

## HOW DO FEMALE RED-WINGED BLACKBIRDS ALLOCATE FOOD WITHIN BROODS?

NICOLE KRAUSS AND KEN YASUKAWA<sup>1</sup>

*Beloit College, Department of Biology, Beloit, WI 53511*

**Abstract.** Nestlings communicate with parents via begging, but what does begging signal and how do parents allocate food to their nestlings? We tested the signal-of-need (SoN) and signal-of-quality (SoQ) hypotheses for nestling begging in the Red-winged Blackbird (*Agelaius phoeniceus*) by attempting to determine whether begging is negatively (SoN) or positively (SoQ) condition dependent, and by attempting to identify the attributes of nestlings that parents use to allocate food within broods. We quantified begging by its mean intensity (scale 0–7) and mean duration and parental allocation by the number of times each nestling was fed. We found that the intensity and duration of begging were not correlated with nestlings' size (estimated by body mass and tarsus length), condition (estimated from the residual of mass regressed on tarsus length), age, sex, or testosterone concentration, so begging did not appear to be negatively or positively condition dependent. A generalized linear model showed that mean intensity of begging, body condition, and log testosterone concentration were significant predictors of the number of feedings. These results are consistent with parents using begging intensity and nestling quality, but not long-term need, to allocate food within broods.

**Key words:** *Agelaius phoeniceus*, begging, condition, hunger, need, quality, Red-winged Blackbird.

### ¿Cómo Asignan los Alimentos entre las Crías las Hembras de *Agelaius phoeniceus*?

**Resumen.** Los pichones mendigan para comunicarse con sus padres, pero ¿qué señal representa esto y cómo los padres asignan los alimentos a sus pichones? Evaluamos las hipótesis de la señal de necesidad (SdN) y la señal de calidad (SdC) para pichones de *Agelaius phoeniceus* que mendigan intentando determinar si la mendicidad depende negativa (SdN) o positivamente (SdC) de la condición, e intentando identificar los atributos de los pichones que usan los padres para asignar los alimentos entre las crías. Cuantificamos la mendicidad de acuerdo a su intensidad media (escala 0–7) y duración media, y la asignación de los padres con el número de veces que cada pichón fue alimentado. Encontramos que la intensidad y la duración de la mendicidad no estuvieron correlacionados con el tamaño del pichón (estimado por la masa corporal y el largo del tarso), la condición (estimado a partir del residuo de la regresión de la masa con el largo del tarso), la edad, el sexo o la concentración de testosterona, por lo que la mendicidad no parece depender positiva o negativamente de la condición. Un modelo lineal generalizado mostró que la intensidad media de la mendicidad, la condición del cuerpo y la concentración logarítmica de la testosterona predijeron significativamente el número de provisiones de alimento. Estos resultados son consistentes con la noción de que los padres usan la intensidad de mendicidad y la calidad del pichón, pero no la necesidad de largo plazo, para asignar los alimentos entre las crías.

## INTRODUCTION

In animals with parental care, communication between parents and offspring is critical (Clutton-Brock 1991). Birds have been the subjects of many studies of parent–offspring communication, and many of these studies have focused on nestlings' begging (Kilner and Johnstone 1997, Budden and Wright 2001, Wright and Leonard 2002). When a parent arrives at the nest with food, nestlings use postures, movement, and vocalizations, display their colorful gapes, and jostle for position (Kilner 2002) to beg (Budden and Wright 2001, Wright and Leonard 2002), but when the parent controls allocation within the brood, it must assess many behavioral, physiological, and morphological traits when deciding which nestling to feed (Budden and Wright 2001, Clark 2002, Mock et al. 2011). We

investigate two related but not identical questions about parental allocation of care. What does begging signal? On what do parents base their allocation decisions?

Clark (2002) divided the signal components of nestlings' begging into three categories: hunger, need, and condition. Mock et al. (2011) discussed these categories by suggesting that parent-in-control hypotheses for nestlings' begging could be divided into three types. The signal-of-hunger (SoH) hypothesis proposes that volitional begging signals act like a fuel gauge (Grodzinski and Lotem 2007) to express a nestling's fullness. The signal-of-need (SoN) hypothesis suggests that parents use begging signals to assess how much a food item will improve the signaler's fitness, allowing parents to favor needy offspring (Godfray 1991, 1995). Finally, according to the signal-of-quality (SoQ) hypothesis, begging

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<sup>1</sup>E-mail: [yasukawa@beloit.edu](mailto:yasukawa@beloit.edu)

indicates a nestling's reproductive value so that parents can preferentially allocate food to offspring of high reproductive value (Grafen 1990). We use the term "signal" to mean informative traits that evolved to change the behavior of receivers (e.g., begging calls) to the benefit of signalers and receivers (Searcy and Nowicki 2005, Ruxton and Schaefer 2011). In contrast, "cues" are informative traits (e.g., size) that did not evolve as signals (Searcy and Nowicki 2005, Ruxton and Schaefer 2011), whereas "attributes" are other characteristics (e.g., age) that do not directly provide information to receivers.

