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Parental favoritism in a wild bird population

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Abstract

In most taxa with altricial young, offspring solicit food from their parents using a combination of visual and acoustic stimuli, but exactly what these young are communicating, and how selection shapes parental responses, remains unresolved. Theory posits that parents' interpretation and response to begging should vary with the likelihood of a return on their investment. We tested this in a wild population of prothonotary warblers (*Protonotaria citrea*), predicting that parents bias food non-randomly toward certain individuals within their broods depending on both the size and number of offspring. We observed parent–offspring interactions and detected strong dependence between brood size and nestling size in shaping parental responses to begging. Larger siblings were less likely to solicit food during feeding events than their smaller siblings, but they received a disproportionate share from parents in nests containing fewer-than-average young, whereas the smaller-than-average nestlings were disproportionately fed in broods containing a greater-than-average number of young. These findings suggest that parents respond to begging signals according to multiple social cues, favoring the stronger siblings with greater survival prospects when few copies of their genes are present, but overtly favoring runts to ensure whole-brood survival when capable of fledging more young. Future experimental studies may shed light on the contributions of parental decision-making and memory, how young nestlings learn in parent–offspring communication systems, and the adaptive significance of these behaviors.

Introduction

To maximize fitness, altricial young should make the most of a critical window of time, early in life, in which to grow and mature prior to having to survive without parental assistance, whereas fitness maximization for parents requires

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the optimization of a trade-off between investment among multiple offspring both within and among reproductive events, thereby constraining the availability of resources for individual young (Williams 1966; Trivers 1974; Smith and Fretwell 1974; Macnair and Parker 1979; Parker et. al. 2002; Royle et al. 2012; Hodges et al. 2015). It follows, then, that intense selection should favor overt solicitations (i.e., begging) by offspring for limiting parental food resources. Indeed, offspring in many taxa, including amphibians, birds, insects, mammals, spiders, and possibly some plants, solicit food from their parents using a combination of stimuli (e.g., Smith and Montgomerie 1991; Kilner and Johnstone 1997; Wright and Leonard 2002; Leonard and Horn 2005; Kölliker et al. 2006; Grodzinski and Lotem 2007; Hinde et al. 2009; Madden et al. 2009; Smiseth et al. 2011; Bowers et al. 2016b; Capodeanu-Nägler et al. 2018a, b; Mattey et al. 2018). However, parents do not always feed begging offspring or even attempt to treat them equally (Mock and Parker 1997; Leonard and Horn 2001; Forbes 2007; Smiseth

et al. 2007; Barnett et al. 2011; Bowers et al. 2011; Wiebe and Slagsvold 2012; Caro et al. 2016a). Indeed, in a variety of vertebrate and invertebrate clades, parents only feed a subset of their offspring, usually just one, during a given provisioning event (Mock and Parker 1997; Manser et al. 2008; Dor and Lotem 2010; Barnett et al. 2012), and how parents choose who to feed remains unresolved.

Begging solicitations are particularly apparent in birds (Fig. 1), in which altricial young make postural gestures that include flaunting conspicuous, brightly colored mouths and repetitively calling to attract parental attention (e.g., Kilner 2002), but the exact causes, consequences, and meaning of begging signals for parents are not always clear (Royle et al. 2002; Grodzinski et al. 2011; Hinde and Godfray 2011; Johnstone and Kilner 2011; Mock et al. 2011; Wright 2011; Caro et al. 2016a). Several hypotheses might explain the information parents glean from begging signals: parents might respond to begging simply as a proximate signal of hunger underlying a nestling's desire to be fed and allowing parents to make a quick decision, or as an ultimate, condition-dependent expression of offspring reproductive value (Godfray 1991; Glassey and Forbes 2002; Wiebe and Slagsvold 2009; Mock et al. 2011; Fresneau et al. 2018). In the latter case, parents might perceive begging as either a signal of need or signal of quality. If parents perceive begging as a signal of need, feeding decisions should be aimed at benefitting the survival prospects of the offspring for whom a unit increase in parental investment yields the greatest marginal increase in survival probability; in other words, parents choose to feed runts (Godfray 1995; Kilner 1995; Price and Ydenberg 1995; Kilner and Johnstone 1997; Cotton et al. 1999; Godfray and Johnstone 2000; Saino et al. 2000a; Koykka and Wild 2018). Alternatively, if begging is a signal of quality, parents should feed the young with the best chance of survival; in other words, parents actively choose to feed the healthiest young that are most likely to survive, as this is least likely to constitute a wasted investment (Grafen 1990; Lotem 1998; Royle et al. 2002; Mock et al. 2005, 2011; Bowers et al. 2019a).

