

# Feeding decisions of eastern bluebirds are situationally influenced by fledgling plumage color

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The relative amount of resources that avian parents provide to individual offspring within a brood represents a strategy that can have large effects on reproductive success. We tested whether parental feeding decisions of eastern bluebirds *Sialia sialis* are influenced by offspring plumage color by presenting pairs of differently colored fledglings side by side and observing how they were provisioned by parents. After a control period, we manipulated blue plumage color so that one sibling in each trial became relatively dark and one became relatively bright. During neither the control nor the experimental periods did either parent consistently feed naturally brighter or experimentally brightened sons more than drab sons. Under specific circumstances, however, both parents directed a higher proportion of their feeding attempts to more brightly colored sons. Paternal feeding attempts to brighter offspring during both the control and experimental periods increased in relation to the brightness of these fledglings relative to their brothers. Maternal feeding decision, on the other hand, were influenced by numerous variables during control and experimental periods including the date of the trial, the difference in mass between fledglings, the feeding behavior of fathers during the trial, the relative investment by fathers during the nestling stage, and the amount of UV chroma in fledgling plumage. Taken together, these results suggest that equal provisioning of offspring is the strategy most commonly adopted by eastern bluebirds but more brightly colored offspring will be fed preferentially when resources for offspring are limited. *Key words:* color, juvenal plumage, ornaments, parent–offspring interactions, plumage, relative parental investment, *Sialia sialis*. [*Behav Ecol* 21:456–464 (2010)]

In bird species with altricial young, parents provide all the food resources for their offspring both while they are in the nest (nestlings) and for a period after they have left the nest (fledglings; Skutch 1976). How food is distributed among offspring in a brood can have profound effects on parents' reproductive success. When food is abundant, parents are expected to distribute food equally among all offspring (Davis et al. 1999). When food is limited, however, parents typically benefit by allocating more resources to the offspring in the best condition (Lack 1968; Davis et al. 1999).

Parents need to be able to accurately assess the condition of their offspring if they are to distribute food based on the future reproductive value of these individuals (Clutton-Brock 1991). Accurate assessment of nestling quality by parents may depend on multiple signals (Johnstone 1995, 1996), and there are a number of cues potentially available to parents to assess the condition of their young. By the time they leave the nest, altricial young have grown most of their juvenal plumage, and differences in plumage coloration may provide a visual cue that could allow parents to accurately assess offspring quality outside of the nest.

Relatively few studies have investigated whether the plumage coloration of juvenile birds may serve as a signal of quality to parents (Lyon et al. 1994; Galván et al. 2008; Tanner and Richner 2008; Griggio et al. 2009), but the idea that feather coloration can signal individual condition in the context of mate choice and aggressive interactions has been the focus of

numerous studies in recent decades (reviewed in Hill and McGraw 2006). Most studies have focused on the condition-dependent nature of pigment-based coloration in birds (reviewed in Hill 2006a), but links between individual condition and expression of structural coloration, such as the blue feather coloration of eastern bluebirds *Sialia sialis*, have also been demonstrated (e.g., Siefferman and Hill 2005a, 2005b). Correlations between structural plumage color and individual condition have been reported in blue grosbeaks *Guiraca caerulea* (Keyser and Hill 2000), blue tits *Cyanistes caeruleus* (Johnsen et al. 2003), and blue-black grassquits *Volatinia jacarina* (Doucet 2002). Additionally, manipulative studies have shown that structural coloration is condition-dependent in adult wild turkeys *Meleagris gallopavo* (Hill et al. 2005), brown-headed cowbirds *Molothrus ater* (McGraw et al. 2002), and adult eastern bluebirds (Siefferman and Hill 2005a, 2005b). The structural plumage color of juveniles also seems to be condition-dependent in blue tits (Jacot and Kempenaers 2007) and eastern bluebirds (Siefferman and Hill 2007). Whether they grow in more or less crowded nest environments affects the brightness of blue wing and tail feathers in juvenile male (but not female) eastern bluebirds (Siefferman and Hill 2007). In this way feather color summarizes the condition of fledglings over the previous several days of growth and development, potentially providing important information that could be used in decisions of resource allocation.

Given the links between expression of structural coloration and individual condition, it seems plausible that parents assess the condition of their offspring by evaluating juvenile feather coloration. Two recent studies have shown that great tit *Parus major* juveniles with experimentally manipulated yellow plumage are fed less frequently than siblings with natural plumage reflectance (Galván et al. 2008; Tanner and Richner 2008). Both of these studies utilized techniques that eliminated the

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Received 24 April 2009; revised 21 December 2009; accepted 31 December 2009.

UV reflectance of feathers, but no study has assessed parental provisioning relative to natural variation in color expression among fledglings.

Resource availability is another variable likely to affect the provisioning strategies of parents. A mathematical model developed by Davis et al. (1999), using western bluebirds *Sialia mexicana* as the focal species, predicts that parents should allocate more resources to “better” (i.e., bigger) chicks when resources are scarce and distribute food more evenly when resources are plentiful. In support of this model, resource availability influenced parental feeding decisions in Alpine swifts *Apus melba* and European starlings *Sturnus vulgaris* (Bize et al. 2006). In both species, UV skin coloration of nestlings is correlated with nestling mass and skeletal size (Bize et al. 2006) and is used by parents to make provisioning decisions. As predicted by Davis et al. (1999), parents attempted to “catch-up” their inferior offspring (no UV reflectance) when there was abundant food but invested maximally in their best offspring (normal UV reflectance) when resources were limited.

Provisioning strategies of parents might be affected not only by temporal and spatial variation in food availability (e.g., Davis et al. 1999; Bize et al. 2006) but also by the relative amount of care provided by a mate (Winkler 1987; McNamara et al. 1999). When one member of a pair provisions offspring at a relatively low rate, the partner is expected to increase investment in the current brood (Winkler 1987; Wright and Cuthill 1989) at a cost to its own future reproductive value (Nur 1988). Increased investment by compensating parents carries increased costs (Clutton-Brock 1991), and food items brought back to the nest become relatively more valuable. Parents mated to partners that invest relatively little in offspring care may face costs similar to those of parents experiencing natural food shortages, namely an inability to adequately provision all offspring. Therefore, we predicted that parents doing a relatively larger share of provisioning young should invest preferentially in superior offspring, like parents in low-quality habitats (Bize et al. 2006).

To test whether the blue structural plumage of juvenile eastern bluebird males influences feeding decisions made by parents, we manipulated the plumage coloration of fledgling juvenile bluebirds within the range of natural variation to create relatively brighter and darker individuals. We predicted that parents would feed sons with brighter blue feathers more than sons with darker feathers if feather coloration serves as a signal of the health and nutritional condition. Because resource allocation decisions are likely to be influenced by food availability, we also looked at how relative levels of parental investment early in offspring development (nestling stage) influenced parental feeding strategies later in development (fledgling stage). We predicted that bluebird parents paired to mates contributing little to nestling provisioning would experience limited ability to provision their entire brood, thereby increasing the likelihood of differential allocation to superior offspring. Parents paired to high-contributing mates should be less limited by food and therefore able to provision offspring more equitably.