#### NESTLING HUNGER, NEED, AND QUALITY

Hunger is the expression of short-term nutritional requirements and is what motivates a nestling to beg and to compete aggressively for food (Budden and Wright 2001, Clark 2002, Mock et al. 2011). Differences in hunger (short-term need) produce variance in intensity of begging, and it presumably benefits a parent to provision the brood at a faster rate in response to more intense begging, and to favor intensely begging nestlings (Budden and Wright 2001, Clark 2002, Mock et al. 2011). Feeding by parents (or ornithologists) therefore reduces the intensity of begging in the short term, whereas experimental food deprivation increases it. Results of many studies of birds support the SoH hypothesis (Budden and Wright 2001, Clark 2002, Kilner 2002, Mock et al. 2011).

Need refers to the food requirements of the nestling over the longer term (Price et al. 1996, Clark 2002). Need could thus represent the amount of food necessary for a nestling to reach fledging or independence and is a function of the nestling's size, condition, age, growth rate, and sex in sexually dimorphic species, among other things. According to the SoN hypothesis, needy offspring should beg intensely and parents should favor them as a result of the marginal benefit to nestlings of receiving extra food (Godfray 1991, 1995). Several studies have demonstrated parental preference for intensely begging and apparently needy nestlings (Budden and Wright 2001, Wright and Leonard 2002, Mock et al. 2011).

Quality reflects a nestling's reproductive value, which is affected by its relative growth, nutritional reserves, hormone concentrations, and immunocompetence (Clark 2002, Saino and Møller 2002, Schwabl and Lipar 2002, Mock et al. 2011). As proposed by Grafen (1990), the best nestlings beg most and parents favor high-quality nestlings to avoid wasting food on young with low reproductive value. An index of condition is often used as a proxy for relative growth or nutritional reserves and is typically estimated as the residual of expected body mass for a given skeletal size (Hochachka and Smith 1991, Rosivall et al. 2005, Vitz and Rodewald 2011). Several studies have documented parental favoritism toward nestlings signaling high quality (Budden and Wright 2001, Wright and Leonard 2002, Clark 2002, Saino and Møller 2002, Mock et al. 2011). Other studies have shown that hormone concentrations affect begging behavior, parental feeding, and fledging success. The concentration of maternal testosterone in egg yolk

is positively correlated with the nestling's effort in begging and with its growth and development (Schwabl 1996, Eising and Groothuis 2003). The nestling's endogenous testosterone is positively correlated with the intensity and duration of begging (Goodship and Buchanan 2006). Increased corticosterone levels facilitate begging and provisioning by parents (Kitaysky et al. 1999, 2001, 2003). Finally, broods with high testosterone are more successful at fledging than are broods with low testosterone (Goodship and Buchanan 2006).

#### RED-WINGED BLACKBIRDS

When an adult Red-winged Blackbird (*Agelaius phoeniceus*), usually the female, arrives with food, the nestlings beg actively and one or more nestlings are fed (Searcy and Yasukawa 1995). Females sometimes put a food item in one nestling's mouth, pull it out, then put it back in or give it to another nestling (Wilson and Clark 2002, pers. obs.). Allocation of food thus appears to be an active choice of the parent.

Several aspects of parent–nestling interaction have been studied in the Red-winged Blackbird. Hunger affects begging behavior (Whittingham and Robertson 1993), and provisioning adults respond to the rate of a brood's begging (Burford et al. 1998, Glassey and Forbes 2002a, but see Clark and Lee 1998) and to the brood's size and age (Yasukawa et al. 1990, 1993). Parents are most likely to feed nestlings that reach highest and beg first (Teather 1992), and parents decrease their provisioning rates when nestlings are temporarily muted (Glassey and Forbes 2002b). Additionally, nestlings that hatch later and are consequently smaller beg more intensely than their older and larger broodmates (Glassey and Forbes 2002a).

Male and female Red-winged Blackbird nestlings grow at different rates and achieve different body sizes (Holcomb and Twiest 1970, Teather 1992, 1993); at fledging males are 30% heavier and require nearly 30% more energy than females (Fiala 1981, Fiala and Congdon 1983). The energy needs of male nestlings are thus greater than those of females, and Teather (1992) found that males received more food than their female siblings. J. Peet and A. B. Clark (cited in Clark 2002) found that this sex difference in feeding does not develop until days 7–9 of the nestling period when the size dimorphism becomes apparent.

Within a clutch, maternally produced testosterone in Red-winged Blackbird egg yolk increases as the eggs are laid regardless of the nestling's sex (Lipar et al. 1999) and may mitigate effects of asynchronous hatching, aid the development of neck muscles necessary for begging, and contribute to overall mass (Lipar and Ketterson 2000, Schwabl and Lipar 2002).

We studied begging of Red-winged Blackbird nestlings and their parents' food allocation by first examining the hunger, need, and quality hypotheses for begging. Given the wealth of data on begging as a signal of short-term need (e.g., Rydén and Bengtsson 1980, Götlander 1987, Stamps et al. 1989, Smith and Montgomerie 1991, Redondo and Castro 1992, Teather 1992, Whittingham and Robertson 1993, McRae et al. 1993, Kacelnik et al. 1995, Cotton et al. 1996,

Leonard and Horn 1996, 1998, Ottosson et al. 1997, Burford et al. 1998, Glassey and Forbes 2002a), we tested whether begging was related to attributes of nestling Red-winged Blackbirds that are presumably related to long-term need or to quality. We examined size, condition, testosterone concentration, sex, and age as nestlings' attributes.