Nestling begging is generally thought of as being costly and, thus, representative of an honest signal (Kilner 2001; Wells 2003; but see also Moreno-Rueda 2007), although such signals do not always need to be costly to be honest (Számadó 2011). But what, exactly, constitutes honesty depends on the message nestlings are conveying. Positively condition-dependent begging, where offspring in better condition beg more intensely, is often assumed to represent dishonest signaling, and it has been observed in just as many species as putatively honest, negatively condition-dependent begging, where nestlings in poor condition beg more intensely (Caro et al. 2016b). However, positively condition-dependent begging would only be dishonest if begging is intended to signal need but would be honest if signaling

quality. For example, a recent field experiment involving the direct manipulation of offspring condition revealed that nestlings in better condition (1) begged more intensely than those in poorer condition, (2) received an increase in parental feedings corresponding to their increased begging, and (3) had a higher likelihood of recruiting into the local population as breeding adults in the future (Bowers et al. 2019a). These findings suggest that positively condition-dependent begging can serve as an honest signal of quality, and that parents further use information about offspring size, condition, and other morphological traits when making feeding decisions (see also Kilner 1997; Saino et al. 2000b; Loiseau et al. 2008b; Dugas 2009; Romano et al. 2016; Pirrello et al. 2017). While nestling phenotype and begging intensity are important to parents in making feeding decisions, it is possible that parents also use previous experience to weigh these decisions. The memory of which nestlings have recently been fed, either through spatial memory of the arrangement of nestlings within the nest or through episodic memory of specific feeding events, could influence parental feeding patterns. Spatial and episodic memory have primarily been tested in food-caching species (Clayton 1998; Salwiczek et al. 2010; Watanabe 2018; Branch et al. 2019); thus, the potential influence of long-term memories on parental investment decisions of non-caching species, if any, is unclear.

Parents may embark on a breeding cycle intending to distribute resources equally and keep all their young alive, but, if conditions deteriorate, fitness maximization may require a different strategy (Caro et al. 2016a; Koykka and Wild 2018; Li et al. 2019). Such a situation arises in birds, in which numerous factors (e.g., brood size, nestling size, resource availability) can shape parents' perception of how their nesting attempt is progressing. Indeed, the number of young produced as eggs usually exceeds the number of young reared to independence, typically because of asymmetric sibling rivalry, low resource availability, or partial nest destruction or parasitism (Mock and Forbes 1995; Forbes et al. 1997, 2002; Hoover and Robinson 2007; Forbes 2011; Louder et al. 2015). Similarly, recent research in a cooperative breeder revealed that responsiveness to begging varied with group composition, suggesting that parents modify their investment according to multiple environmental cues (MacLeod and Brouwer 2018). Thus, parental responses to begging signals likely vary with ecological conditions and the anticipated return on parental investment (Roulin et al. 2010; Caro et al. 2016a; Koykka and Wild 2018).

In this observational study, we analyze parental responsiveness to condition-dependent nestling begging in a wild population of prothonotary warblers (*Protonotaria citrea*), predicting that, if parental responsiveness varies with the expected return on their investment, then responses to nestling begging should vary with both brood size and nestling