## MATERIALS AND METHODS

### Study site

We conducted this study on a banded population of eastern bluebirds in Lee County, Alabama (lat 32°35'N, long 82°28'W) between March 2008 and August 2008. We monitored approximately 150 nest-boxes throughout the breeding season and recorded the date of the first egg laid and the date of hatching for each nest.

### Experimental protocol

We selected 2 male nestlings from each nest when nestlings were between 15 and 18 days of age. We determined the sex of nestlings in the field by examining the amount of blue in emerging flight feathers (Pinkowski 1974) and later confirmed these assignments using molecular techniques. Eastern bluebird nestlings typically fledge 15–18 days after hatching, and we chose specific trial dates on a nest-by-nest basis depending on the development of nestlings in each brood. To ensure that juveniles in separate trials exhibited approximately equal plumage development at the time of testing, we tested faster growing broods with advanced feather growth at younger ages than broods containing slow developing juveniles. When broods contained more than 2 male nestlings, we tested the 2 brothers closest to one another in mass, and in cases where there were multiple possible pairings we tested the heaviest pair (average mass of heavier male 26.50 g  $\pm$  standard deviation [SD] 1.58, average mass of lighter male 25.59 g  $\pm$  1.56, average difference 0.91 g  $\pm$  0.75).

On the day of the trial, we gathered all nestlings from a given box to measure their mass individually. After recording the mass of each nestling we fed each juvenile one mealworm. This early morning feeding served to minimize the effects that different hunger levels might have on begging behavior. We returned all members of the brood to the natal nest-box and sealed the entrance to prevent any feeding attempts by the parents. We then left the immediate area for 30 min to allow the nestlings to digest the recently consumed mealworms. After the 30 min pretrial period, we returned to the nest-box, selected the predetermined males, and placed them separately in a divided wire cage near ( $\sim$ 5 m) the natal nest-box. A solid partition prevented any physical or visual contact between siblings in the wire cage. To create a location from which bluebird parents could assess their offspring, we placed a 50 cm tall perch one meter away from the front of the cage. By placing the fledglings (formerly nestlings) in the experimental cage we were able to measure parental feeding decisions to recently fledged offspring under seminatural, and equal, ambient lighting conditions. The cage allowed us to keep mobile fledglings from separating, made possible our use of video cameras to record parental feeding behavior, and enabled bluebird parents to directly compare 2 of their offspring. We kept all remaining juveniles in a cloth box and fed them mealworms throughout the duration of the trial.

Parent bluebirds quickly adjusted to the experimental setup and began to feed their offspring through the wire mesh of the cage in as little as 45 s. We used a tripod-mounted video camera (Sony Hi-8) to record parent and chick interactions during each trial, consisting of a control period followed by a manipulation period. Initially, we used a control period of 30 min ( $\pm$  5 min) but, after briefly investigating several of these trials ( $n = 14$ ), we discovered that this duration was not long enough to consistently observe a sufficient number of feeding attempts from parent bluebirds (number of trials with 30 min control periods excluded from the final analyses due to incomplete data = 6). Subsequently, we used 1 h ( $\pm$  5 min) control periods. After the control period, we returned to the area, manipulated the plumage of the chicks (see Color manipulation below), and resumed recording parent–chick interactions for 2 h. After each trial, we collected the fledglings from the cage and returned them to their nest-box along with their siblings.

Parental investment was quantified from videotapes by observers blind to color differences and plumage manipulations. We were unable to reliably assess the size of food items brought to fledglings during the trial, but previous research indicates that prey size does not vary with feeding rate in this

population (Siefferman and Hill 2007). Food handling and transfer difficulties between parents and offspring, exacerbated by the wire mesh separating them, often caused parents to temporarily abandon feeding one fledgling and begin attempting to feed the other fledgling. Due to the inconsistency of food transfer, we used long-distance parental approaches to juveniles as a proximate measure of investment. Every time an adult directly approached one of the juveniles from outside the frame of the video screen or from the perch one meter in front of the cage, we scored the event as a feeding attempt. Instances in which adults approached one juvenile, failed to deliver the food item, and immediately (and without retreat) approached the second juvenile with the food item were scored only as an approach for the first offspring. This scoring method best captures the choices that parents make when delivering food and minimizes the effects that delivery complications and fledgling behavior had on parental feeding decisions.

Although we attempted to control for differences in hunger between juveniles within trials (by feeding each juvenile, see above), our method was likely imperfect at creating equally hungry fledglings (owing to preexisting differences between juveniles with respect to hunger and body condition). We did not know how differences in hunger levels, although minimized by our pretrial feedings, might contribute to differences in begging behavior and the subsequent feeding behavior of parents. Therefore, to determine the degree to which differences in begging behavior influenced parental feeding decisions, we analyzed a subset ( $n = 6$ ) of trials in which we recorded all instances of parental feeding attempts preceded (within 10 s) by fledgling begging.

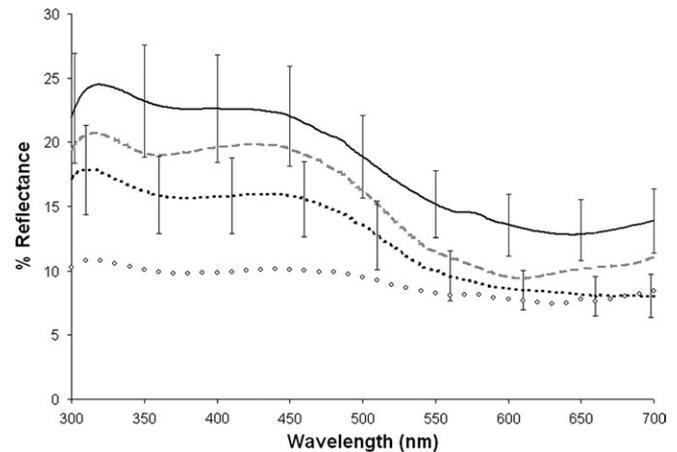
### Color manipulation

After the control period in each trial, the plumage of one fledgling (alternating between the heavier and the lighter bird between trials) was treated with a violet permanent marker (PM-60: violet mist; Prismacolor, Sanford L.P., Oak Brook, IL), whereas the plumage of the second juvenile was treated with a nontoxic black permanent marker (permanent marker: black; Sharpie). We attempted to apply marker ink to all the blue feathers of each juvenile bluebird we manipulated (these feathers are limited to the wings and tail). Because the blue coloration of bluebirds results from microstructure rather than pigments, feathers colored with these markers still looked blue to a human observer, and the reflectance from such feathers still had the spectral shape characteristic of blue (ink from the pens absorb a percentage of light reaching the microstructures, uniformly reducing the brightness of coloration; Ballentine and Hill 2003; Liu et al. 2007).

