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Original Article

Parental control: ecology drives plasticity in parental response to offspring signals

Shana M. Caro[1,2,3,*], Adara C. Velasco[1,4], Tjomme van Mastrigt[1,5], Kees van Oers[5], Ashleigh S. Griffin[6], Stuart A West[6] and Camilla A. Hinde[1]

[1]Behavioural Ecology Group, Wageningen University & Research, De Elst 1, 6708 WD, The Netherlands
[2]Department of Biology, Adelphi University, 1 South Avenue, Garden City, NY 11530, USA
[3]Department of Integrative Biology, The University of Texas at Austin, 2415 Speedway, Austin, TX 78712, USA
[4]Department of Evolutionary Ecology, National Museum of Natural Sciences, Spanish National Research Council (MNCN-CSIC), Calle de José Gutiérrez Abascal 2, 28006 Madrid, Spain.
[5]Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), PO Box 50, 6700 AB, Wageningen, The Netherlands.
[6]Department of Biological Sciences, University of Oxford, 11a Mansfield Road, Oxford, OX1 3SZ, UK.

[*]Corresponding author: Shana Caro, Department of Biology, Adelphi University, 1 South Avenue, Garden City NY 11530, USA. Email: Shana_Caro@post.harvard.edu
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Birds differ in their parent-offspring interactions, and these differences may be caused by environmental variation. When food is plentiful, chicks that are begging more are fed more. When food is scarce, parents instead feed larger offspring. This change could be due to offspring adjusting their behavior, or to confounding factors not directly related to current food availability, such as brood size. Alternatively, it could be due to parents responding to signals differently based on their experience of food availability in the recent past. We tested these competing explanations experimentally by manipulating food availability in wild great tits, *Parus major*. We then standardized food availability, and manipulated offspring size and behavior by creating mixed cross-fostered broods just before filming. This isolated the effect of parental strategies while holding food availability and offspring begging and size constant across treatments. We found that when parents received supplemented food prior to filming, they were: (1) more likely to preferentially feed chicks that were begging more; and (2) less likely to preferentially feed larger chicks. Chicks, conversely, did not differ in their begging in relation to prior environmental conditions, but instead begged in relation to their immediate feeding history and their nestmates' begging intensity. Overall, our results suggest that parents have more control over food distribution than suggested by scramble competition models, and that parents can flexibly adjust how they respond to offspring signals and cues in response to food availability. Consequently, different signaling systems and parental plasticity are favored depending on environmental conditions.

Keywords: begging; parent-offspring communication; *Parus major;* plasticity; signaling.

Introduction

In species where parents care for multiple offspring in the same breeding attempt, families must negotiate how much parents will invest in each offspring. Multiple frameworks for explaining parental food allocation and parent-offspring communication have been put forward, arguing alternatively that parents prefer feeding their offspring in the worst condition (Signal of Need), best condition (Signal of Quality), hungriest (Signal of Hunger), or that offspring and not parents control food distribution (Scramble Competition) (Godfray 1995; Kilner 1995; Kilner and Johnstone 1997; Parker et al. 2002; Wright and Leonard 2002; Mock et al. 2011). Yet the outcome of these negotiations differs across bird species (Caro et al. 2016). In some species, chicks in worse condition beg the most, and parents almost always feed the chick begging the most. In other species, begging appears to be less important: the largest chicks obtain the most food. Evolutionary theory and a comparative, across-species study have suggested that this pattern reflects parents' adjusting their feeding strategy in response to food availability (Davis et al. 1999; Kilner 2002; Mock et al. 2011; Grodzinski and Johnstone 2012; Caro et al. 2016; Koykka and Wild 2018). When food is plentiful, parents will be able to rear all their offspring, and so should preferentially feed the offspring in greatest need, which can be signaled by begging (Godfray 1995; Davis et al. 1999). In contrast, when food is scarce and only a fraction of offspring can be raised, parents should preferentially feed the best quality offspring based on size cues (Caro et al. 2016). This environmental flexibility hypothesis posits that parents adjust their responses to offspring information depending on environmental conditions. This implies parents of many bird species have a similar response strategy with variation in phenotypic plasticity based on food abundance.

Plasticity is expected to evolve in species where individual parents experience variable ecological conditions within or between successive breeding bouts (Royle et al. 2014; Forsman 2015; Wong and Candolin 2015; Lea et al. 2020). If a bird species evolved without sufficient variability at the appropriate timescale, we might instead expect parents to follow a fixed strategy. For instance, if a species evolved in a stable environment with abundant food, it might adopt a fixed strategy to feed the chick that is begging most. In contrast, a species from an unstable environment

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with scarce food, might have evolved a fixed strategy to always feed the largest chick. Parents may also use a combination of size and begging to make choices, and how they balance that information may vary with the environment. Either way, fixed parental food allocation strategies result in patterns where the relative importance of begging signals and size cues does not change with food availability, but where species from different environments display different strategies. Completely fixed parental strategies may be unlikely (Royle et al. 2014), but it may be that apparent plasticity in feeding strategies at the individual level are driven primarily by either differences between species, or variation in begging.