condition. The number of young fledged is among the strongest determinants of parental fitness in wild birds (McCleery et al. 2004; Williams 2012), and getting as many offspring through to fledging as possible necessitates keeping even the runts of the brood alive; thus, we predicted that when rearing broods with relatively more young, parents may respond to signals of need and preferentially feed smaller siblings. However, offspring body mass is also commonly associated with parental fitness, as individual differences in body mass among offspring prior to independence positively predict their survival and recruitment as breeding adults in most species studied to date (e.g., Clutton-Brock and Sheldon 2010). This latter effect on parental fitness is not as strong as the number of fledglings produced (McCleery et al. 2004; Williams 2012). Thus, we posit that, when brood size is reduced, thereby reducing the number of copies of parents' genes that can possibly be transmitted, parents should respond to signals of quality, biasing food toward the larger offspring in better condition (see also Saino et al. 2000a, b; Caro et al. 2016a; Koykka and Wild 2018) so as to maximize their probability of post-fledging survival. We weighed all nestlings before and after observing parental feedings within the nest, predicting that any parental feeding preferences should also shape nestling weight gain during our observations in addition to prefledging mass, size, and survival.

Methods

Study species and site

Prothonotary warblers are small (14–16 g), insectivorous, cavity-nesting songbirds. They are Neotropical–Nearctic migrants whose endemic breeding range lies predominantly in the southeastern United States (Tonra et al. 2019; Youtz et al. 2020), and they frequently nest in human-made nest boxes when available (Twedt and Henne-Kerr 2001; Slevin et al. 2018; Mueller et al. 2019b). The number of eggs laid by the female per clutch is typically four or five, averaging 4.2 ± 0.1 eggs (mean $\pm$ SE), and can vary in part with maternal age (Blem et al. 1999), whereas brood size at fledging is 3.4 ± 0.1 young (mean $\pm$ SE), typically a result of brood reduction in asynchronously hatched broods (Petit 1989). Only the female incubates eggs and broods ectothermic hatchlings, but these young are typically provisioned with arthropod prey by both parents (Petit 1999). Nests are often targeted by the brood parasitic brown-headed cowbird (*Molothrus ater*), which can be a major cause of nest failure (Petit 1999). However, none of the broods being provisioned in this study contained any parasitic cowbird young.

This study was conducted on a wild population of prothonotary warblers in the 2019 breeding season at the Meeman Biological Station, lying east of the Mississippi River in southwestern Tennessee (35.363° N, 90.017° W). From 2017–2018, there were 220 nestboxes distributed over ca. 100 ha of the forest; prior to the 2019 field season, we expanded this network to 600 nest boxes distributed over ca. 250 ha. available for breeding prothonotary warblers. Nestboxes rest ca. 1.5 m aboveground atop a 51-cm-diameter aluminum predator baffle (further details in Mueller et al. 2019a, b), and the surrounding habitat is mostly mature, secondary deciduous forest comprised of white and red oak (*Quercus* spp.), American beech (*Fagus grandifolia*), tulip poplar (*Liriodendron tulipifera*), and sweetgum (*Liquidambar styraciflua*).

Procedures

During the 2019 breeding season, we visited all nestboxes twice per week to determine clutch-initiation dates. Beginning about halfway through incubation, which lasts ca. 13–14 days (Mueller et al. 2019a), we captured all females on the nest while incubating, and we captured adult males using song playback and mist nets located near the nest. Both females and males received a uniquely numbered, aluminum leg band, and males received three additional, colored leg bands arranged in unique combinations so they could subsequently be identified visually (males are more difficult to recapture than females). We then monitored the progress and status of each nest and, six days after hatching began, we collected digital videos from both inside (SQ11 mini HD camera) and outside (Kodak Zx1 or Zx5) each nest. Videos typically lasted an hour per nest, demonstrating nestling and parent behaviors and allowing us to observe begging by individual nestlings (vocally and by gaping open their mouths) and assess who was fed using the internal cameras. For simplicity, we consider nestlings raising their head and gaping open their mouths to reflect a begging solicitation (Fig. 1), providing an objective, non-qualitative metric indicating whether nestlings either did or did not solicit food. In some species, provisioning behavior and parental care may differ according to parent sex (Leonard and Horn 1996); thus, to determine whether provisioning behavior differed between males and females in our study, we identified parents visiting the nest to feed as either the resident male or female using the external cameras. We were able to uniquely identify the individual nestlings in the internal videos by placing, at random, a dab of nontoxic white paint in various locations on the nestlings' heads. Before filming each nest, we weighed nestlings (± 0.1 g) using an electronic balance and marked them with white paint as described above. We then weighed each nestling again after the recording was completed, and we used these pre- and post-video weight measurements to analyze changes in nestling mass during our observations. We subsequently visited each nest on day 8 post-hatching to process nestlings prior to fledging and obtain measures

of phenotypic condition (Sakaluk et al. 2014; Barnett et al. 2015). This involved banding all nestlings and obtaining measures of pre-fledging mass (± 0.1 g), tarsus length (± 0.1 mm), and wing-chord length (± 0.5 mm).