The quality and need hypotheses make distinct predictions, so can be treated as alternatives in hypothesis testing (Kölliker 2003, 2011). For example, the SoQ hypothesis predicts that nestlings in good condition should beg more and be preferentially fed by parents, whereas the SoN hypothesis predicts the opposite. Our use of the viewpoint of signaling to study nestlings' begging and parental allocation, however, leads us to separate begging and allocation in our hypothesis tests. Lotem (1998a) pointed out that the optimal level of signaling and a signaler's quality (condition) may be either positively or negatively correlated. If begging were a negatively correlated condition-dependent signal, then we should expect begging to be intense in nestlings likely to require substantial food resources to reach independence. In contrast, if begging were a positively correlated condition-dependent signal, then we should expect begging to be intense in nestlings with high reproductive value. Our specific predictions for the nestling's attributes of size, body condition, testosterone concentration, sex, and age are shown in Table 1.

Regardless of whether nestlings' begging is reliably correlated with hunger or condition, we expect parents to respond adaptively to signals, cues, and other attributes as they allocate food among the nestlings in a brood. Godfray

(1991), for example, assumed that quality and need are cryptic (provide no cues) in his initial explanation of the evolution of honest begging. We therefore attempted to determine whether nestlings' attributes affect parents' decisions to allocate. If parents respond to begging, then nestlings that beg strongly will be fed more than weaker beggars. If allocation is negatively condition dependent, then needy nestlings will be fed more than less needy ones. If allocation is positively condition dependent, then better nestlings will be fed more than less valuable nestlings. Our specific predictions for nestlings' attributes are shown in Table 1.

We tested our predictions by observing parental feeding and begging of nestling Red-winged Blackbirds at Newark Road Prairie, Wisconsin.

## METHODS

### FIELD METHODS

We studied Red-winged Blackbirds at Newark Road Prairie (42° 32' N, 89° 08' W), a 13.5-ha remnant prairie in south-central Rock County, Wisconsin (Yasukawa 1989), in May–July 2008–2010. Thirty 1-hr videos were recorded at nests containing 2–4 nestlings on day 8 of the nestling period (nestlings were 4–7 days old) between 06:30 and 10:00 CDT. We marked bills with a nontoxic, permanent marker (Sharpie 15001, Sanford Corporation, Bellwood, IL) for recognition of individuals. We placed a Velbon Stratos 460Q tripod (Velbon Corporation, Nakandoke, Japan) and a Sony HDR XR520 video camera (Sony Corp. of America, New York, NY) within

TABLE 1. Predictions of begging-signal and food-allocation hypotheses for nestling Red-winged Blackbirds.

Nestling attribute	Condition dependence	
	Negatively condition dependent	Positively condition dependent
Size	Negative correlation	Positive correlation
Condition	Negative correlation	Positive correlation
Endogenous testosterone	Negative correlation	Positive correlation
Sex	Males > females	Ambiguous <sup>a</sup>
Age	Negative correlation	Positive correlation
	Food-allocation hypotheses	
	Negatively condition dependent	Positively condition dependent
Begging behavior	Favor intense beggars	Favor intense beggars
Size	Favor smaller	Favor larger
Condition	Favor low condition	Favor high condition
Endogenous testosterone	Favor low <i>T</i>	Favor high <i>T</i>
Sex	Favor males	Ambiguous <sup>a</sup>
Age	Favor younger	Favor older

<sup>a</sup>It is unclear whether male or female nestlings should have higher reproductive value. Early growth may affect reproductive success more in males than in females, so that males in good condition (or males that are attractive to females) may have high reproductive value in a polygynous species such as the Red-winged Blackbird, especially if the parents are also attractive and in good condition, whereas unattractive males in poor condition may have low reproductive value (e.g., Trivers and Willard 1973, Burley 1977, Clutton-Brock 1991).

0.5 m of the nest to be recorded and started the camera after we observed a parent feeding the nestlings. After recording, we measured the nestlings' body mass with a 50-g Pesola scale (Pesola AG, Baar, Switzerland) and tarsus length with General 144-mm calipers (General Tools, New York, NY), and we collected a 100- $\mu$ L blood sample from the wing vein of each nestling with a BD 27½-gauge hypodermic needle (Becton, Dickinson and Company, Franklin Lakes, NJ) and a 370- $\mu$ L heparinized Caraway tube (Fisher Scientific, Waltham, MA). Blood samples were stored in 1-mL microfuge tubes (Fisher Scientific, Waltham, MA) and immediately placed on ice. As soon as we returned from the field, we centrifuged the blood (Eppendorf 5415 Microcentrifuge; Eppendorf, New York, NY) to separate the plasma and cells. Plasma was frozen for later hormone assay. Cells were placed in Queen's lysis buffer ([www.aou.org/committees/collections/recipes\\_dna\\_buffers.php](http://www.aou.org/committees/collections/recipes_dna_buffers.php)) and stored at 4 °C for later sex identification. The Beloit College Institutional Animal Care and Use Committee approved all protocols. Blood collection was endorsed by the U. S. Geological Survey (banding permit 20438).

We watched the videos to score each nestling's intensity of begging and to record the duration of begging at each visit by a parent to feed. We devised a scale of begging intensity (Table 2) by using the begging behavior described by Redondo and Castro (1992) and Teather (1993). This scale combined multiple aspects of begging behavior, including posture, calling, gaping, and jostling for position (Kilner 2002). We averaged scores of intensity and durations of begging for each nestling over the 1-hr observation. We also recorded the number of times each nestling was fed during the hour.

