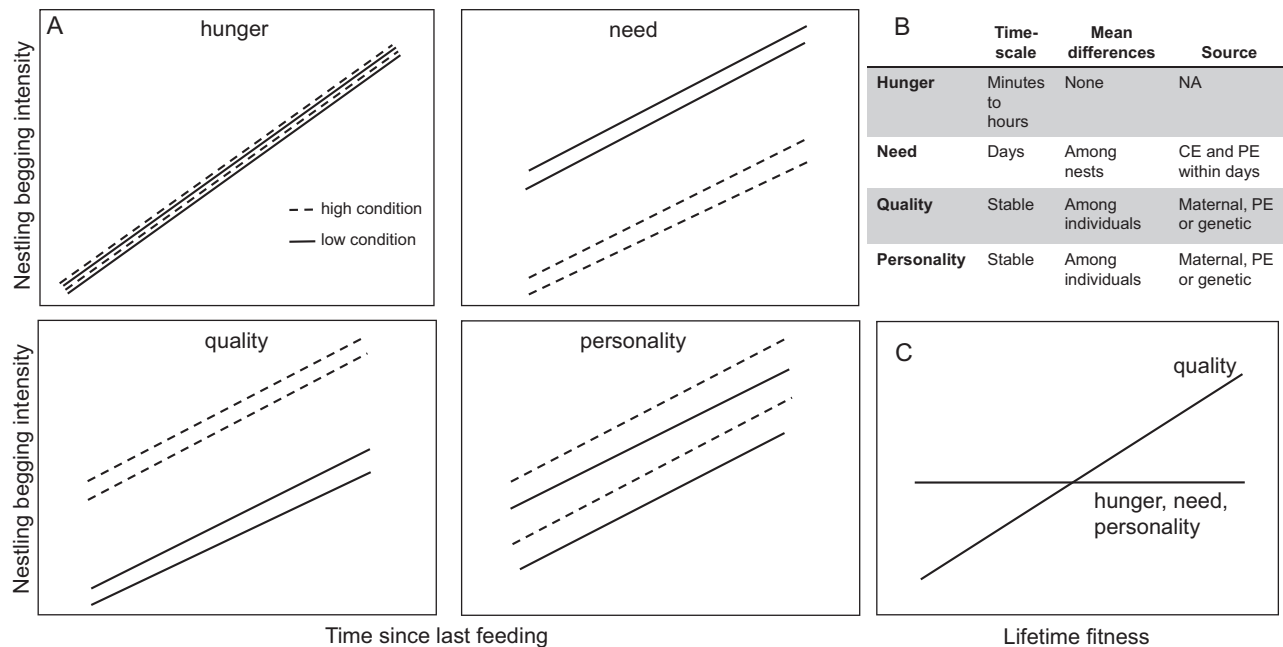
Figure 1: Alternative hypotheses and their predictions based on timescale and sources of variation in begging behavior. *A*, Patterns of variation in begging behavior among four hypothetical nestlings within a brood. Almost all studies show a hunger effect, and for all hypotheses begging intensity should increase in relation to the time since last feeding. However, if differences among individuals at any given time point are explained only by hunger, then mean differences overall will not be related to nestling condition (*top left*). If begging signals need, then high-condition nestlings should have lower mean begging intensity than low-condition nestlings (*top right*), and the opposite is true if begging signals offspring quality (*bottom left*). If differences in begging intensity reflect personality differences among nestlings, then mean begging intensity should not be related to condition despite consistent differences among individuals (*bottom right*). *B*, Hypotheses make alternative predictions about the timescale of variation, whether there are mean differences among nests or individuals and the sources of variation in begging behavior. While both the quality hypothesis and the personality hypothesis predict stable differences in begging behavior that could be due to diverse sources, only the quality hypothesis predicts a relationship with lifetime fitness (*C*). CE = common-environment effects; PE = permanent-environment effects.

of resources over time. In this case, we expect to see high repeatability within days but low repeatability across days. Moreover, the average intensity of begging variation among siblings may converge over the course of the nestling period if parental responses are effective in meeting the need of individual nestlings over time. Given this, we expect that for a signal of need, the main source of variation in begging intensity will be the common nest environment, as nestmates share a parental feeding environment (fig. 1*A*, 1*B*).

For both the signal-of-quality hypothesis and the consistent individual differences hypotheses, we expect a significant repeatability of begging intensity across the nestling period, reflecting permanent differences among siblings in either early developmental environment or genetic variation (fig. 1*A*, 1*B*). Note that the signal-of-quality hypothesis does not necessarily invoke or rely on the concept of genetic quality, which has historically been difficult to assess precisely. Rather, the signal-of-quality hypothesis implies only that a signal will reduce uncertainty about an individual's relative fitness potential in the future.

Thus, the signal-of-quality hypothesis is also the only hypothesis that predicts that offspring that beg more strongly should have higher fitness, a widely assumed but rarely tested prediction (Dale et al. 2001; Mock et al. 2011*b*; Bowers et al. 2019). Links to condition during the nestling period and fitness in adulthood are not necessarily expected if variation in begging intensity simply reflects consistent individual differences among nestlings, even though this last hypothesis also predicts significant repeatability in begging intensity (fig. 1*B*, 1*C*). Because these hypotheses make alternative predictions about sources of variation and fitness consequences of begging behavior, using a quantitative genetic approach is an ideal way of testing them.