Nests are defended to an extent from ground-dwelling predators by baffles under the nest boxes, and enjoy high rates of fledging success (73.3% of 191 warbler nests produced from the onset of the study in 2017 through 2019 successfully fledged young); of the nests that successfully fledge any young, ca. 60% of them fledge all of the offspring produced as eggs. However, nearly 40% of successful breeding pairs fail to rear all their offspring to fledging.

Data and analyses

All analyses were conducted using Statistical Analysis Software (ver. 9.4), with two-tailed hypotheses ($\alpha = 0.05$). In total, we compiled behavioral observations of parents and offspring at 61 nests produced by a total of 42 unique females; thus, we included maternal identity as a random effect where appropriate to account for the non-independence of nests produced by the same female (in only a few instances did a female produce multiple broods sired by different males). Similarly, when analyzing individual nestlings, we also included nest as a random effect to account for the non-independence of siblings within broods. We analyzed begging and feeding as binary outcomes (i.e., nestlings either did or did not beg, and were or were not fed), using generalized linear mixed models (GLMMs) with binomial error distributions. Initially, we analyzed the begging behavior of nestlings in relation to the sex of the feeding parent, which revealed no difference between male and female parents in the nestlings' probability of begging ($F_{1, 870.6} = 0.01$; $P = 0.917$), nor was there any interaction between parent sex and nestlings' relative mass prior to our observation in their effect on the probability of begging ($F_{1, 827.7} = 1.02$; $P = 0.313$). Similarly, the probability of any individual nestling getting fed did not differ between the male and female parent ($F_{1, 868} = 0.00$; $P = 0.965$), and neither did parent sex interact with nestlings' relative mass to influence their probability of being fed ($F_{1, 868} = 0.05$; $P = 0.829$). Thus, we pooled individual feedings by male and female parents when analyzing nestling begging.

We then used pre- and post-observation masses to calculate individual masses relative to the rest of the brood (i.e., relative mass) as the difference between an individual nestling and the brood mean. Thus, positive relative mass values indicate above-average siblings and negative values below-average siblings. We analyzed these changes in nestling mass as the dependent variable in relation to differences in pre-observation mass and brood size. We also used these relative masses as an independent variable in predicting begging and feeding. We then tested, for individual nestlings,

whether its relative mass interacted with the size of the brood in influencing (1) the nestling's probability of begging and being fed during parental feeding visits (using a GLMM as described above), and (2) growth during and after our observations (using linear mixed models).

Results

Undersized nestlings (i.e., runts with a smaller relative mass prior to our observations) begged more frequently overall during our observations than larger nestlings (estimate $\pm$ SE $= -0.367 \pm 0.099$; $F_{1, 203} = 13.60$; $P < 0.001$; Fig. 2a), and nestlings that begged more received more food (estimate $\pm$ SE $= 0.205 \pm 0.030$; $F_{1, 203} = 46.44$; $P < 0.001$; Fig. 2b inset). However, parents did not respond uniformly to nestling begging solicitations. Some nestlings were fed every time they begged, whereas others were not fed at all during our observations despite soliciting food from parents. On average, parents made 5.6 ± 2.5 feeding trips per observation (mean $\pm$ SD), and a given nestling was fed on $40.5 \pm 30.9\%$ of feeding trips during which they solicited food (mean $\pm$ SD; Fig. 2b).