Our use of number of feedings as the dependent variable assumes that visits to feed are relatively uniform. To meet this assumption, prey items should be of similar size and similar numbers of prey should be delivered at each visit. Deliveries should also be to individual nestlings. We therefore attempted

to identify the food items delivered to the nestlings. In many cases, we could not confidently identify food items, but we could determine how many items were delivered, and we could assign items to one of three size classes (small, medium, and large). We could also determine whether the delivery was allocated to a single nestling or divided among broodmates. Nearly all (98%) deliveries were made by females, consisted of a single prey item (90%), and were allocated to a single nestling (88%). The vast majority of food items (81%) were medium-sized prey, and most medium-sized items (63%) appeared to be cabbageworms (*Pieris* spp.). Smaller prey accounted for 16% of delivered items, and the remaining 3% were larger prey.

BODY CONDITION

We calculated an index of body condition from residuals of stepwise polynomial regression of body mass on tarsus length (Hochachka and Smith 1991). This index compared a nestling's body mass to that predicted for its tarsus length; a relatively heavy nestling received a positive condition score, whereas a lighter-than-expected nestling received a negative score. Recent examinations of condition estimates based on regression residuals have emphasized problems with this method, including unwarranted assumption of linearity and lack of validation (Green 2001, Labocha and Hayes 2011). Stepwise polynomial regression addresses limitations of linearity. We assessed validity in two ways. Nestlings that became fledglings ( $n = 59$ ) had mean body-condition indices ( $0.62 \pm 0.34$ ) significantly higher ( $t_{82} = 3.73, P = 0.0002$ ) than those of nestlings that did not survive the nestling period ( $n = 25; -1.71 \pm 0.52$ ). Logistic regression showed that our body-condition index was a significant predictor of fledging success ( $\chi^2_1 = 14.4, P = 0.003$ ). We conclude that our method of estimating body condition is valid for Red-winged Blackbird nestlings.

TESTOSTERONE ASSAY

We assayed nestlings' testosterone concentration by enzyme immunoassay (EIA) techniques (Ginther et al. 2001). Hormones were extracted, separated, and assayed at the University of Wisconsin-Whitewater. We extracted plasma samples in anhydrous ethyl ether, then separated them by celite chromatography (Abraham et al. 1972), using external recoveries to estimate loss of hormone through extraction and chromatography. Extracted samples were dried and then reconstituted in 4% ethyl acetate in isoctane. We separated testosterone from other hormones including dihydrotestosterone by eluting it with 20% ethyl acetate in isoctane. Microtiter plates (Nunc-Immuno Plate Maxisorb F96 certified; VWR Scientific, Chicago, IL) were coated with androgen antibody (R156, University of California, Davis; diluted 1:20 000). Standard curves on each plate were created from 10 testosterone standards, (0.489–250 pg well<sup>-1</sup>). Absorbance was read at 415 nm with a correction at 570 nm on an Emax (Molecular Devices Corp., Sunnyvale, CA). Using 4-parameter estimation,

TABLE 2. Begging-intensity scores for nestling Red-winged Blackbirds (based on Redondo and Castro 1992, Teather 1993).

Score	Behavior
0	No begging
1	Partial gape or opening and closing of bill
2	Head up, full-gape
3	Head up, full gape, vocalization
4	Stretching neck up, full gape, vocalization
5	Blocks other nestlings, stretching neck up, full gape, vocalization
6	Wings outstretched, blocks other nestlings, stretching neck up, full gape, vocalization
7	Legs outstretched, wings outstretched, blocks other nestlings, stretching neck up, full gape, vocalization
8	Wings outstretched and flapping, legs outstretched, blocks other nestlings, stretching neck up, full gape, vocalization

we calculated testosterone concentrations with Softmax Pro software (Molecular Devices Corp., Sunnyvale, CA) and report them as pg L<sup>-1</sup> of plasma. The sensitivity of the EIA at 90% binding was 0.50 pg. Quality-control pools were assayed for each hormone. The intra-assay and inter-assay coefficients of variation were 11% and 30%, respectively. The mean external recovery was 91%.

#### SEX IDENTIFICATION

Nestlings were sexed at the University of Wisconsin–Milwaukee by chromosomal markers. DNA was extracted from blood samples with a 5-M salt solution (Miller et al. 1988). We used P8 and P2 primers to amplify conserved regions within an intron in both CHD1-W and CHD1-Z genes (Griffiths et al. 1998). Each PCR contained 50–100 ng of genomic DNA, 0.5 μM of each primer, 10 mM Tris-HCL (pH 8.3), 1.5 mM MgCl<sub>2</sub>, 0.8 mM dNTPs and 0.5 U *Taq* polymerase in a 10-μL total reaction volume. The thermal program for amplification included an initial 2-min denaturation at 94 °C followed by 29 cycles of 94 °C for 30 sec, 47 °C for 45 sec, and 72 °C for 45 sec, and one final cycle of 48 °C for 1 min and 72 °C for 5 min. In the Red-winged Blackbird, the amplified W and Z fragments do not differ greatly in size, so we separated PCR products by electrophoresis for 120 min at 7 V cm<sup>-1</sup> in a 3% NuSieve 3:1 agarose (FMC Corporation, Philadelphia, PA) gel stained with ethidium bromide. We visualized digested PCR products under UV light and scored one band as male and two bands as female. To confirm the accuracy of the sex identification, we amplified DNA of two adults of known sex (one male and one female) in each PCR reaction and ran it on each agarose gel. In both cases the molecular method correctly identified the sex of these adults.