Here, we combine multiple assessments of begging intensity in isolation and in whole-brood conditions (defined below) with a cross-fostering experiment and quantitative genetic analyses in western bluebirds (*Sialia mexicana*) to determine the sources of variation in begging behavior and how stable this signal is within individuals. Western bluebirds are a nest box species with low

nest predation, making it possible to acquire multiple measures of begging behavior across the nestling period. In addition, use of artificial nest boxes allows individual offspring to be removed from nestmates for isolated observation with minimal disturbance to the nest. Moreover, western bluebird offspring have a high return rate to their natal population, facilitating the measurement of both begging behavior during the nestling period and fitness components in adulthood. Finally, we have a detailed multigenerational pedigree for the population used in this study (Duckworth and Kruuk 2009), allowing accurate estimates of quantitative genetic parameters.

Methods

Study Population

To investigate patterns of within-individual variation in begging behavior, we collected data on nestling western bluebirds during the 2012 and 2013 breeding seasons at two sites in western Montana (one near Missoula [MSO] and one in the Blackfoot Valley [BFV]), where nests have been monitored and adults have been banded since 2001 (for a detailed description of field sites, see Duckworth 2017). During the breeding season (mid-April to mid-August), all breeding adults at MSO and a subset of adults at BFV were captured and marked with a unique color band combination for individual recognition. At this time, we also obtained a blood sample (for paternity analysis) and standard morphological measurements. Occupied nest boxes were visited at least once weekly to monitor nest progress and mark eggs and to band, bleed, and measure nestlings.

Assessment of Nestling Begging Behavior and Parental Response

We collected data on begging behavior using two methods. For younger nestlings (measured at 4–7 days of age), we recorded the behavior of each nestling using portable nest boxes that were designed for acquiring controlled begging measurements in the field. Two nestlings were removed from their nest, fed to satiation with mealworms, and placed in two separate trial boxes that were placed far enough from both the focal nest box and each other (>50 m) that nestlings could not hear their parents or siblings. The trial boxes were outfitted with a Sony HDR-CX220 video camera to record begging responses over a 1-h period. To maintain a constant temperature during the course of the begging trial, nestlings were placed on a HeatMax HotHands hand warmer placed in a sand-filled pouch to prevent direct contact with nestlings. The nestling was not disturbed for the first 20 min to allow acclimation to the trial box and then was stimulated to beg using recordings

of parental feeding calls that were played at 20, 30, 40, 50, and 60 min. Nestling begging intensity was coded from the videos according to four levels following Kilner (1995): 0, no response; 1, nestling was gaping; 2, nestling was gaping and extending neck; and 3, nestling was gaping, extending neck, and standing on tarsi. The start time of trials for each nestling was recorded.

These trials (hereafter, "isolation trials") could be carried out only in young nestlings that still had their eyes closed, as by day 8, nestlings were no longer responsive to parental contact calls in the controlled trial setup. Therefore, to measure begging intensity in older nestlings, we made recordings in the natural context of the brood (hereafter, "whole-brood trials"). We fitted active nests with motion-activated cameras (Spy On A Bird IP207W) in the nest box lid to record begging over one 4–6-h period between days 10 and 12. We marked nestlings with unique symbols on their head using white correction fluid so that data on individual patterns of begging response could be assessed from videos. To measure begging in this context, we used the same scoring system that was used in the isolation trials and also recorded the rate at which each individual nestling was fed during the observation period (the number of times an individual was fed per hour), the overall per-nestling feeding rate at the nest (the number of feeding trips per hour divided by brood size), the time since last feeding for each nestling, and the time of day.

For approximately half of nests, we measured nestling begging multiple times over the nesting period, resulting in two or three measures of begging across trial days for a subset of nestlings ($N = 103$). Begging intensity was also measured multiple times within trials (isolation trials = 5; for whole-brood trials, mean = 34.88, range = 11–95 repeated measures), resulting in 3,296 observations of begging of 225 nestlings in 51 broods. A major assumption of our hypotheses is that more intense begging results in greater parental responses. Therefore, we assessed parental responses to offspring begging in the whole-brood trials using the GLIMMIX procedure in SAS software (ver. 9.4; SAS Institute, Cary, NC) where nestlings received a zero or one depending on whether they were fed or not fed, respectively. We modeled this with a logit link function and a binomial error term and included nest ID as a random effect with mean begging intensity as a fixed effect and time since last feeding as a covariate.

Measurement of Condition and Fitness

To assess condition, we collected data on nestling body mass on each day when begging intensity was measured. We calculated condition as the residuals of a regression of body mass and nestling age, as there was a strong linear increase in mass across the age measured ($F = 1,411.98$, $P < .001$,

$b_{ST} = 0.90$), with substantial variation in mass among nestlings measured at a given age (see fig. A1A). Moreover, this measure of condition was strongly related to nestling survival (logistic regression: Wald $\chi^2 = 10.89$, $P < .001$), with nestlings that are lighter for a given age having a lower probability of surviving to fledge (fig. A1B). To assess the relationship between offspring condition and begging intensity, we used mixed models with mean begging intensity as the dependent variable and residual mass as the independent variable. We also included nest, individual identity, and individual identity nested within nest as random effects and nest attempt (first vs. second) and time of day as covariates.