In contrast to the results of previously published work that relied on violet markers to increase the brightness of adult bluebird contour feathers (Liu et al. 2007), we found that these markers actually reduced the mean total brightness of the blue juvenile feathers in our experiments (Figure 1). However, treatment with black markers reduced mean total brightness to an even greater degree. Because we compared only the relative values of each color variable (see below), these treatments still produced the desired color changes between siblings. For the sake of simplicity, we refer to violet marker-treated individuals as relatively brightened and black marker-treated individuals as relatively darkened.

### Color measurements

To examine whether the premanipulation color of juveniles played a role in parental provisioning during the control period, we obtained measurements of juvenal plumage color



**Figure 1**  
Average reflectance curves for unmanipulated juvenile male eastern bluebirds ( $\pm$ SD, solid black line), violet marker treated (relatively brightened) juvenile males (dashed gray line), black marker treated (relatively darkened) juvenile males ( $\pm$ SD, dashed black line), and 8 naturally dull juvenile males (circles).

following the procedures described in Siefferman and Hill (2007). Briefly, we collected  $\sim 2$  cm of the fifth primary from each juvenile and taped these feathers to a piece of black construction paper. We then used an S-2000 spectroradiometer with a deuterium-halogen lamp (Ocean Optics, Dunedin, FL) and a micron fiber-optic probe at a  $90^\circ$  angle to the feather surface to measure the spectral characteristics of each feather. The spectral processing program (ColouR v1.7, Queens, Ontario) was then used to quantify 2 standard descriptors of reflectance data for each individual: mean brightness and UV chroma. Mean brightness is the average reflectance ( $R_{av}$ ) in the 300- to 700-nm interval, and UV chroma is the proportion of total reflectance that is in the UV range ( $R_{300-400}/R_{300-700}$ ). Hue, defined as the wavelength of peak reflectance, was not used because the flattened shape of the reflectance curve in the UV-blue region (Figure 1) meant that wide variation in hue values was possible with minimal differences in the actual shape of the reflectance curve. In addition to measuring the natural color of juvenile feathers, we also measured the color of feathers after they were manipulated.

Because relative differences in trait expression between offspring likely provide the most informative cues to parents when assessing their current brood, we used relative measures of color in all analyses. During the control period, we analyzed color differences between fledglings by subtracting the color values of darker fledglings from those of their naturally brighter siblings. During the experimental period, postmanipulation, we analyzed color differences between relatively brightened (violet marker treated) fledglings and relatively darkened (black marker-treated) fledglings by subtracting the color values of darkened offspring from those of brightened offspring.

To ensure that our color manipulations did not influence the perceived sex of the fledglings in our experiment (i.e., sons not perceived as daughters by parents), we compared plumage color variables between darkened sons and unmanipulated daughters. We found that the plumage of daughters had significantly less UV chroma than that of darkened males ( $t$ -test,  $t_{164} = 21.64$ ,  $P < 0.0001$ ), significantly less reflectance in the UV ( $t$ -test  $t_{164} = 4.79$ ,  $P < 0.0001$ ), but did not differ in mean brightness ( $t$ -test,  $t_{164} = -0.50$ ,  $P = 0.62$ ). Overall, the spectral shape of the female plumage was flatter (more achromatic)

than that of darkened males, with lower reflectance at shorter wavelengths. Therefore, we feel that parents could accurately distinguish between darkened males and females.

### Relative parental investment during the nestling stage

To compare the relative investment of mothers and fathers during the nestling stage, we recorded parental visits to nest-boxes with a Hi-8 video camera for approximately 2 h (beginning between 0600 and 0730 h) when nestlings were 10 (nests recorded = 7), 11 ( $n = 50$ ), 12 ( $n = 11$ ), or 13 ( $n = 3$ ) days old. Within this range, mean feeding rates did not differ by age (One-way analysis of variance,  $F_{3,67} = 0.58$ ,  $P = 0.63$ ). We excluded recordings in which neither parent returned to the box for an extended period of time ( $>45$  min), and, to control for differences between parents with respect to human-induced behavioral changes, the first 20 min of each tape were not analyzed. In a study utilizing 12 h of radio-transponder data to determine feeding rates of blue tits, Johnsen et al. (2005) found no difference between their observations and those obtained from 1 h direct feeding observations. Additionally, previous research on this population of bluebirds found no difference in feeding rates between 4-h recordings and 2-h recordings (Siefferman L, personal communication). The length of our observation periods therefore captures the relevant information regarding relative parental feeding rates.

Individual feeding rates of the parents (feeds/chick/hour) were used to calculate the relative investment of parents to nestlings by dividing paternal feeding rates by maternal feeding rates.

### Analyses

To examine whether parents differed in their overall investment to fledglings, we used paired  $t$ -tests comparing the number of maternal and paternal feeding attempts during both the control and experimental periods. We also used paired  $t$ -tests to determine whether parents consistently fed naturally brighter offspring during the control period and whether parents consistently fed experimentally brightened offspring during the experimental period. In addition to paired  $t$ -tests, we also examined the influence of numerous covariates on parental feeding decisions using generalized linear models. Our experimental design forced the bluebird parents in our study to repeatedly choose between 1 of 2 offspring when delivering food, resulting in binomially distributed data. Therefore, we analyzed data from our control and experimental periods with generalized linear models (PROC GENMOD in SAS) with binomial error distributions and logit link functions. Generalized linear models are appropriate for binary and proportional data and can incorporate both continuous and categorical explanatory variables (Lewis 2004). We incorporated differences in plumage coloration between fledglings, differences in mass between fledglings, trial date, relative parental investment during the nestling stage, mate's feeding behavior during the trial, and the number of offspring in each brood as potential explanatory variables in our feeding behavior models for the control period. Because parents did not feed offspring at all in a few trials and because we lacked data for certain variables in other trials, our final models for the control period were constructed from 54 feeding trials. In our model of feeding behavior during the experimental period, we incorporated differences in manipulated plumage color, date, relative parental investment during the nestling stage, differences in natural plumage color, mate's feeding behavior during the experimental period, mate's feeding behavior during the control period, each parent's own feeding behavior during the control period, mass

differences between offspring, and brood size as explanatory variables. These models were constructed from 52 separate trials containing complete data sets.