#### STATISTICAL ANALYSES

We used mean intensity (0–7) and mean duration (sec) of begging to estimate nestlings' begging and body mass (g), tarsus length (mm), body condition, sex, age (days), and log testosterone concentration ( $T$ , pg L<sup>-1</sup>) as nestlings' attributes. We calculated partial correlation coefficients between begging and these attributes to test for negative condition dependence and positive condition dependence. We used a log transformation to correct for the lack of normality in estimated  $T$ .

We also attempted to identify the attributes of nestlings that affect the number of feedings they receive. To reduce collinearity, we examined intercorrelations among variables and used those results to select mean score for begging, tarsus length, body condition, sex, and log  $T$  as effects and number of feedings as the response variable in an analysis with hierarchical generalized linear model (GLM). We also included the brood's identity as a factor in an attempt to account for the lack of independence of nestlings within a brood (Forbes 2002, Rosivall et al. 2005). Although the proportion of feedings allocated to each nestling in a brood might also be informative,

we do not report GLM results for that metric here for two reasons. First, we believe that number of feedings is better than proportion of feedings as an estimate of the amount of food a nestling receives because it accounts for the overall rate of feeding. For example, a nestling that was allocated 3 of 4 items delivered to the brood received less food than another fed 5 of 10 items. Second, the results of GLM analyses using proportion of feedings were similar to those with number of feedings and therefore added little information.

GLMs use maximum-likelihood estimations to estimate parameters. We used an information-theoretic approach to evaluate support for 19 a priori candidate models that might affect the number of feedings (Table 3). Our candidate models included a global model with all explanatory variables (brood identity + mean begging intensity + tarsus length + body condition + sex + log  $T$ ). We used a normal distribution to model all response variables. Models were then fit by the Generalized Linear Model personality and Identity link function in JMP Fit Model (JMP User Guide, Release 8, SAS Institute, Cary, NC). We used Akaike's second-order information criterion (AIC<sub>c</sub>), which is well suited to fit smaller sample sizes (Burnham and Anderson 2002), to identify the best-fit model. As only one model received strong support ( $\Delta\text{AIC}_c < 2$ ), we used parameter estimates from that model.

All statistical tests were done in JMP (version 8, SAS Institute, Inc., Cary, NC). We accepted statistical significance at  $\alpha = 0.05$ .

#### RESULTS

We obtained partial data for 114 nestlings, which we used in correlation analyses. As shown in Table 4, none of the partial correlations between the two variables for begging (mean intensity and mean duration) and other attributes of nestlings were significant. Thus nestlings' begging did not appear to be negatively or positively condition dependent in the Red-winged Blackbird.

The two estimates of nestlings' begging (intensity and duration) were significantly correlated ( $r_{81} = 0.367$ ,  $P < 0.01$ ), so we limited further analysis to intensity. The two estimates of size (tarsus length and mass) were also significantly correlated ( $r_{82} = 0.806$ ,  $P < 0.01$ ). Because mass varies through the day, we used tarsus length in the subsequent analysis. Finally, body condition and age were significantly correlated as well ( $r_{84} = 0.233$ ,  $P = 0.033$ ). As the age distribution was highly skewed (73% of the nestlings were 7 days old, 23% were 6 days old, 4% were 5 days old, and only 1 nestling was 4 days old), we used body condition in the GLM.

We obtained data for all variables on 54 nestlings in 18 broods. GLM using these data produced 10 models (Table 5) with significant goodness of fit (deviance value/df). Only one of these models (brood identity + mean begging intensity + body condition + log  $T$ ), however, received strong support ( $\Delta\text{AIC}_c < 2$ ).

TABLE 3. The 19 candidate models used in GLM analysis of factors affecting rate of feeding of nestling Red-winged Blackbirds.

Brood identity + one factor	
1.	Brood identity + mean begging intensity
2.	Brood identity + tarsus length
3.	Brood identity + body condition
4.	Brood identity + sex
5.	Brood identity + log <i>T</i>
Brood identity + mean begging intensity + one other factor	
6.	Brood identity + mean begging intensity + tarsus length
7.	Brood identity + mean begging intensity + body condition
8.	Brood identity + mean begging intensity + sex
9.	Brood identity + mean begging intensity + log <i>T</i>
Brood identity + mean begging intensity + two other factors	
10.	Brood identity + mean begging intensity + tarsus length + body condition
11.	Brood identity + mean begging intensity + tarsus length + sex
12.	Brood identity + mean begging intensity + tarsus length + log <i>T</i>
13.	Brood identity + mean begging intensity + body condition + log <i>T</i>
14.	Brood identity + mean begging intensity + sex + body condition
15.	Brood identity + mean begging intensity + sex + log <i>T</i>
Brood identity + mean begging intensity + three other factors	
16.	Brood identity + mean begging intensity + tarsus length + sex + body condition
17.	Brood identity + mean begging intensity + tarsus length + sex + log <i>T</i>
18.	Brood identity + mean begging intensity + sex + body condition + log <i>T</i>
19.	Global

We used that model to calculate parameter estimates (Table 6). Mean begging intensity (+), body condition (+), and log *T* (+) were all significant predictors of number of feedings. Nestlings that begged intensely, were in good condition, and had high testosterone concentrations were favored by feeding adults over less intense beggars in poor condition with low values of *T*.