To examine whether begging intensity was related to fitness, we assessed whether offspring that begged more intensely were more likely to survive to fledging using the GLIMMIX procedure in SAS with a logit link function and a binomial error term and included nest ID as a random effect. A total of 22 nestlings that were measured for begging behavior subsequently returned as adults and established breeding territories, allowing us to quantify their lifetime fitness as the total number of offspring each individual fledged summed across all of the years they bred in the population. Western bluebirds have high site fidelity in adulthood (Guinan et al. 2000), so we assumed that of these philopatric individuals, those that failed to return across breeding seasons did not survive over winter. To examine the relationship between begging behavior and lifetime fitness, we used Pearson correlation (after verifying normal distribution of both variables) with mean begging intensity (averaged across all repeated measures) as the dependent variable and lifetime fitness as the independent variable. Finally, to determine whether parental feeding rates of broods (measured only during the whole-brood trials) influenced offspring condition, we used a mixed model with residual body mass as the dependent variable, feeding rate of the brood divided by brood size as the independent variable, and nest ID as a random effect.

Cross-Fostering Experiment

To distinguish common environmental effects from genetic effects, we cross-fostered offspring from a subset of nests in 2013 during egg laying before incubation onset. We exchanged one to three eggs between two nests that were matched for their timing of nest initiation, and from this experiment we were able to measure begging behavior of 53 offspring from 16 nests. Eggs were numbered to keep track of lay order, and we swapped eggs that had been laid on the same day, alternating between pairs of cross-fostered nests whether we started with the first or second egg. In this population, clutch sizes vary from three to seven eggs; therefore, for most nests, roughly half of the clutch was exchanged. We did not keep track of which offspring were cross-fostered

at hatch, and therefore we were blind to this information during assessment of begging behavior. For analyses, cross-fostered offspring were identified post hoc using microsatellite markers to identify parents (see below for details). Cross-fostering eggs enabled us to distinguish common environmental influences from genetic influences on begging that occur in the nest environment after laying; however, similar to other cross-fostering studies, we cannot distinguish genetic influences from maternal influences that are present at the time of laying.

In addition to estimating variance components using the animal model (see below), we also directly compared resemblance of begging behavior between cross-fostered nestlings and their unrelated nestmates as well as their full siblings from their nest of origin. For this analysis, we used the mean begging scores of these groups in Pearson correlation analysis.

Pedigree Construction

For quantitative genetic analyses, we constructed a pedigree that spanned five generations with 2,055 individuals, including 199 sires and 230 dams. Western bluebirds have a moderate level of extrapair offspring (10%–20% of offspring; Potticary and Duckworth 2018), and thus the identity of each offspring's genetic father and cross-fostering status were verified using five microsatellites (for details, see Ferree et al. 2008). The pedigree contained both paternal half-siblings (due to extrapair paternity) as well as maternal and paternal full siblings reared separately (due to cross-fostering). Moreover, using pedigree-based analyses allowed us to account for the relatedness structure among adults within the population. Because this population has several related patrilines (Aguillon and Duckworth 2015), incorporating pedigree information enables more accurate estimation of quantitative genetic parameters (Kruuk 2004). Parentage was assessed for each nest by comparing genotypes of offspring and the attending adults. We were unable to obtain a blood sample from the parents at 13% of nests, and in these cases we assumed that the social parents were the genetic parents of the nest. This assumption is warranted because social fathers sire most offspring in a nest and egg dumping is rarely observed in this species (Dickinson and Akre 1998; Potticary and Duckworth 2018). Missing maternal genotypes from one nest prevented us from reconstructing cross-fostering status of four nestlings, and these nestlings were excluded from further analysis. In cases where offspring genotype did not match the social father's genotype, we assigned paternity to another male if the microsatellite data matched completely with only one other male in the population in the same year. In cases where two males at the site matched the genotype of an extrapair nestling, we genotyped with additional markers (Smex 2, 4, 5, 7, 9, 11,

and 13; Ferree et al. 2008) to assign paternity. We were able to successfully assign more than 83% of offspring to their genetic father in the pedigree.

Estimation of Variance Components

To determine fixed effects for quantitative genetic analysis, we first fitted mixed models in SAS with individual identity, nest ID, year, and site included as random factors and type of trial (isolation vs. whole brood), nestling age, and their interaction, as well as time since last feeding, Julian date, time of day, brood size, and nest attempt (first vs. second) as fixed effects. All data were standardized to mean of zero and standard deviation of one for analysis. Neither brood size nor Julian date was related to begging intensity (brood size: $F_{1,3,048} = 0.57$, $P = .450$; Julian date: $F_{1,3,048} = 1.54$, $P = .215$), so they were removed from subsequent analyses. All other fixed effects that were significant or had significant interactions (see "Results") were retained in the animal model. Moreover, begging intensity did not differ across years ($Z = 0.55$, $P = .293$) or sites ($Z = 0.68$, $P = .248$), so these were not included as random effects in the final models.