Fig. 1 Nestlings begging for food. Parents typically encounter solicitations from multiple young simultaneously, despite only having a single prey item with which to feed an individual nestling

Fig. 2 Proportion of parental feeding trips during which nestlings solicited food in relation to their relative mass prior to our observation (**a**), and the frequency, expressed as a proportion, with which nestlings were fed on any given provisioning trip during which they solicited food (**b**). Inset is the relationship between the number of times nestlings were fed and begged relative to their brood-mates during our observations. Light dots depict individual observations, dark dots overlapping observations
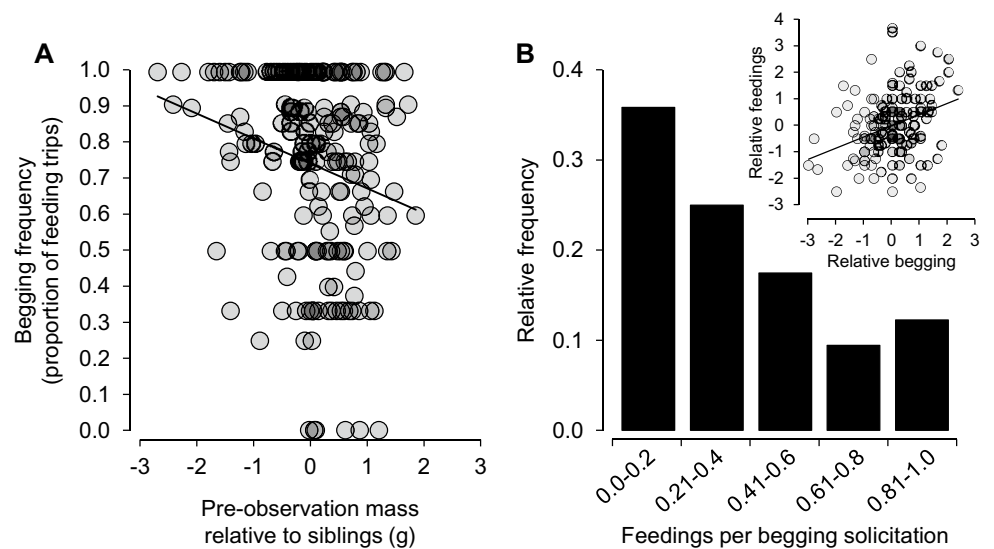
Parents biased feedings toward nestlings primarily on the basis of size-differences among siblings within broods, but this bias was dependent upon brood size as reflected by an interaction between these effects on the probability of a nestling being fed (Table 1; Fig. 3a–c). Follow-up tests to tease apart this interaction revealed that parents actively biased food toward larger nestlings beyond what would be expected by chance when rearing broods with only a few young (effect of nestling mass on feeding frequency: estimate $\pm$ SE $= 0.519 \pm 0.155$; $F_{1, 61} = 11.27$; $P = 0.001$; Fig. 3a), but parents expressed the opposite behavior, favoring runts when rearing relatively more young (estimate $\pm$ SE $= -0.453 \pm 0.220$; $F_{1, 55} = 4.23$; $P = 0.044$; Fig. 3c).

Parental favoritism had consequences for the amount of mass nestlings gained, as the amount of feedings a nestling received during our observations positively affected their change in mass over this time (effect of feeding frequency on mass gained: estimate $\pm$ SE $= 0.055 \pm 0.019$; $F_{1, 203} = 8.06$; $P = 0.005$). Thus, consistent with the feeding biases we observed (Fig. 3a–c), there was a similar interaction between brood size and initial size-differences among siblings in their effect on mass gained (Table 1; Fig. 3d–f). Specifically, within enlarged broods in which parents biased food toward runts (Fig. 3c), these runts gained more mass during our observations than their initially bigger siblings (estimate $\pm$ SE $= -0.197 \pm 0.049$; $F_{1, 66} = 15.96$; $P < 0.001$; Fig. 3f); on the other hand, initial size differences persisted within broods containing fewer young in which parents did not attempt to ameliorate the runts' initial disadvantage (estimate $\pm$ SE $= -0.023 \pm 0.040$; $F_{1, 66} = 0.33$; $P = 0.569$; Fig. 3d). These changes in mass during our observations were also associated with nestling survival, as the average change in mass among nestlings at the brood level was positively correlated overall with the proportion of young surviving to fledge (estimate $\pm$ SE $= 2.537 \pm 1.049$; $F_{1, 59} = 5.84$; $P = 0.019$). Finally, prior to fledging, nestlings that had received more food per begging solicitation were heavier and had longer, better-developed wing chords while controlling for their initial size differences (Table 2).