## RESULTS

### Total investment

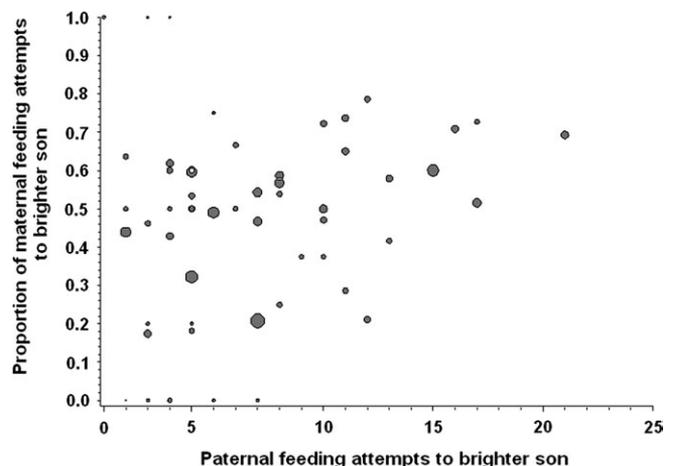
During the control period mothers averaged 18.21 total feeding attempts ( $\pm$ SD =  $\pm 15.78$ ) and fathers averaged 13.24 ( $\pm 9.74$ ) attempts. During the experimental period, mothers fed fledglings an average of 26.11 ( $\pm 19.02$ ) times and fathers 19.05 ( $\pm 12.50$ ) times. The differences in feeding rates between mothers and fathers were significant in both the control (paired  $t$ -test,  $t_{68} = 2.68$ ,  $P < 0.01$ ) and experimental (paired  $t$ -test,  $t_{72} = 2.62$ ,  $P = 0.01$ ) periods.

### Influence of begging behavior on parental feeding attempts

Analysis of 6 trials in which we recorded whether begging occurred in the 10 s prior to parental approaches revealed that begging did not significantly impact parental feeding decisions. In only 0.05% (2/366) of the feeding attempts recorded during these 6 trials did a juvenile beg before its parent approached.

### Control period

During the control period, mothers did not consistently feed naturally brighter sons (average feeding attempts =  $8.9 \pm 7.6$ ) more than naturally darker sons ( $\bar{x} = 9.3 \pm 10.0$ ; paired  $t$ -test,  $t_{80} = -0.46$ ,  $P = 0.65$ ). However, when we incorporated explanatory variables into our generalized linear models, we found that the proportion of maternal feeding attempts directed toward naturally brighter sons during the control period was positively correlated with natural differences in mass between sons, as well as the total number of paternal feeding attempts to naturally brighter sons (Figure 2; Table 1). This means that mothers were more likely to feed naturally brighter sons if they were heavier than their naturally darker brothers, and more likely to feed naturally brighter sons if fathers fed these same sons more during the control period.



**Figure 2**

The relationship between female eastern bluebird feeding behavior during the control period (proportion of total feeding attempts toward naturally brighter sons) and the number of feeding attempts that fathers directed toward naturally brighter sons during the same period. To facilitate a more accurate interpretation of the relative weights of each trial to the final model, symbol sizes are proportional to the number of maternal feeding attempts in each trial.

Table 1

Generalized Linear Model using binomial error and logit link for the proportion of feeding attempts that eastern bluebird mothers directed toward naturally brighter sons during the control period

Parameter	Estimate	Standard error	Wald 95% confidence limits		Chi square	<i>P</i> value
Intercept	1.64	0.65	0.37	2.91	6.44	<b>&lt;0.05</b>
Brightness difference <sup>a</sup>	0.07	0.06	-0.06	0.19	1.17	0.28
UV chroma difference <sup>b</sup>	8.67	5.26	-1.63	18.98	2.72	0.10
Mass difference <sup>c</sup>	0.17	0.05	0.06	0.27	9.91	<b>&lt;0.01</b>
Date of trial	-0.01	0.00	-0.02	0.00	12.75	<b>&lt;0.001</b>
Relative parental investment <sup>d</sup>	0.04	0.10	-0.17	0.24	0.12	0.73
Paternal feeding <sup>e</sup>	0.06	0.01	0.03	0.09	16.91	<b>&lt;0.0001</b>
Brood size	-0.15	0.08	-0.31	0.02	3.14	0.08

Significant explanatory values in bold.

<sup>a</sup> Difference in brightness between naturally brighter and naturally darker sons.

<sup>b</sup> Difference in UV chroma between naturally brighter and naturally darker sons.

<sup>c</sup> Difference in mass between naturally brighter and naturally darker sons.

<sup>d</sup> Ratio of paternal/maternal feeding rates to nestlings prior to fledging.

<sup>e</sup> Number of paternal feeding attempts to naturally brighter sons during the control period.

Additionally, mothers exhibited an increased proportion of feeding attempts to naturally brighter sons earlier in the season (Table 1). Relative plumage brightness did not appear to influence maternal feeding attempts during the control period, but there was a nonsignificant trend for mothers to increase feeding attempts to brighter nestlings with more UV chromatic plumage (Table 1). Maternal investment during the control period was not influenced by the relative investment of fathers during the nestling stage.

Overall, during the control period fathers did not feed brighter fledglings ( $\bar{x} = 6.7 \pm 5.4$ ) more than darker fledglings ( $\bar{x} = 6.5 \pm 5.6$ ) fledglings (paired *t*-test,  $t_{72} = 0.35$ ,  $P = 0.73$ ). However, the proportion of paternal feeding attempts directed toward naturally brighter sons during the control period was positively correlated to natural differences in brightness between sons (Figure 3; Table 2). In other words, the proportion of feeding attempts that the brightest fledgling received from his father increased with increasing color difference between it and its sibling. Natural differences in UV chroma between brothers did not appear to influence

paternal feeding patterns during the control period nor did differences in fledgling mass, the date of the trial, the relative paternal investment during the nestling stage, feeding attempts of mothers to brighter sons, or brood size (Table 2).

### Experimental period

Overall, bluebird mothers showed no significant difference in feeding attempts between experimentally brightened sons ( $\bar{x} = 12.6 \pm 10.1$ ) and experimentally darkened sons ( $\bar{x} = 13.5 \pm 10.4$ ) during the experimental period (paired *t*-test,  $t_{79} = -1.03$ ,  $P = 0.30$ ). However, our generalized linear model indicated that mothers invested more in brightened sons earlier in the breeding season and when fathers contributed less to offspring provisioning during the nestling stage (Figure 4; Table 3). Additionally, the proportion of maternal feeding attempts to experimentally brightened sons was positively correlated to natural differences in plumage brightness, mass, and the feeding behavior of fathers during the experimental period (Table 3). Mothers also increased feeding attempts to experimentally brightened sons if their plumage was more chromatic in the ultraviolet region than their brothers during the experimental period (Table 3).

During the experimental period, fathers fed experimentally brightened ( $\bar{x} = 9.1 \pm 6.7$ ) and experimentally darkened fledglings ( $\bar{x} = 9.97 \pm 7.3$ ) at similar rates (paired *t*-test,  $t_{75} = -1.15$ ,  $P = 0.26$ ). However, the model we created incorporating multiple explanatory variables indicated that fathers increased feeding attempts to brightened sons in relation to the degree they were brighter than their brothers (Figure 5; Table 4). That is, brightened sons who were much brighter than their darkened siblings received more feeding attempts from their fathers. Additionally, fathers were more likely to feed experimentally brightened fledglings when broods were larger (Table 4). No other variable was significant predictor of paternal feeding patterns in the experimental period.