DISCUSSION

The lack of significant correlations between estimates of begging and attributes of nestlings indicates that begging

TABLE 4. Partial correlation matrix of nestling Red-winged Blackbird begging behavior and other attributes. None of the partial correlations is significant.

Attribute	Begging behavior	
	Mean intensity	Mean duration
Tarsus length	-0.201	0.108
Body mass	0.175	-0.149
Body condition	-0.171	0.178
Sex	0.068	-0.146
Age	-0.113	-0.042
Log <i>T</i>	-0.149	0.148

TABLE 5. Results of GLM selection of 19 candidate models examining factors affecting number of feedings of nestling Red-winged Blackbirds; only 10 models with significant goodness of fit are shown. Only one model (in bold) had strong support ( $\Delta AIC_c < 2$ ); parameter estimates were calculated from that model (Table 6).  $\Delta AIC_c$  = the scaled value of Akaike's information criterion corrected for small sample sizes.  $P < 0.001$  for all models shown.

Model	$\Delta AIC_c$	$\chi^2$
<b>Brood identity + mean begging intensity + body condition + log <i>T</i></b>	<b>0<sup>a</sup></b>	<b>99.3</b>
Brood identity + mean begging intensity + tarsus length + sex + log <i>T</i>	14.9	114.5
Brood identity + body condition	17.0	124.1
Brood identity + mean begging intensity + tarsus length + body condition	22.8	114.7
Brood identity + mean begging intensity + sex + body condition	24.4	117.5
Brood identity + mean begging intensity + tarsus length + sex + body condition	28.6	114.4
Brood identity + mean begging intensity + sex + log <i>T</i>	42.7	124.2
Brood identity + mean begging intensity + sex	62.7	139.0
Brood identity + mean begging intensity	117.9	161.2
Brood identity + log <i>T</i>	161.7	448.2

<sup>a</sup> $AIC_c = 287.5$ .

is neither positively nor negatively condition dependent. We interpret this result to mean that begging does not signal need or quality in the Red-winged Blackbird. Even if begging is not a signal of need or quality, provisioning parents could still allocate food among nestlings in a brood on the basis of the intensity of their begging because it honestly indicates short-term need. They can also favor nestlings with high need or of high quality if they can assess need or quality accurately by other means. Our results show that provisioning Red-winged Blackbirds favor nestlings that beg intensely, are in good condition, and have a high concentration of testosterone.

Interest in nestlings' begging has a long history in ornithology, although the focus of that interest has changed over time. Initially, interest centered on the seeming cooperation between offspring and parents, but then changed when

TABLE 6. Generalized linear model parameter estimates of number of feedings of Red-winged Blackbird nestlings as a function of the nestlings' mean intensity of begging, body condition, and log testosterone concentration.

Source	<i>b</i>	SE	df	$\chi^2$	<i>P</i>
Mean begging intensity	0.244	0.132	1	4.37	0.037
Body condition	0.374	0.110	1	10.7	0.011
Log <i>T</i>	0.207	0.072	1	3.88	0.049

Trivers (1974) discussed parent–offspring conflict. Later, the focus shifted to the question of whether begging is honest and how honesty is maintained (e.g., Zahavi 1977, Godfray 1991, 1995). More recently, attention has refocused on the signal function of begging (e.g., Clark 2002, Mock et al. 2011, Johnstone and Kilner 2011, Kölliker 2011, Wright 2011, Grodzinski et al. 2011). Controversy continues, for example, on the meaning of nestling need and whether short-term and long-term need are distinct (e.g., Mock et al. 2011, cf. Grodzinski et al. 2011, Johnstone and Kilner 2011), as well as whether signal-of-hunger models provide sufficiently adaptive explanations (Wright 2011).

#### HUNGER

Our result that intensity of begging affects feeding is consistent with many studies of nestlings' begging and parental provisioning. Mock et al. (2011) stated that no one doubts that begging signals hunger, and Kilner (2002) asserted that virtually all studies show that parents respond to the intensity (postural) of begging. Teather (1992) concluded that provisioning Red-winged Blackbirds respond to the heights to which nestlings reach, and we included reach height in our index of begging intensity. Other potential features such as structural characteristics (Yasukawa et al. 2008) or loudness of the begging call (Horn and Leonard 2002) and the nestling's position in the nest may have affected feeding rate as well (Kilner 2002, Saino and Møller 2002), but we did not study them.

Hunger has been viewed variously as a short-term component of need (e.g., Budden and Wright 2001, Johnstone and Godfray 2002, Johnstone and Kilner 2011), an indication of digestive-system fullness analogous to a fuel gauge (Grodzinski and Lotem 2007, Grodzinski et al. 2011), and a nestling's motivation to beg (e.g., Clark 2002). In our view, hunger is a short-term, transient feature that varies for all individuals, so a clear distinction between hunger and need is not essential; hunger can be defined operationally as the amount of food necessary to reach satiation, at which point begging ceases temporarily. Short-term need of individuals with both high and low long-term need therefore varies (e.g., Iacovides and Evans 1998) even if needy individuals become hungry sooner than less needy ones (Budden and Wright 2001). There is little doubt that provisioners pay attention to nestlings' short-term need.