We estimated variance components using a pedigree-based restricted maximum likelihood mixed model or animal model (Lynch and Walsh 1998; Kruuk 2004). Diagnostics for the model confirmed the assumption of normal error structure. Components of variance were estimated in ASReml version 4 (VSN International). We used a univariate model with repeated measures of begging behavior, including all measurements for each individual both within and across trial days. Observations for successive begging trials of the same nestling were assumed to be repeated observations of the same trait. The total phenotypic variance in begging intensity (V_P) was partitioned as a sum of component parts:

$$V_P = V_A + V_C + V_{PE} + V_T + V_R,$$

where V_A is the additive genetic variance, V_C is the environmental component of variance attributable to a common nest environment, V_{PE} is the permanent-environment effect, V_T is among-individual differences in environmental conditions causing short-term consistency (measured as repeated sampling of begging behavior of the same individual within a trial day; sensu Araya-Ajoy et al. 2015), and V_R is the residual variance. We also ran a second model replacing V_C, the common-nest-environment effect (based on nest of rearing), with a nest-of-origin effect, V_M. This nest-of-origin effect would encompass any effects of the common laying environment, so it would encompass any maternal effects present in the egg at laying. We attempted to fit a model with both of these nest effects; however, this model

was likely overspecified and did not converge. Because we did not have multiple nests with the same social mother in our data set, we were unable to separate the influence of maternal effects due to rearing environment from other aspects of the common nest environment. By fitting both V_{PE} and V_T in the models, we could calculate both short-term (within trial days) and long-term (across days) repeatability of begging intensity to determine at what scale individuals modify their begging, if at all (Araya-Ajoy et al. 2015). We assessed random effects in the full model and sequentially removed effects using likelihood ratio tests to determine the significance of variance components (Pinheiro and Bates 2000). We calculated short-term and long-term repeatability ($R_{short-term}$ and $R_{long-term}$, respectively) as
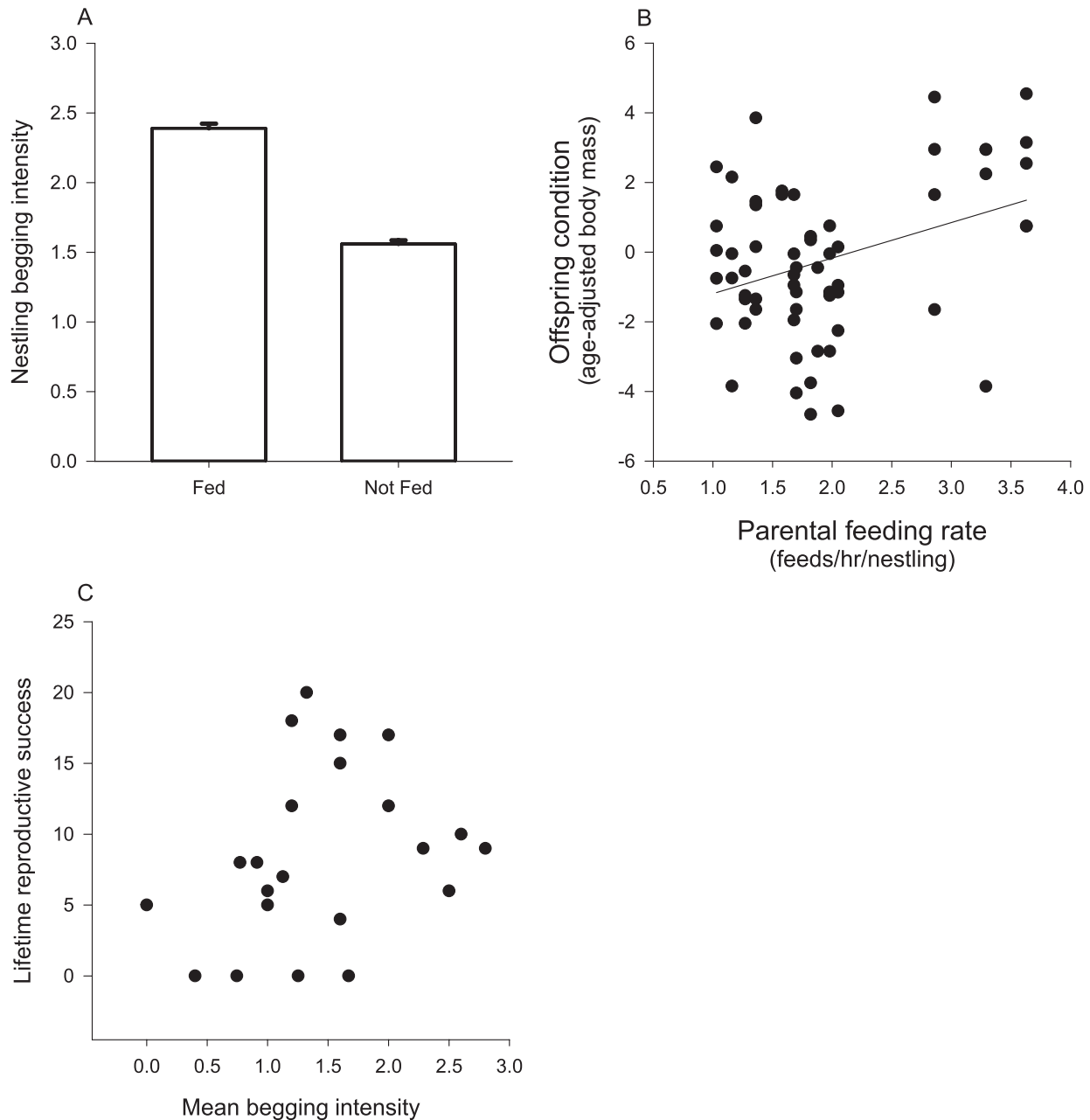
$$R_{short-term} = \frac{V_A + V_C + V_{PE} + V_T}{V_P},$$
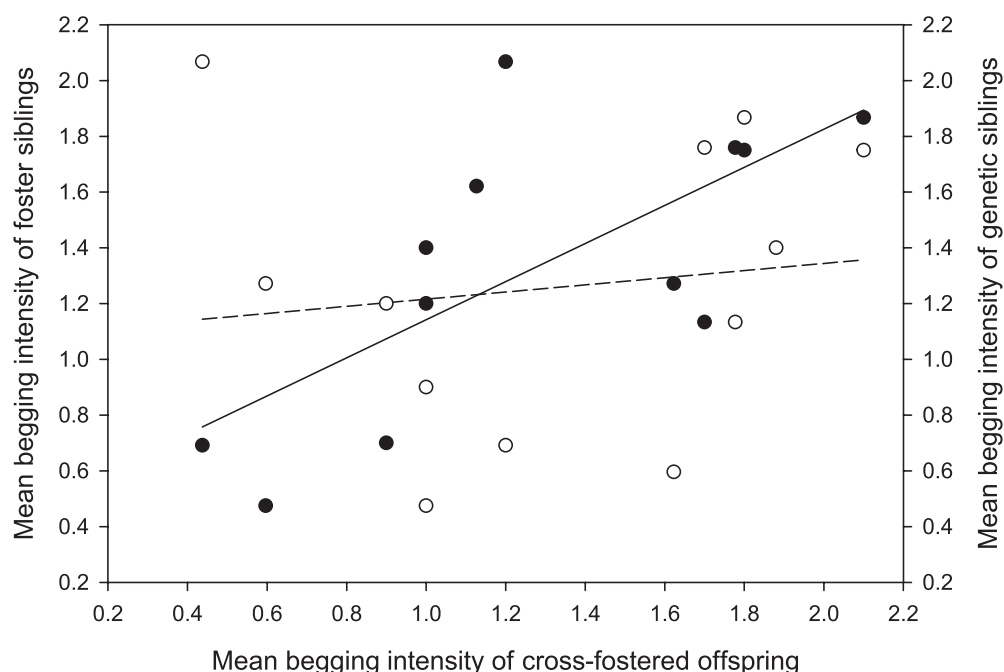
$$R_{long-term} = \frac{V_A + V_C + V_{PE}}{V_P}.$$