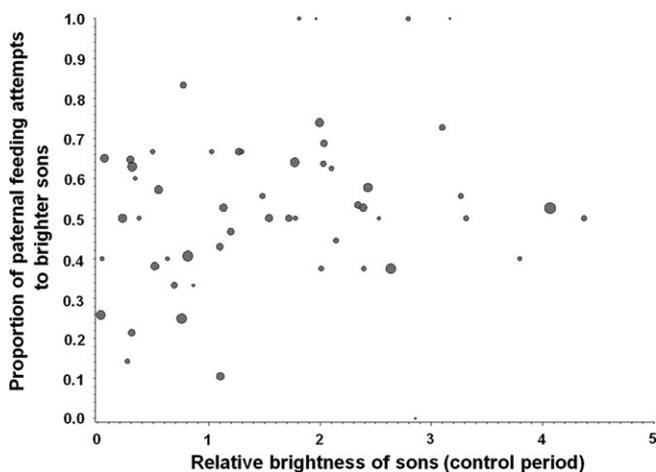


Figure 3

The relationship between male eastern bluebird feeding behavior during the control period (proportion of total feeding attempts toward naturally brighter sons) and the relative plumage brightness of the sons being fed. Symbol sizes are proportional to the number of paternal feeding attempts in each trial.

### DISCUSSION

On fledging, the context in which bluebird offspring are fed changes dramatically. Young bluebirds leave the restrictive confines of the nest-box and spread out into the bright, open-field habitats typically occupied by the species. The change in both feeding environment and offspring proximity means that many of the signals used by bluebird parents to assess fledgling

Table 2

Generalized Linear Model using binomial error and logit link for the proportion of feeding attempts that eastern bluebird fathers directed toward naturally brighter sons during the control period

Parameter	Estimate	Standard error	Wald 95% confidence limits		Chi square	P value
Intercept	-1.38	0.74	-2.82	0.07	3.50	0.06
Brightness difference <sup>a</sup>	0.17	0.07	0.02	0.31	5.08	<b>&lt;0.05</b>
UV chroma difference <sup>b</sup>	0.87	5.81	-10.51	12.25	0.02	0.88
Mass difference <sup>c</sup>	-0.01	0.07	-0.14	0.12	0.02	0.88
Date of trial	0.00	0.00	0.00	0.01	1.39	0.24
Relative parental investment <sup>d</sup>	-0.02	0.12	-0.25	0.22	0.02	0.90
Maternal feeding <sup>e</sup>	0.00	0.01	-0.02	0.02	0.10	0.75
Brood size	0.13	0.09	-0.05	0.30	2.03	0.15

Significant explanatory values in bold.

<sup>a</sup> Difference in brightness between naturally brighter and naturally darker sons.

<sup>b</sup> Difference in UV chroma between naturally brighter and naturally darker sons.

<sup>c</sup> Difference in mass between naturally brighter and naturally darker sons.

<sup>d</sup> Ratio of paternal/maternal feeding rates to nestlings prior to fledging.

<sup>e</sup> Number of maternal feeding attempts to naturally brighter sons during the control period.

quality should be different than signals used to assess nestling quality. Mouth color, used by adults of many bird species to assess nestling need and quality (Gotmark and Ahlstrom 1997; de Ayala et al. 2007; Ewen et al. 2008), is probably not as useful as signal outside the confines of the nest because fledged offspring are less likely to beg simultaneously when spatially separated (Ligon RA, personal observation), at least early in the fledgling stage. However, the flanges of many recently fledged passerine birds remain enlarged for a period of time after offspring have left the nest and these may serve as a signal for provisioning parents (e.g., de Ayala et al. 2007; Dugas 2009), both within and outside of the nest. Relative begging volume may also be more difficult for parents to assess after fledging, when nestlings are spatially separated (Mennill D, personal communication). Juvenile begging displays also attract predators (Haskell 1994; Leech and Leonard 1997) and may therefore carry greater costs outside of the nest. In the wild bluebirds that we watched, begging commenced only when parents approached fledglings, and this constrained behavior likely reflects the risks associated with extended periods of begging. By assessing condition-dependent plumage traits, parents are able to assess the relative quality of their

offspring without forcing them to reveal themselves through overt begging displays.

Using feather brightness as a cue for assessing offspring quality makes sense because the brightness of blue primary feathers is a condition-dependent trait in juvenile bluebirds. Young male bluebirds raised in less crowded nests with access to more food grow brighter feathers (Siefferman and Hill 2007). Prior studies with other bird species also found that juvenal plumage coloration can be a signal that alters the amount of food provided by parents. Direct (Tanner and Richner 2008) and indirect (Galván et al. 2008) measures of parental investment indicate that UV plumage coloration of great tit *P. major* offspring influences the feeding decisions of parents. In both studies (Galván et al. 2008; Tanner and Richner 2008) UV blocking techniques were used that reduced UV reflectance of yellow juvenal plumage outside the range of natural variation. These studies provide important insights into the potential for juvenal plumage to serve a signaling function, but because they involve the virtual removal of UV reflectance, neither study shows how parents respond to natural variation in color expression (Hill 2006b).

By presenting bluebird parents with pairs of their offspring that differed in feather coloration, we tested for preferential feeding based on plumage coloration. In simple comparisons of food delivery attempts to fledglings with natural feather coloration, we found no significant bias in either males or females to feed brighter offspring more. When we used marking pens to color the plumage of the paired fledglings, making one relatively brighter and one relatively darker, we again found no significant bias in the food delivery of parents related to offspring color. From these observations, we conclude that provisioning without regard to feather coloration is a common behavioral tactic in eastern bluebirds.

When we added more details to our analyses about the circumstances in which the feeding trials were performed, interesting patterns of provisioning related to feather coloration began to emerge. In the control period, females provisioned naturally brighter sons more when they were heavier than darker brothers, when trials occurred earlier in the breeding season and when fathers fed these sons more during the control period. During this control period, males preferentially fed brighter sons in relation to the degree that these sons were brighter than their brothers. Thus, while the simple paired comparisons, in which siblings were ranked simply as brighter or drabber regardless of the difference in feather coloration, showed no pattern of preferential feeding, when additional

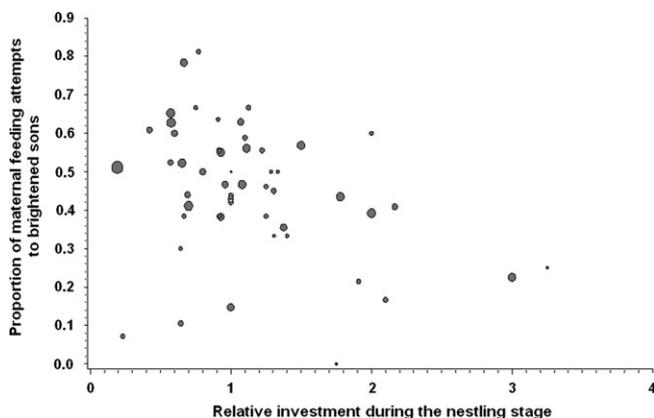


Figure 4

The relationship between female eastern bluebird feeding behavior during the experimental period (proportion of total feeding attempts toward experimentally brightened sons) and the relative parental investment during the nestling stage. Symbol sizes are proportional to the number of maternal feeding attempts in each trial.