#### NEED

We found little evidence to support signal-of-need hypotheses in the Red-winged Blackbird. Intensity of begging was not correlated with attributes of the nestling (Table 4) that might reflect need (Table 1). Further, if allocation were negatively condition dependent, we would expect nestlings in poor condition and with low testosterone concentration to be fed at high rates (Table 1), but we found the opposite (Table 6). Our lack of support for SoN is similar to that reported from other studies (e.g. Røskoft and Slagsvold 1985, Redondo and Castro 1992, Leonard et al. 1994, Whittingham et al. 2003).

In contrast, several tests of Godfray's (1991, 1995) SoN model have supported the prediction that, all else being equal, begging should increase with offspring need. For example, Price et al. (1996), Iacovides and Evans (1998), and Lotem (1998b) used experiments that controlled for hunger to show that nestlings in poor condition and nestlings with higher long-term need begged more than nestlings in good condition or with lower long-term need. Other studies have demonstrated parental favoritism on the apparent basis of need. Stamps et al. (1985) found that female Budgerigars (*Melopsittacus undulatus*) favored their smallest and youngest (= neediest) nestlings, actively searching under "a squirming pile of begging older nestlings" (p. 13) to feed a younger, nonbegging nestling. Anderson et al. (1993), Nishiumi et al. (1996), and Price et al. (1996) all suggested that sex-biased feeding reflects the greater need of the larger sex when nestlings are sexually dimorphic in size.

One possible factor in whether results support SoN is the effect of asynchronous hatching on nestlings' survival. Some studies have shown that parents favor larger, less needy core nestlings, which are produced by asynchronous hatching (Forbes et al. 1997, Mock and Parker 1997, Glassey and Forbes 2002a). Given that in our study we observed asynchronous hatching (nearly a quarter of the nestlings that we recorded hatched a day or more after the core brood) and marginal (later hatched) nestlings suffer reduced survival (Forbes et al. 1997, Glassey and Forbes 2002a), it is perhaps not surprising that Red-winged Blackbirds discriminate against needy marginal nestlings. In the Budgerigar, however, Stamps et al. (1989) found that late in the nestling period, last-hatched chicks begged more often, were fed more often, and fledged at heavier weights than their older nestmates. Thus the marginal value of feeding late-hatched (noncore) nestlings appears to vary by species or with environmental circumstances such as food abundance.

#### QUALITY

Although aspects of begging that we did not study may be condition dependent, we conclude that begging does not signal quality in the Red-winged Blackbird. In contrast, other studies show that intensity of begging is positively correlated with nestling condition (Göttlander 1987, Price 1996, Lotem 1998b, Cotton et al. 1999).

Our results support the hypothesis that allocation is positively condition dependent. Our best candidate model in the hierarchical GLM analysis showed that nestlings in superior body condition and with high levels of testosterone were fed at higher rates than their siblings in poor condition with low levels of testosterone. We interpret these results to mean that parents favor nestlings of high reproductive value (= quality). These results are consistent with those of other studies, which show that, for a given level of begging effort, parents favor nestlings in better condition over those in poorer condition (Göttlander 1987, Price 1996, Lotem 1998b, Cotton et al. 1999). For example,

experimentally supplemented House Sparrow (*Passer domesticus*) broods begged more loudly, received more food, and produced more recruits to the breeding population than did un-supplemented broods (Mock et al. 2005), and parents allocated more food to larger than to smaller nestlings (Mock et al. 2009). Dugas (2009) used paint to manipulate rictal flange color so that parents encountered one nestling with flanges resembling a signal of good condition (carotenoid-rich) and another resembling a signal of poor condition (carotenoid-poor) signal. Provisioning House Sparrows (especially females) favored the nestlings in apparently good condition.

Some other studies have shown that testosterone can also affect both begging behavior and nestling condition. For example, 7-day-old Pied Flycatcher (*Ficedula hypoleuca*) nestlings that begged most intensely had the highest endogenous testosterone levels and broods with high testosterone levels had high fledging success (Goodship and Buchanan 2006). Although hatching is asynchronous in both the Pied Flycatcher and Red-winged Blackbird, in contrast to the redwing, asynchronous hatching does not appear to result in brood reduction in the flycatcher (Amundsen and Slagsvold 1991). Perhaps this difference explains why begging intensity reflects endogenous testosterone in the flycatcher but not in the redwing. Studies of maternally produced testosterone in the yolk of domestic canary (*Serinus canaria*) and House Finch (*Carpodacus mexicanus*) eggs showed that yolk testosterone enhances the frequency of nestlings' begging, which results in enhanced growth in both males and females and in juvenile canaries is positively correlated with social status (Schwabl 1993, 1996, Navara et al. 2006). Experimental manipulation of yolk androgen levels within the physiological range affects behavior, growth, morphology, immune function, and survival of the offspring, in some cases even long after fledging (Groothuis et al. 2005).