Repeatability calculations were based on the model including the common-environment effect.

Results

Begging intensity increased with time since last feeding ($F_{1,3,050} = 18.06$, $t = 4.25$, $P < .001$). Time of day and brood number also influenced begging intensity, with nestlings begging more intensely both later in the day ($F_{1,3,050} = 4.67$, $t = 2.16$, $P = .030$) and in second broods (mean intensity $= 1.87 \pm 0.03$) compared with first broods (mean intensity $= 1.53 \pm 0.02$; $F_{1,3,050} = 15.36$, $P < .001$). Both type of trial and age were unrelated to begging intensity as main effects (type of trial, whole-brood trials vs. isolation trials: $F_{1,3,050} = 1.37$, $P = .241$; nestling age: $F_{1,3,050} = 0.11$, $P = .745$), but there was a significant interaction between them ($F_{1,3,050} = 5.76$, $P = .017$) such that begging intensity decreased with age in the isolation trials ($t_{1,1,120} = -3.45$, $P < .001$) and increased with age in the whole-brood trials ($t_{1,1,868} = 2.09$, $P = .037$).

There was a negative relationship between an individual's mean begging intensity on a given trial day and its age-adjusted mass on that same day—individuals with higher relative mass for their age begged less intensely compared with individuals in poorer condition ($F_{1,110} = 6.73$, $t = -2.59$, $P = .011$). Moreover, in the whole-brood trials parents were more likely to feed nestlings that begged more intensely ($F_{1,1,859} = 113.85$, $P < .001$; mean begging intensity of fed vs. not-fed nestlings: 2.39 ± 0.03 vs. 1.56 ± 0.03; fig. 2A). Nestlings within broods that had a higher feeding rate were in better condition compared with nestlings in broods with lower parental feeding rates ($F_{1,46} = 5.44$, $t = 2.33$, $P =$

Figure 2: Links between begging intensity, parental feeding rates, and lifetime reproductive success. *A*, Offspring that are fed during parental feeding trips are begging more intensely than offspring that are not fed. *B*, Offspring condition is higher in broods with a higher parental feeding rate. *C*, Mean begging intensity as a nestling was not related to an individual's lifetime reproductive success.

.024; fig. 2*B*). Therefore, nestlings that begged more intensely were fed more, and feeding rate was, in turn, positively correlated with nestling condition.

Begging Behavior and Measures of Fitness

Of the 225 offspring with measurements of begging intensity, only 25 (11%) did not survive to fledging. A significant amount of variance in survival probability was explained by nest ID (Wald test: $Z = 2.61$, $P = .005$), but offspring that begged more intensely on average during the nestling period were no more likely to fledge compared with offspring that did not beg as intensely ($F_{1, 174} = 0.14$, $P = .705$). Moreover, there was no significant relationship between an individual's mean begging score and its lifetime fitness (Pearson $r = 0.30$, $P = .181$; fig. 2*C*).

Figure 3: Cross-fostered nestlings resemble their foster siblings' begging behavior (filled circles, solid line) more than their genetic siblings (open circles, dashed line). Shown are mean begging intensities for siblings within a nest grouped by their cross-foster status.

However, the relationship was positive, and given our sample of 22 individuals, we cannot rule out a weak or moderate association between begging intensity and lifetime fitness; despite this, power analysis revealed that we had a greater than 70% chance of detecting an $r > 0.50$ (Cohen 1988).