Table 3

Generalized linear model using binomial error and logit link for the proportion of feeding attempts that eastern bluebird mothers directed toward experimentally brightened sons during the experimental period

Parameter	Estimate	Standard error	Wald 95% confidence limits		Chi square	P value
Intercept	1.75	0.58	0.62	2.88	9.20	<b>&lt;0.01</b>
Brightness difference, exp <sup>a</sup>	-0.03	0.03	-0.08	0.02	1.72	0.19
UV chroma difference, exp <sup>b</sup>	11.80	4.26	3.45	20.14	7.68	<b>&lt;0.01</b>
Date of trial	-0.01	0.00	-0.02	-0.01	16.11	<b>&lt;0.0001</b>
Relative parental investment <sup>c</sup>	-0.61	0.12	-0.84	-0.37	26.09	<b>&lt;0.0001</b>
Brightness difference <sup>d</sup>	0.07	0.03	0.01	0.14	4.97	<b>&lt;0.05</b>
UV chroma difference <sup>e</sup>	-8.91	5.04	-18.78	0.96	3.13	0.08
Paternal feeding, control <sup>f</sup>	-0.01	0.01	-0.03	0.02	0.13	0.72
Maternal feeding, control <sup>g</sup>	-0.01	0.01	-0.02	0.01	0.96	0.33
Paternal feeding, exp <sup>h</sup>	0.03	0.01	0.00	0.05	5.49	<b>&lt;0.05</b>
Mass difference <sup>i</sup>	0.14	0.06	0.03	0.24	5.95	<b>&lt;0.05</b>
Brood size	0.11	0.07	-0.03	0.25	2.48	0.12

Significant explanatory values in bold.

<sup>a</sup> Difference in brightness between experimentally brightened and experimentally darkened sons, see text for details.

<sup>b</sup> Difference in UV chroma between experimentally brightened and experimentally darkened sons.

<sup>c</sup> Ratio of paternal/maternal feeding rate to nestlings prior to fledging.

<sup>d</sup> Natural difference in brightness between experimentally brightened and experimentally darkened sons during the control period.

<sup>e</sup> Natural difference in UV chroma between experimentally brightened and experimentally darkened sons during the control period.

<sup>f</sup> Number of paternal feeding attempts to experimentally brightened sons during the control period.

<sup>g</sup> Number of maternal feeding attempts to experimentally brightened sons during the control period.

<sup>h</sup> Number of paternal feeding attempts to experimentally brightened sons during the experimental period.

<sup>i</sup> Difference in mass between experimentally brightened and experimentally darkened sons.

variables were considered it became apparent that females shifted to provisioning brighter sons more when circumstances favored greater allocation to superior offspring. Males did not show the same sort of subtle shifts in strategy but rather seemed to respond only to the magnitude of difference in ornamental display, which could be interpreted as responding to the magnitude of difference in the quality of offspring.

When considering multiple explanatory variables during the experimental period, we found that mothers increased provisioning attempts to relatively brightened offspring if they had higher UV chroma, if they were naturally brighter, if it was earlier in the season, if they were heavier, if fathers fed them

more during the experimental period, and if fathers contributed relatively less to nestling provisioning. Hence, as in the control period, when certain conditions favored preferential food delivery to superior offspring, females shifted to greater allocation of food to brighter chicks. Paternal feeding rates during the experimental period were influenced by relatively few variables, with males responding only to brood size and differences in manipulated brightness between sons. The brighter that sons were relative to their brothers during this period, the more feeding attempts they received from their fathers. This relationship was strongest in fathers of large broods, likely because of the increased burden placed on fathers provisioning multiple offspring.

Although brood size and relative differences in the brightness of fledglings were the only variables influencing paternal feeding decisions, several factors influenced the relationship between maternal feeding decisions and fledgling plumage color. In both control and experimental periods, females increased feeding attempts to brighter or brightened sons early in the season, at a time when temperatures are consistently cooler. Lower daytime and nighttime temperatures might reduce the abundance of arthropod prey items necessary for self and nestling provisioning (e.g., Williams 1961; Kamata and Igarashi 1995) and increase thermoregulatory requirements of nestlings (Thessing 2000). Nestlings that must invest proportionally higher energy in homeostasis would have higher nutritional requirements than nestlings raised without such constraints (Dawson et al. 2005). Increased nutritional requirements of offspring could limit parental ability to adequately provide sufficient food for all nestlings, thus increasing the likelihood that parents might invest preferentially in those offspring most likely to survive, that is, those exhibiting the highest expression of a condition-dependent plumage trait. Additionally, increased thermoregulatory requirements of nestlings earlier in the season might also place undue pressure on brooding eastern bluebird mothers (eastern bluebird fathers do not brood; Gowaty and Plissner 1998) contributing to the female-specific influence of date on feeding decisions.

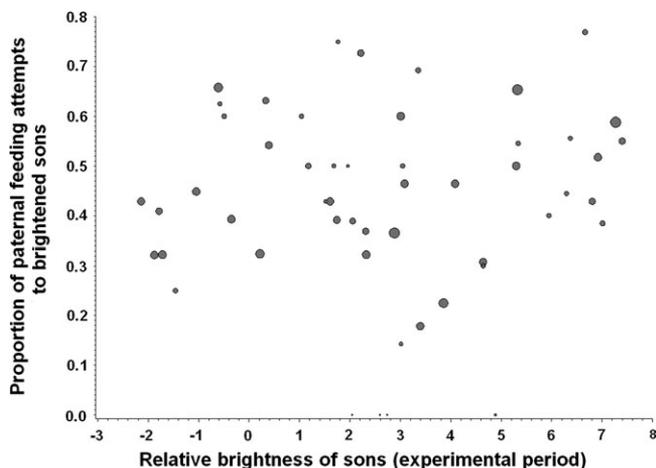


Figure 5

The relationship between male eastern bluebird feeding behavior during the experimental period (proportion of total feeding attempts toward experimentally brightened sons) and the relative plumage brightness of the sons being fed. Symbol sizes are proportional to the number of paternal feeding attempts in each trial.

Table 4

Generalized linear model using binomial error and logit link for the proportion of feeding attempts that eastern bluebird fathers directed toward experimentally brightened sons during the experimental period

Parameter	Estimate	Standard error	Wald 95% confidence limits		Chi square	<i>P</i> value
Intercept	-1.12	0.72	-2.52	0.29	2.44	0.12
Brightness difference, exp <sup>a</sup>	0.06	0.03	0.00	0.12	4.52	<0.05
UV chroma difference, exp <sup>b</sup>	5.26	4.60	-3.76	14.29	1.31	0.25
Date of trial	0.00	0.00	0.00	0.01	0.28	0.60
Relative parental investment <sup>c</sup>	-0.13	0.10	-0.33	0.06	1.80	0.18
Brightness difference <sup>d</sup>	-0.01	0.04	-0.09	0.07	0.03	0.85
UV chroma difference <sup>e</sup>	-2.79	5.26	-13.09	7.52	0.28	0.60
Maternal feeding, control <sup>f</sup>	0.01	0.01	-0.01	0.03	1.04	0.31
Paternal feeding, control <sup>g</sup>	0.02	0.01	-0.01	0.04	1.46	0.23
Maternal feeding, exp <sup>h</sup>	-0.01	0.01	-0.03	0.01	1.80	0.18
Mass difference <sup>i</sup>	-0.06	0.06	-0.17	0.05	1.19	0.28
Brood size	0.15	0.08	0.00	0.30	4.07	<0.05

Significant explanatory values in bold.