On the other hand, high testosterone levels can have deleterious effects on immunity (Peters 2000, Duckworth et al. 2001, Navara et al. 2005) and metabolic rate (Buchanan et al. 2001), whereas depressed levels may be associated with increased stress (Quillfeldt et al. 2006). Navara et al. (2005) found that yolk testosterone exerts complex effects in the Eastern Bluebird. Experimentally elevated testosterone was detrimental to hatching success, but moderate doses stimulated skeletal growth during the embryonic period, and high doses resulted in heavier nestlings that were more mature at fledging but had a compromised T-cell immune response. Navara et al. (2006) suggested that the effects of yolk testosterone depend on food availability, which varies widely. It is not known, however, whether endogenously produced testosterone has similar effects in nestlings (Schwabl and Lipar 2002).

High levels of testosterone in species such as the Red-winged Blackbird with asynchronous hatching that results in brood reduction may confer compensatory growth advantages when food for the entire brood is adequate (Lipar and Ketterson 2000) and may aid in the development of neck muscles

necessary for begging (Lipar and Ketterson 2000). We did find a significant positive effect of testosterone concentration and body condition on number of feedings of nestling Red-winged Blackbirds. Perhaps testosterone enhances mass gain and females attempted to compensate for the condition disadvantages of asynchronous hatching by increasing testosterone with hatching order (Lipar and Ketterson 2000). Testosterone may also have organizational effects on steroidogenic tissue (Schwabl and Lipar 2002).

Lipar and Ketterson (2000) found that Red-winged Blackbird nestlings hatched from eggs with higher testosterone concentrations in yolk begged more intensely than those from eggs with lower concentrations. In contrast, although we found that testosterone affected number of feedings, it was not correlated with begging behavior. One obvious difference in the two studies is the source (maternal or endogenous) of testosterone. It is likely that the effect of maternal testosterone had dissipated in our 7-day-old nestlings. For example, Navara et al. (2006) found that injection of a physiological dose of testosterone into House Finch eggs produced growth effects in 2-day-old nestlings, but by 8 days after hatching this effect had disappeared. It is also unknown how maternal testosterone in yolk affects endogenous production of testosterone in nestlings.

#### NESTLING BEGGING AND PARENTAL ALLOCATION

Begging is complex (Kilner 2002) and effective (Horn and Leonard 2002), but does it signal hunger, need, quality, or some combination of them (Johnstone and Grafen 1993, Price et al. 2002, Clark 2002, Mock et al. 2011)? Despite numerous studies of many species, this question remains relevant. Although begging does not appear to signal need or quality in nestling Red-winged Blackbirds, we did find that nestlings in good body condition with high levels of testosterone were favored. In species with asynchronous hatching such favoritism would be adaptive to avoid investment in nestlings that are unlikely to survive (e.g., Godfray 1991, 1995, Budden and Wright 2001, Mock et al. 2011). It is possible, however, that parents might use a signal of need initially to maintain the whole brood and then switch to a signal of quality when brood reduction becomes advantageous (Mock et al. 2011). Need and condition might be used simultaneously as well if male and female parents use different signals. For example, females of some species favor their smallest nestlings, whereas males feed indiscriminately and thereby passively favor larger nestlings (Stamps et al. 1985, Götthlander 1987, Krebs 2002).

Mock et al. (2011) suggested that begging might not provide useful information about a nestling's important attributes if those traits can be assessed by cues that the nestling cannot hide. In our study, parents perhaps had access to information in the public domain about nestlings' body condition and testosterone level. There is another explanation, however. McLinn and Stephens (2006) modeled the effects of signal honesty ("reliability,"  $q$ ) and the statistical distribution of public-domain information ("environmental uncertainty,"  $p$ ) on animal

signaling. This model predicts that receivers should use signals when both signal reliability and environmental uncertainty are high. If applied to begging, this model predicts that parents should tend to pay attention to begging when it is an honest signal, but tend to ignore it when environmental certainty about a state is high (e.g., when a given state is always true). For example, if all nestlings in a brood have the same reproductive value (all high or all low), there is no environmental uncertainty and begging should have no effect on allocation. In contrast, if some offspring are in a high state while others are in a low state, and if that state cannot be assessed directly (is cryptic), then a reliable signal from begging can become useful.

With respect to our results, we can ask whether hunger (short-term need), long-term need, or quality (reproductive value) is likely to meet the criteria of high reliability, high uncertainty, and crypticity of the signal. Our results seem to show that long-term need and quality are not reliably signaled by begging intensity and can be assessed with information (cues) in the public domain (e.g., size, body condition, vigor). In contrast, hunger (short-term need) is reliably signaled by begging intensity and is seemingly otherwise cryptic to provisioners, so it is not surprising that parents should allocate food on the basis of begging intensity in the Red-winged Blackbird as well as many other species.

#### FUTURE STUDIES

Our poor understanding of the mechanisms by which testosterone exerts its effects calls for continued study (e.g., Groot-huis and Schwabl 2008). For example, the cues by which allocation is affected by maternal and endogenous testosterone might include the nestling's size or condition, gape size or color, mouth-flange color, begging-call structure, and position in the nest. In addition, parents might base their allocation decisions on begging behavior during previous visits (Glasse 2000, Clark 2002), and parents that deliver multiple items might favor one kind of offspring (e.g., males) with the first item and another kind (e.g., females) with subsequent items (Wilson and Clark 2002). Parental decisions are probably also affected by environmental circumstances such as food availability. When food is abundant, parents may favor needy nestlings, but when food is scarce, they may sacrifice them. Clearly much research remains to be done.

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