Effects of Cross-Fostering and Components of Variance in Begging Intensity

Of the 16 nests that included cross-fostered offspring, we were able to directly compare the mean begging intensity of foster nestlings with both their foster siblings and their full genetic siblings for 12 nests. Nests that we could not include in this analysis had mortality of cross-fostered and/or nonfostered offspring, had offspring for which we could not verify parents (because of lack of a DNA sample), or had extrapair genetic siblings making them only half-siblings to the cross-fostered nestlings (these were excluded from this analysis but included in the pedigree-based analysis). Despite the small sample size for comparisons, we found that there was a strong positive correlation between mean begging intensity of cross-fostered nestlings and their foster siblings (Pearson $r = 0.70$, $P = .011$) but not between cross-fostered nestlings and their genetic siblings (Pearson $r = 0.13$, $P = .681$; fig. 3).

Similar to the results of the cross-fostering nest comparisons, there was a strong effect of the common nest environment on begging intensity, but there was no evidence of additive genetic variance for this behavior when this effect was included in the model (table 1). Moreover, nest of origin did not explain any variance in begging intensity when included in the model. Finally, while there was significant repeatability of the behavior within a trial, there was no significant repeatability across days (table 1). Data for all results have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.wstqjq2nr; Gurguis and Duckworth 2021).

Discussion

Behavioral traits span a spectrum of flexibility from highly changeable behaviors that are modified rapidly in response to current environmental conditions to behaviors that remain relatively stable throughout life. This variation in flexibility is often thought to reflect a tension between selection for the ability to track changing state or environmental conditions versus intrinsic constraints to how rapidly certain behaviors can change (Sih et al. 2004; Stamps 2007; Duckworth 2015). Thus, characterizing the timescale of changes in behavioral expression is important because it can shed light on both behavioral function and evolution.

Table 1: Estimates of variance components for begging intensity from animal models using pedigree information including either nest of rearing or nest of origin as random effects

Model information, source	Variance components (SE)	Proportion of total (SE)	P
1. (Nest of rearing/provisioning-based parental effect):			
V_A	.000 ± .000	.00 ± .00	1.00
V_C	.117 ± .038	.112 ± .033	.003
V_{PE}	.037 ± .037	.036 ± .035	.365
V_T	.178 ± .039	.171 ± .036	<.0001
V_R	.709 ± .018	.681 ± .030	
2. (Nest of origin/egg-based maternal effect):			
V_A	.185 ± .048	.176 ± 4.10	.058
V_M	.000 ± .000	.00 ± .00	1.00
V_{PE}	.000 + .000	.00 ± .00	1.00
V_T	.156 ± .033	.149 ± 3.11	<.0001
V_R	.708 ± .018	.675 ± 2.82	
$R_{short-term}$		.332	
$R_{long-term}$		.154	
N		3,296 records, 225 nestlings, 51 nests	
Mean ± SE		1.683 ± .018	

Note: Repeatabilities ($R_{short-term}$ and $R_{long-term}$) are based on model 1. V_A = additive genetic variance; V_C = variance attributable to common nest environment; V_M = variance attributable to egg-based maternal effects; V_{PE} = permanent-environment effect variance across trials; V_T = variance attributable to among-individual differences in environmental conditions across trials; V_R = residual variance; N = sample size.

In this study, we found strong support for the idea that offspring begging conveys information on relatively short timescales but no support for the idea that it is either constrained in flexibility or integrates information about more stable aspects of offspring phenotypic variation. These conclusions are based on several lines of evidence. First, begging behavior was highly repeatable within trial days, but not across days, and there was no evidence for genetic or permanent-environment effect variation in begging behavior (table 1). In fact, cross-fostered nestlings converged with their nestmates and did not resemble their genetic siblings in mean begging intensity (fig. 3). Second, in both isolation trials and whole-brood trials, there was a strong link between the amount of time that had elapsed since an individual's last feeding and their begging intensity, indicating that it changes on the scale of minutes in response to hunger state. This result was not surprising, as many studies have shown similar patterns and it is now well established that begging often signals hunger (Mock et al. 2011*b*). Finally, we also found that mean begging intensity within a trial was correlated with offspring condition—offspring in better condition begged less intensely than offspring in poor condition, a finding that is consistent with predictions of the signal-of-need hypothesis but not the signal-of-quality hypothesis.

These results raise several points. First, they suggest that begging can simultaneously signal offspring's longer-term need for extra food resources and their immediate short-term readiness for another meal. Condition is expected to change more slowly than hunger and is dependent on separate physiological and neurological systems. In birds, for example, hunger is controlled by two regions of the hypothalamus—the ventromedial nucleus controls the sensation of satiety while the lateral hypothalamic area controls the drive to eat (Tachibana and Tsutsui 2016). These drives are regulated by the hormone ghrelin and other gut hormones that are, in turn, directly related to the time since last feeding (reviewed in Honda et al. 2017). Need, on the other hand, may be more closely related to differences in basal metabolic rate and energy utilization, which change on longer timescales (Piersma and Van Gils 2011). Differences in need among nestlings may thus depend on a complex interplay between cumulative effects of hunger, differences in parental feeding rates, and intrinsic differences in physiological and neurobiological systems (Ahima and Antwi 2008).