Table 1 Effects of nestling mass and brood size on parental responsiveness to nestling begging and on mass gains by nestlings during our observations

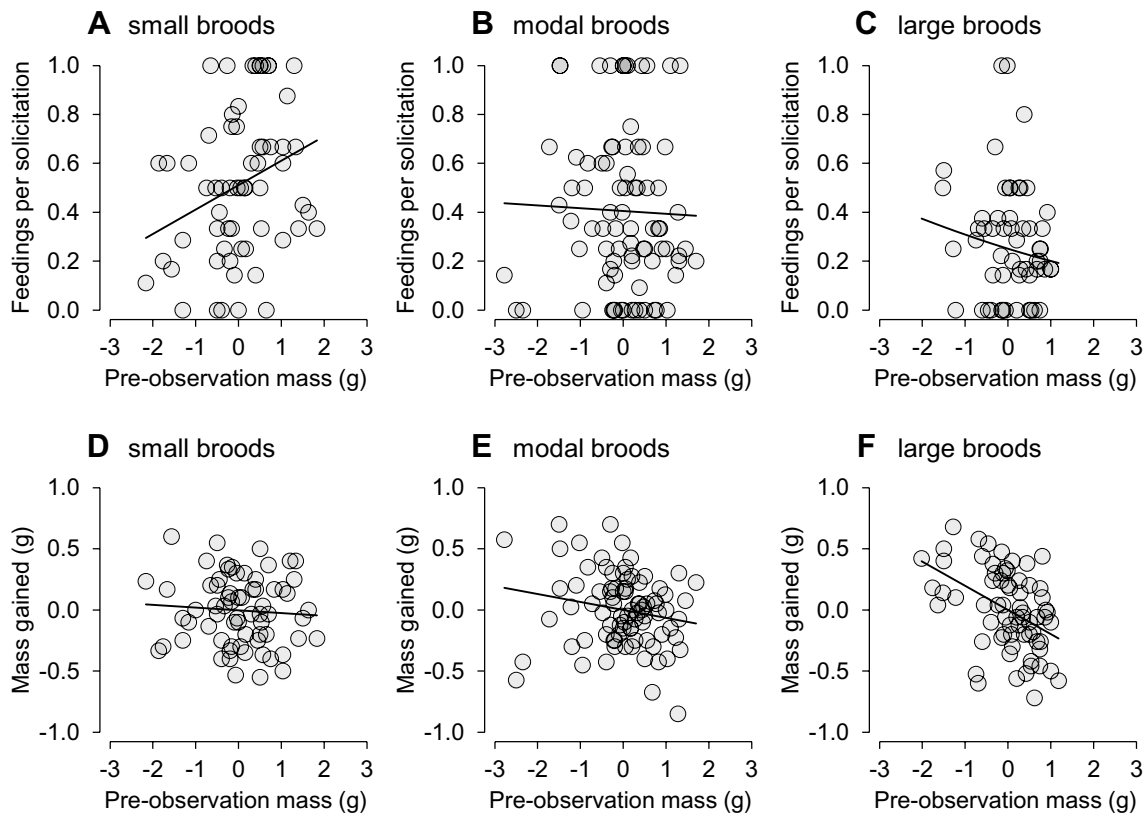|	Estimate $\pm$ SE	F	df	P
Parental feedings per solicitation				
Relative mass	1.362 ± 0.431	10.00	1, 195.0	0.002
Brood size	-0.487 ± 0.085	33.07	1, 54.1	<0.001
Relative mass $\times$ brood size	-0.348 ± 0.112	9.66	1, 195.0	0.002
Intercept	1.288 ± 0.339			
Mass gained				
Relative mass	0.176 ± 0.113	2.40	1, 217	0.123
Brood size	0.001 ± 0.022	0.00	1, 217	0.956
Relative mass $\times$ brood size	-0.067 ± 0.029	5.44	1, 217	0.021
Intercept	-0.006 ± 0.088			