<sup>a</sup> Difference in brightness between experimentally brightened and experimentally darkened sons, see text for details.

<sup>b</sup> Difference in UV chroma between experimentally brightened and experimentally darkened sons.

<sup>c</sup> Ratio of paternal/maternal feeding rates to nestlings prior to fledging.

<sup>d</sup> Difference in brightness between experimentally brightened and experimentally darkened sons during the control period.

<sup>e</sup> Difference in UV chroma between experimentally brightened and experimentally darkened sons during the control period.

<sup>f</sup> Number of maternal feeding attempts to experimentally brightened sons during the control period.

<sup>g</sup> Number of paternal feeding attempts to experimentally brightened sons during the control period.

<sup>h</sup> Number of maternal feeding attempts to experimentally brightened sons during the experimental period.

<sup>i</sup> Difference in mass between experimentally brightened and experimentally darkened sons.

Another variable that influenced maternal feeding decisions in both control and experimental periods was the relative mass of the fledglings. Females fed both naturally brighter and experimentally brightened sons more when they were heavier than their brothers. Juvenal plumage ornamentation and mass are probably not independent characters, given that previous research has shown juvenile males raised in enlarged broods with lower feeding rates have duller feathers (Siefferman and Hill 2007). This relationship may explain some of the observed correlation between mass and maternal feeding preferences for naturally brighter offspring. However, the fact that experimentally brightened fledglings were also more likely to receive increased maternal investment if they were heavier than their siblings suggests that mothers can assess mass or mass-related character differences between fledglings. When analyzing offspring and making feeding decisions that optimize their own reproductive success, parents likely rely on a suite of cues to determine the relative quality and qualities of their offspring. Based on its influence on maternal feeding decisions in both control and experimental periods, the relative mass of fledglings appears to be one such cue.

Although differential fitness payoffs for mothers and fathers in different environments and contexts can lead to different investment strategies (e.g., Krebs and Magrath 2000; Kilner 2002; Quillfeldt et al. 2004), both parents are generally better off when their offspring survive. A certain degree of correlation in feeding behaviors between mothers and fathers is therefore not unexpected and we found that eastern bluebird mothers were more likely to feed naturally brighter and experimentally brightened offspring if their mates fed these same offspring at higher rates. However, the fact that paternal investment was not related to maternal feeding decisions is interesting. Given that female investment strategies appear to incorporate several sources of information (e.g., date, mass, color) it would seem that males could benefit by incorporating maternal feeding strategies into their own optimal provisioning decisions. However, given that paternal investment during the fledgling stage is lower than that of mothers, the

benefits of assessing multiple sources of information to optimize feeding strategies (as females appear to do) may be low, resulting in an optimal paternal strategy that incorporates only direct and easy-to-assess fledgling cues like plumage brightness and brood size.

The importance of reliable signals of offspring quality likely varies with resource availability and the costs of obtaining food. Such signals should be less important when resources are abundant and the costs of provisioning an entire brood are low. When resources are limited or the cost of obtaining resources is high, however, signals of offspring quality may be very valuable because they allow parents to maximize reproductive success by investing heavily in high-quality offspring. Habitat quality, time of year, and the relative investment of one's mate are just a few of the many factors could influence the costs of provisioning an entire brood. In our experiment, mothers increased the proportion of feeding attempts to experimentally brightened sons when the relative investment of fathers during the nestling stage was low. Fathers that provision nestlings at low rates increase the demands on mothers, thereby limiting the ability of mothers to provide adequate food for their entire brood. The increased demands on mothers mated to low investing fathers may make mothers more discriminating when delivering food items to offspring, in order to maximize their own reproductive success. Fathers with larger broods were also more likely to increase investment in experimentally brightened offspring suggesting that the increased costs of raising more offspring also influences the feeding rules and decisions of fathers. It would be interesting to measure additional factors such as food abundance and habitat quality to determine the impact of these variables on parental feeding decisions.

Natural selection and phylogenetic constraints have long been assumed to shape the appearance of juvenal plumage, but the juvenal plumages of some birds have characteristics of complex intraspecific signals of condition. Species such as the eastern bluebird, with well-understood, sexually selected signals of quality and condition, provide opportunities for exploring the potential intraspecific signaling functions of

juvenile traits. Recent studies show that the coloration and pattern of juvenal plumage function in much more than camouflage. Future studies should focus on the types of signals used in parent-offspring communication, the environmental conditions that favor the use of such signals, and the mechanisms ensuring the honesty and stability of these traits.

## FUNDING

National Institute of Allergy and Infectious Diseases (R01AI049724 to G.E.H.); Birmingham Audubon Society (to R.A.L.); Sigma Xi (to R.A.L.); American Ornithologists' Union (to R.A.L.).

We would like to thank J.D. Ligon, L. Siefferman, 2 anonymous reviewers, and members of the Hill lab for suggestions that greatly improved this manuscript. Additionally, we would like to thank M. Liu for guidance with laboratory procedures, M. Buschow and J. Hill for assistance with data collection in the field, A. Langston for assistance with data collection in the laboratory, M. Wooten for statistical assistance, R. Montgomery for the use of his program Colour, and V. Rebal for her assistance taping thousands of feathers and her support to R.A.L. throughout the duration of this project.