An interesting finding was the interaction between the effects of nestling age and the type of trial on begging intensity. This interaction could reflect a truly nonlinear relationship between begging intensity and age where the youngest and oldest nestlings beg more intensely. In altricial nestlings, several important physiological events happen about midway through the nestling stage, including the development of vision (Schaller and Emlen 1961), the development of a stress response (Wada et al. 2007), and the switch from ectotherm to endotherm (Price and Dzialowski

2018). It is possible that there is a decrease in begging intensity associated with one or more of these critical developmental switch points. However, because we had to use two different types of trials (isolated and whole brood) at different ages to measure begging, it is also possible that these patterns are associated with trial type rather than general changes in behavior with age.

Nestlings in the same nest environment converged in begging behavior, as substantial variance was explained by the common nest environment and there was a strong correlation between social but not genetic siblings in the cross-fostering experiment. Such convergence could be due to several factors. First, offspring may be directly influenced by their nestmates' begging intensity. In social species, individuals often mimic the behavior of other individuals, such as siblings, with whom they are bonded (Emery et al. 2007; Sapolsky 2017). Therefore, direct stimulatory or inhibitory influences of nestmates' behavior could lead to convergence in begging intensity within a brood (Leonard and Horn 1998). A second possibility is that broods converge on a particular level of begging intensity because they share a provisioning environment that influences their condition, making the overall brood converge in their need for resources (e.g., Saino et al. 2000). Parents were more likely to feed offspring that begged more intensely (fig. 3B; for a similar result, see also Smith et al. 2017), and higher provisioning rates positively influenced nestling condition. Moreover, nestlings begged more intensely in second broods, which in the study populations are known to suffer greater parasitism by blowfly larvae (R. A. Duckworth, personal observation), which may negatively impact nestling condition (Johnson and Albrecht 1993; O'Brien et al. 2001). Thus, links between begging behavior, parental response, and offspring condition suggest that differences among broods in their begging intensity could reflect differences in either parental quality or territory quality, such that broods receiving less or lower-quality food may converge on overall higher mean begging intensities.

Variation in begging intensity did not predict an individual's chances of surviving to fledge. This, combined with the lack of consistency in expression of begging behavior across the nestling period and the negative relationship with condition, provides little support for the signal-of-quality hypothesis. However, a recent phylogenetic analysis of begging behavior (Caro et al. 2016) finds that signals of quality tend to evolve in poor environmental conditions where food is unpredictable and/or scarce. In this context parents feed larger offspring, and ultimately selection favors brood-reducing strategies, such as infanticide or siblicide (Parker et al. 1989). Given this link between environmental conditions and parental strategies, we cannot rule out the possibility that parental responses to begging in bluebirds are context dependent. In this study, we observed very little

offspring mortality (<10%), indicating that environmental conditions were overall good during the years of this study. However, in other years at these sites, we have observed substantial offspring mortality due to late-spring cold snaps that can cause more than 50% nestling mortality (Duckworth 2006; Duckworth et al. 2017). Thus, the possibility remains that under poor environmental conditions, differences in offspring quality may become more prominent, and parents could change their responses to offspring begging, enforcing it as a signal of quality that is linked to offspring survival. After all, partial brood reduction is common in this species in years in which extreme cold snaps occur (Duckworth et al. 2017).

Unlike other studies of passerine begging behavior (Kölliker et al. 2000; Dor and Lotem 2009), we found little evidence of additive genetic variance in begging intensity. There are three main explanations for why our results may differ from these studies. First, unlike other studies, we used a pedigree-based animal model approach to assess heritability of begging. This approach, which allows us to explicitly include fixed effects and multiple random effects, is less biased by potentially confounding environmental variation than other types of analyses (e.g., parent-offspring or sib-sib analyses, which inflate estimates of heritability; Lynch and Walsh 1998; Kruuk 2004). Moreover, its use of covariances across all possible pairs of relatives further reduces the impact of shared-environment effects on heritability estimates. In our study, while we had only 2 years of begging measures and few parent-offspring measures, there are several related patrilines at the site, so there were many measures of second-order relatives, such as cousins, uncles, and nephews. Thus, using the animal model to include multiple measurements of individuals over time at different ages allowed us to simultaneously estimate heritability as well as permanent- and common-environment effects. Most other studies of begging behavior have been unable to examine these latter two environmental effects (but see Wetzel et al. 2020), which are potentially important sources of consistent individual differences. Second, it could be that heritability of begging is lower in western bluebirds compared with other studied species because they are at a different evolutionary point in their coevolutionary dynamics with parents. Strong selection for accurate signaling of hunger and need may have made this signal particularly sensitive to environmental variation, ultimately depleting additive genetic variation in mean begging intensity. However, our findings do not rule out genetic variation for plasticity itself. Finally, as noted above, environmental conditions during our study were particularly good. It may be that genetic variation for begging is masked in such conditions. Stress can unmask hidden genetic variation and simultaneously constitute a particularly strong selective environment (Badyaev 2005). Dor and Lotem (2009) found substantial differences in

heritability across years with negligible heritability in the second year of their study. Thus, while our study finds clear support for the widely held but rarely tested assumption that begging is a highly flexible behavioral trait that is not limited by genetic or developmental constraints, it also is consistent with findings from other studies that suggest selection on begging may be evolutionarily relevant only in a subset of environmental conditions.