Fig. 3 Parental provisions received per begging solicitation in relation to nestling's pre-observation mass within **a** small broods, **b** modal broods, and **c** large broods. Nestling mass gains during our observations in relation to their pre-observation mass within **d** small, **e** modal, and **f** large broods. Pre-observation mass and mass gained are values relative to the rest of the brood. Light dots depict individual observations, dark dots overlapping observations

Discussion

Environmental conditions, including the social environment, early in life can often have a profound effect on fitness (Lindström 1999; Bowers et al. 2015, 2017; but see also Drummond and Ancona 2015). In altricial birds that depend upon parents for food at a young age, a particularly critical period of neonatal development with long-term consequences appears to involve a narrow window of time shortly after hatching. Indeed, parental provisioning of food to offspring at this time positively predicts whether or not offspring survive and reproduce as adults within local breeding populations (Schwagmeyer and Mock 2008; Bowers et al. 2014a), a result that is not unexpected given the critical window of time for offspring to maximize growth prior to encountering the energetic demands of endothermy and to obtain the nutritional resources they will need to survive outside the nest. It follows, then, that selection might favor overt solicitations from these offspring for parental food resources to enhance offspring survival and parents' inclusive fitness.

We found that size differences between siblings within the nest prior to our observations significantly predicted

begging during parental visits. Undersized runts begged for food more frequently during feeding trips, whereas their larger, presumably better-satiated siblings in better condition refrained from begging on ca. one-third of parental visits, on average (Fig. 2a). Such a result is consistent with the hypothesis that selfishness among older, dominant siblings might be tempered by the inclusive-fitness benefit of letting younger siblings obtain food instead (Parker et al. 1989; Forbes 2007; Romano et al. 2016; Roulin et al. 2016); at a proximate level, this abstaining from begging by larger siblings may simply be mediated by hunger (Glassey and Forbes 2002; Mock et al. 2011; Fresneau et al. 2018), but this does not negate the potential inclusive-fitness benefit of helping younger siblings stay alive. Although begging was negatively condition-dependent, parental responses to these begging signals clearly depended on nestling size, suggesting that (1) nestling begging may reflect a form of cooperation associated with feeding (Roulin 2002; Dreiss et al. 2010, 2015; Mock et al. 2011), but that parents ultimately determine who is fed and that (2) parents do not respond to begging merely for fast decision making.

Table 2 Effects on nestling pre-fledging body mass, tarsus length, and wing-chord length (relative to siblings)

	Estimate ± SE	F	df	P
Body mass				
Feedings per solicitation	0.075 ± 0.032	5.63	1, 186	0.019
Initial mass	0.612 ± 0.043	200.18	1, 186	< 0.001
Brood size	0.049 ± 0.038	1.69	1, 186	0.195
Intercept	− 0.232 ± 0.149			
Tarsus length				
Feedings per solicitation	0.064 ± 0.039	2.67	1, 186	0.104
Initial mass	0.504 ± 0.053	89.64	1, 186	< 0.001
Brood size	0.056 ± 0.046	1.44	1, 186	0.231
Intercept	− 0.240 ± 0.183			
Wing length				
Feedings per solicitation	0.259 ± 0.096	7.22	1, 186	0.008
Initial mass	1.523 ± 0.132	132.70	1, 186	< 0.001
Brood size	0.255 ± 0.115	4.89	1, 186	0.028
Intercept	− 1.001 ± 0.455			

Feedings per solicitation are the residuals of a feedings × solicitations linear regression, and initial masses are relative values (i.e., relative to siblings) during our behavioral observations two days prior

Not unexpectedly, nestlings begging more than their siblings were fed more frequently, but although this relationship was relatively strong (Fig. 2b), it was noisy, and most nestlings received relatively little food given their begging rate, whereas ca. 10% of nestlings in the population received a prey item nearly every time they solicited food. Why should such a subset of nestlings be disproportionately more likely to be fed than their siblings? Future experiments manipulating age structure, nestling satiety, and condition will shed light on this. One potential explanation for this pattern, given the distribution of feedings we observed (Fig. 2b) is that parents discriminate among their young and make non-random feeding decisions. Parents provisioning larger-than-average broods appeared to follow the signal of need hypothesis, demonstrating a preference for undersized runts and feeding their young based on their level of need. This may be necessary with increasing brood sizes, as food will be spread over a relatively larger number of young, thereby reducing per-capita intake among nestlings and increasing the risk of starvation. On the other hand, parents of broods in which not all offspring were present discriminated against the runts and preferentially fed the larger siblings. These differences in feeding rate were not inconsequential, as they also predicted nestlings' subsequent survival to fledging and pre-fledging mass and size, traits that generally predict the survival and recruitment of offspring as breeding adults in future years

(Both et al. 1999; Clutton-Brock and Sheldon 2010; Wolfe et al. 2013; Bowers et al. 2014b, 2019a).