## REFERENCES

- de Ayala RM, Saino N, Moller AP, Anselmi C. 2007. Mouth coloration of nestlings covaries with offspring quality and influences parental feeding behavior. *Behav Ecol*. 18:526–534.
- Ballentine B, Hill GE. 2003. Female mate choice in relation to structural plumage coloration in blue grosbeaks. *Condor*. 105:593–598.
- Bize P, Piau R, Moureau B, Heeb P. 2006. A UV signal of offspring condition mediates context-dependent parental favouritism. *Proc R Soc Lond B Biol Sci*. 273:2063–2068.
- Clutton-Brock TH. 1991. The evolution of parental care. Princeton (NJ): Princeton University Press.
- Davis JN, Todd PM, Bullock S. 1999. Environment quality predicts parental provisioning decisions. *Proc R Soc Lond B Biol Sci*. 266:1791–1797.
- Dawson RD, Lawri CC, O'Brien EL. 2005. The importance of microclimate variation in determining size, growth, and survival of avian offspring: experimental evidence from a cavity nesting passerine. *Oecologia*. 144:499–507.
- Doucet SM. 2002. Structural plumage coloration, male body size, and condition in the blue-black grassquit. *Condor*. 104:30–38.
- Dugas MB. 2009. House sparrow, *Passer domesticus*, parents preferentially feed nestlings with mouth colors that appear carotenoid-rich. *Anim Behav*. 78:767–772.
- Ewen JG, Thorogood R, Karadas F, Cassey P. 2008. Condition dependence of nestling mouth colour and the effect of supplementing carotenoids on parental behavior in the hihi *Notiomystis cinctea*. *Oecologia*. 157:361–368.
- Galván I, Amo L, Sanz JJ. 2008. Ultraviolet-blue reflectance of some nestling plumage patches mediates parental favouritism in great tits *Parus major*. *J Avian Biol*. 39:277–282.
- Gotmark F, Ahlstrom M. 1997. Parental preference for red mouth of chicks in a songbird. *Proc R Soc Lond B Biol Sci*. 264:959–962.
- Gowaty PA, Plissner JH. 1998. Eastern Bluebird (*Sialia sialis*). In: Poole A, editor. The birds of North America, No. 381. Ithaca (NY): Cornell Lab of Ornithology. doi:10.2173/bna.381. Available from: <http://bna.birds.cornell.edu/bna/species/381>.
- Griggio M, Morosinotto C, Pilastro A. 2009. Nestlings' carotenoid feather ornamentation affects parental allocation strategy and reduces maternal survival. *J Evol Biol*. 22:2077–2085.
- Haskell D. 1994. Experimental evidence that nestling begging behavior incurs a cost due to nest predation. *Proc R Soc Lond B Biol Sci*. 257:161–164.
- Hill GE. 2006a. Environmental regulation of ornamental coloration. In: Hill GE, McGraw KJ, editors. Bird coloration volume I: mechanisms and measurements. Cambridge (MA): Harvard University Press. p. 507–560.
- Hill GE. 2006b. Female mate choice for ornamental coloration. In: Hill GE, McGraw KJ, editors. Bird coloration volume II: function and evolution. Cambridge (MA): Harvard University Press. p. 137–200.
- Hill GE, Doucet SM, Buchholz R. 2005. The effect of coccidial infection on iridescent plumage coloration in wild turkeys. *Anim Behav*. 69:387–394.
- Hill GE, McGraw KJ, editors. 2006. Bird coloration volume II: function and evolution. Cambridge (MA): Harvard University Press.
- Jacot A, Kempenaers B. 2007. Effects of nesting condition on UV plumage traits in blue tits: an experimental approach. *Behav Ecol*. 18:34–40.
- Johnsen A, Delhey K, Andersson S, Kempenaers B. 2003. Plumage colour in nestling blue tits: sexual dichromatism, condition dependence and genetic effects. *Proc Roy Soc London B*. 270:1263–1270.
- Johnsen A, Delhey K, Schlicht E, Peters A, Kempenaers B. 2004. Male sexual attractiveness and parental effort in blue tits: a test of the differential allocation hypothesis. *Anim Behav*. 70:877–888.
- Johnstone RA. 1995. Honest advertisement of multiple qualities using multiple signals. *J Theor Biol*. 177:87–94.
- Johnstone RA. 1996. Multiple displays in animal communication: 'backup signals' and 'multiple messages'. *Philos Trans R Soc Lond B Biol Sci*. 351:329–338.
- Kamata N, Igarashi M. 1995. Diurnal change of adult behavior, daily oviposition and influence of temperature on adult emergence and light trapping data of the beech caterpillar, *Quadralcalcarifera punctatella* (Motsch) (Lep, Notodontidae). *J Appl Entomol*. 119:177–183.
- Keyser AJ, Hill GE. 2000. Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behav Ecol*. 11:202–209.
- Kilner RM. 2002. Sex differences in canary (*Serinus canaria*) provisioning rules. *Behav Ecol Sociobiol*. 52:400–407.
- Krebs EA, Magrath RD. 2000. Food allocation in crimson rosella broods: parents differ in their responses to chick hunger. *Anim Behav*. 59:739–751.
- Lack D. 1968. Ecological adaptations for breeding birds. London: Chapman & Hall.
- Leech SM, Leonard ML. 1997. Begging and the risk of predation in nestling birds. *Behav Ecol*. 8:644–646.
- Lewis KP. 2004. How important is the statistical approach for analyzing categorical data? A critique using artificial nests. *Oikos*. 104:305–315.
- Liu M, Siefferman L, Hill GE. 2007. An experimental test of female choice relative to male structural coloration in eastern bluebirds. *Behav Ecol Sociobiol*. 61:623–630.
- Lyon BE, Eadie JM, Hamilton LD. 1994. Parental choice selects for ornamental plumage in American coot chicks. *Nature*. 371:240–243.
- McGraw KJ, Mackillop EA, Dale J, Hauber ME. 2002. Different colors reveal different information: how nutritional stress affects the expression of melanin and structurally based ornamental plumage. *J Exp Biol*. 205:3747–3755.
- McNamara JM, Gasson CE, Houston AI. 1999. Incorporating rules for responding into evolutionary games. *Nature*. 401:368–371.
- Nur N. 1998. The cost of reproduction in birds: an examination of the evidence. *Ardea*. 76:155–168.
- Pinkowski BC. 1974. Criteria for sexing eastern bluebirds in juvenile plumage. *Inland Bird Banding News*. 46:88–91.
- Quillfeldt P, Masello JF, Hamer KC. 2004. Sex differences in provisioning rules and honest signalling of need in Manx shearwaters, *Puffinus puffinus*. *Anim Behav*. 68:613–620.
- Siefferman L, Hill GE. 2005a. Evidence for sexual selection on structural plumage coloration in female eastern bluebirds (*Sialia sialis*). *Evolution*. 59:1819–1828.
- Siefferman L, Hill GE. 2005b. Male eastern bluebirds trade future ornamentation for current reproductive investment. *Biol Lett*. 1:208–211.
- Siefferman L, Hill GE. 2007. The effect of rearing environment on blue structural coloration of eastern bluebirds (*Sialia sialis*). *Behav Ecol Sociobiol*. 61:1839–1846.
- Skutch AF. 1976. Parent birds and their young. Austin (TX): University of Texas Press.
- Tanner M, Richner H. 2008. Ultraviolet reflectance of plumage for parent-offspring communication in the great tit (*Parus major*). *Behav Ecol*. 19:369–373.
- Thessing A. 2000. Growth and final size of Willow Tit *Parus montanus* under different environmental conditions. *Ardea*. 88:215–224.
- Williams CB. 1961. Studies in the effect of weather conditions on the activity and abundance of insect populations. *Philos Trans R Soc Lond B Biol Sci*. 244:331–378.
- Winkler DW. 1987. A general model for parental care. *Am Nat*. 130:526–543.
- Wright J, Cuthill IC. 1989. Manipulation of sex differences in parental care. *Behav Ecol Sociobiol*. 25:171–181.