There was no evidence of an early maternal effect on begging behavior. Later maternal effects (e.g., due to parental feeding rates) are confounded with the common environment, since we cross-fostered eggs (see "Methods"). This result is surprising given previous findings about the importance of maternal effects on behavior in this system where variation in dispersal and aggression is known to be mediated via androgens allocated to eggs (Duckworth et al. 2015). However, these results are consistent with recent work showing that female western bluebirds do not change androgens deposited in eggs in response to predation risk, a situation that would be expected to influence begging behavior (Mouton et al. 2022).

A major assumption underlying many studies in behavioral ecology is that individuals are highly flexible in their behavior and can change it in response to internal state or external conditions. Yet this assumption is rarely tested. Here, using quantitative genetic methods, we show that begging behavior is a highly flexible trait that appears to be unconstrained by both genetic influences and developmental influences. Our results suggest that begging signals have evolved to signal the offspring's short-term internal state and condition and that parents' responses to these signals ensure an even distribution of resources to offspring. More generally, our examination of conspicuous begging behavior demonstrates the clear utility of assessing a dynamic signal across multiple timescales to understand its function.

Statement of Authorship

Both R.A.D. and C.I.G. were responsible for conceptualization, methods development, experimental design, providing resources, and writing the original draft as well as reviewing and editing. R.A.D. also contributed to funding acquisition, data analysis and visualization, and supervision, while C.I.G. contributed to data collection and data validation.

APPENDIX
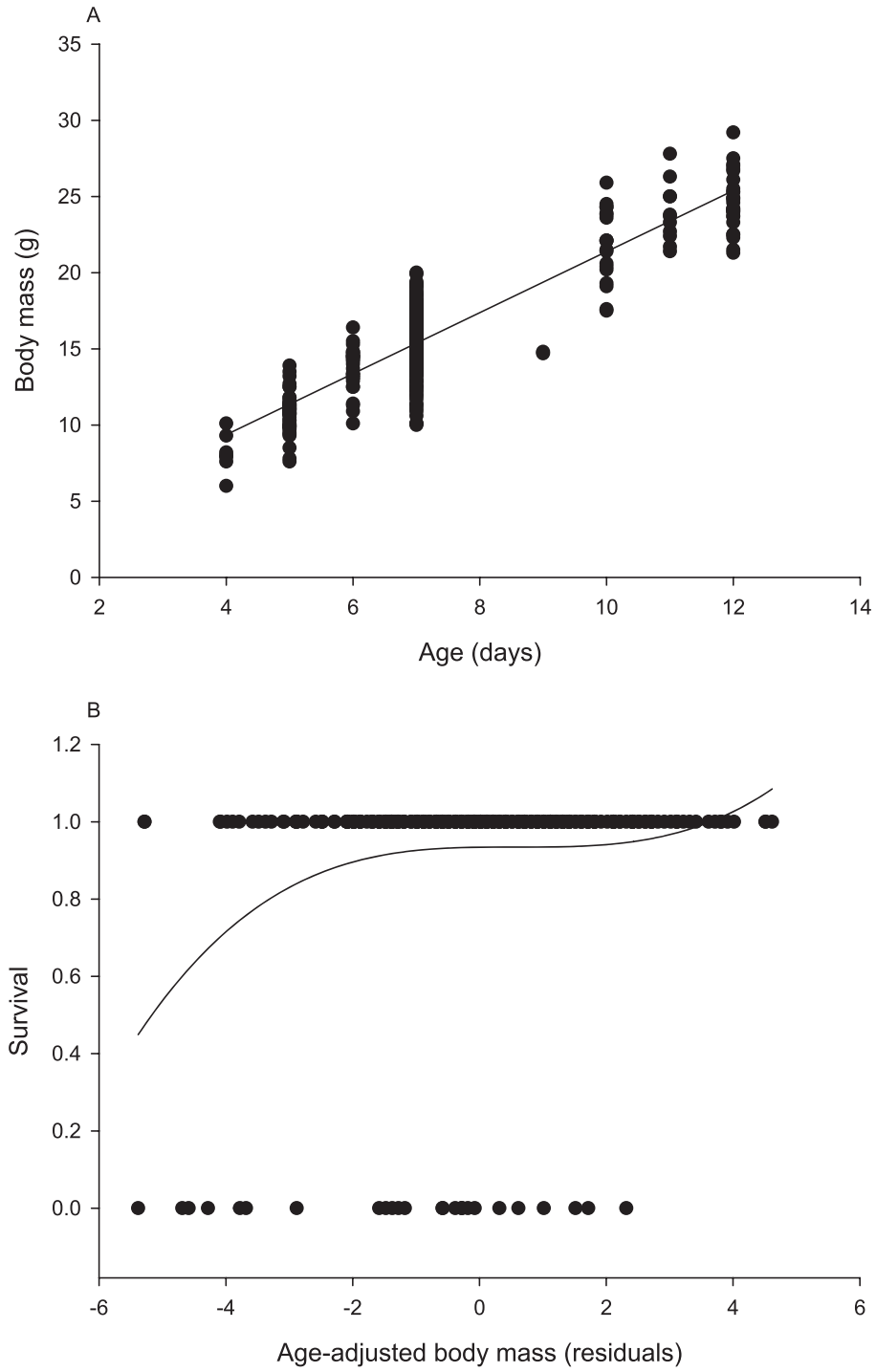
Figure A1: Measurement of condition. *A*, Body mass was significantly related to nestling age and varied substantially within ages. *B*, Age-adjusted body mass was significantly related to nestling survival to fledging, with relative higher-weight nestlings more likely to fledge.

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