It must be noted that this study is an observational one, whereas inferences of causation require experimentation. For example, the patterns we report may be a response by parents to changes in brood size over the course of the nestling period (i.e., as nestlings are lost through brood reduction or partial nest destruction or depredation). On the other hand, these correlations might also be underlain by inherent differences in parental behavior, whereby a subset of parents adopt a signal-of-quality strategy from the outset of the breeding cycle, actively favoring the strongest, dominant siblings, and potentially even encouraging the mortality of the youngest, less-competitive nestlings. Indeed, even though our study is an observational one, it suggests that parental responses to the begging of any particular nestling vary with its size relative to siblings. Since nestling size changes rapidly with fluctuations in feeding and as the nestling stage progresses, parental learning and memory of feeding events may allow for behavioral plasticity in feeding decisions (Healy and Hurly 2004). Aside from remembering recent feeding trips, parental memory of the investment strategy that incurred the greatest benefit in previous broods can shape decisions for future broods. Additionally, parents may adopt one feeding strategy early in the nestling stage and later switch to a different strategy after learning what works best to ensure the survival of the young (Shizuka and Lyon 2012). The role of cognitive processes such as these in shaping parental investment decisions warrants further study, but, ultimately, the ability to adapt to changing nestling signals using phenotypic and/or memory cues should increase parental fitness.

Begging is likely not without costs (Kilner 2001; Moreno-Rueda 2007; Wright and Leonard 2002), thereby ensuring signal honesty and reliability. However, the exact interpretation of begging signals for parents remains unclear, with widely variable results across studies and species (Lotem 1998; Mock et al. 2011). Some degree of this variability is likely attributable to variation in ecological conditions and resource availability (Caro et al. 2016a; Koykka and Wild 2018), as territory quality is known to shape the investment strategies of breeding birds (Martin 1987), including the number, quality, and sex ratio of offspring (Janiszewski et al. 2013; Krist and Munclinger 2015; Krist et al. 2015; Bowers et al. 2016a, 2017; Poorboy et al. 2018). Such a situation may be especially likely to occur in birds, as ecological conditions are known to shape maternal hormone levels during the reproductive cycle, influencing hormone concentrations within egg yolks that shape subsequent variation in nestling begging, parental care, and offspring survival (Scwabl and Lipar 2002; Müller et al. 2007; Loiseau et al. 2008a; Bowers et al. 2016b, 2019b; Weber et al. 2018). Future manipulative experiments will shed further light on the interplay between

maternal hormone deposition in eggs and intrafamilial conflict in shaping nestling learning early in life (e.g., when begging goes unrewarded; see also Kedar et al. 2000; Budden and Wright 2008; Grodzinski et al. 2008).

In conclusion, we found that larger siblings were generally less likely to beg than their smaller siblings during parental feeding trips. However, despite this reduced begging rate, these larger-than-average siblings received a disproportionate share of food in those nests with fewer-than-average young. On the other hand, the smaller-than-average nestlings were disproportionately fed in broods with a greater-than-average number of young. Collectively, these results suggest that parents respond to begging signals within a given breeding cycle according to their own assessment of how many copies of their genes might be passed on, a possibility that awaits testing in future experimental studies.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

Ethics approval All activities followed guidelines provided by ABS/ASAB, with approval from (1) the Institutional Animal Care Committee of the University of Memphis, (2) the United States Geological Survey, and (3) the Tennessee Wildlife Resources Agency.

Consent for publication All persons entitled to authorship are so named and consented to publication of this work.

Code availability Available upon request to the corresponding author.

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