The mechanism by which parental flexibility is achieved needs to be better understood. For example, blue tit parents of enlarged or reduced broods respond differently to signals of their offspring, specifically by varying their likelihood of offering chicks prey in relation to their UV coloration rather than their begging (García-Campa et al. 2021, 2023). In suboptimal environments, if all offspring beg at maximum intensity, parents may not be able to use begging to distinguish between offspring, even if they are selected to feed offspring begging most. This would reduce the correlation between begging and the likelihood of being fed, without any change in parental strategy. Similarly, in optimal environments, all offspring may be roughly the same size, constraining parents' ability to distinguish between chicks of different sizes and chicks' scope for direct competition. This would reduce the correlation between offspring size or quality and the likelihood of being fed, again without any change in parental preference or strategy. Thus, offspring effects need to be accounted for when determining if environmentally-associated differences in parent-offspring communication are due to parental flexibility.

This environmental flexibility hypothesis would be supported by a shift in parental feeding strategies when food abundance is experimentally manipulated and offspring signals, cues, and scramble competition behavior are constant. Any such change in parental feeding strategy would indicate that parents are flexible, even within-species, and that the environment causes changes in parental strategies. Any difference in food distribution patterns when offspring behavior and cues are held constant across environmental treatments would indicate that parents do control feeding and are responding to differently to begging signals and cues "on purpose" and not simply because they lack sufficient variation to use the information to distinguish offspring. Specifically, we predict that as food abundance increases, parents will pay more attention to begging and/or prefer smaller offspring, as is seen across species (Caro et al. 2016). Here, we used an experimental approach to directly test whether parents respond differently to begging depending upon the food availability they had previously experienced using the great tit, *Parus major*, as a model species. This species lives in temperate regions and is exposed to variable breeding conditions across years and is therefore expected to have evolved plasticity in response to offspring signals and cues. To distinguish between parental and offspring responses to food availability, we temporarily provided supplemental food to some parents and subsequently cross-fostered offspring to balance brood nutritional backgrounds and brood size before observing feeding visits. This allowed us to observe parents that had previously experienced different food abundance treatments, interacting with foster broods that were similar in begging intensity, chick size cues, and chick competitive asymmetry and supplementation history.

Materials and methods

Study area and species

Great tits (*Parus major*) are a common passerine bird distributed across Eurasia. They are primarily insectivorous while feeding young, with highly variable food availability both geographically and temporally (van Balen 1973). This variation in ecological conditions within and between breeding bouts makes great tits a prime candidate for studying the evolution of flexibility in parental provisioning strategies. We studied a wild population of great tits living in a mixed pine-deciduous forest (Boslust) covering approximately 75 ha in The Netherlands (5°85'E, 52°01'N). From March through June 2017, we monitored 130 nest boxes, and were able to include 34 broods in our study. We checked nest boxes every other day to determine the onset of egg laying and clutch size. We began visiting nests daily the day before hatching was expected to determine hatch date (day 0), brood size and mortality rates. Mean clutch size was 9.29 ± 0.23 SE eggs, and mean brood size at hatching was 8.82 ± 0.26 SE in our study population. All of the study broods hatched within 9 days of each other. Across all broods, 11% of chicks (33 of 302 chicks) died in the first week after hatching, prior to our cross-fostering and filming experiment.

Experimental procedures

To simulate variation in ecological conditions, we experimentally manipulated food availability in an alternating pattern: half of the broods received supplemental food (mealworms and wax worms) in a feeding tray given to parents, while the other half experienced natural conditions (Fig. 1). To isolate the effect of parental strategies on food distribution, we made cross-fostered broods so that on filming day, there was no variation in how chicks behaved or looked *across* parental environmental treatments. Thus, on filming day, a parent who had received extra food interacted with a foster brood that looked and acted the same as the foster brood of a parent who had not received extra food. In order to generate enough within-brood variation in chick begging for parents to be able to use that information when making decisions, we handfed half the brood to satiation immediately before filming. Satiated chicks beg less, and so this manipulation reduced begging in half of the brood. If most chicks begged at the highest intensity on most feeding visits, parents would have been constrained in their ability to use begging to distinguish between chicks. Handfeeding also decoupled begging intensity from chick size, to ensure not all small chicks begged at maximum intensity the whole time, and allowed us to determine whether parents were feeding based on begging or size. We also ensured there was size variation between chicks within broods through our cross-fostering protocol: parents in both treatments interacted with a brood that had small, medium and large chicks.

Details for experimental manipulation of environmental quality

To ensure only experimental broods received extra food, and to avoid changes to nest defence associated with positioning the food near the nest box, we installed a small feeding tray inside each nest box (Grieco 2003; Eeva et al. 2009). This was done during incubation at all nests. No broods were deserted after the introduction of the tray. Each day for the first week after hatching, we provided a *c.* 20g mixture of live meal worms (*Tenebrio molitor*) and rehydrated wax worm larvae (*Galleria mellonella*) cut into 0.25 cm pieces to supplemented nests. This represents approximately 20% of the daily nutritional needs of the brood (van

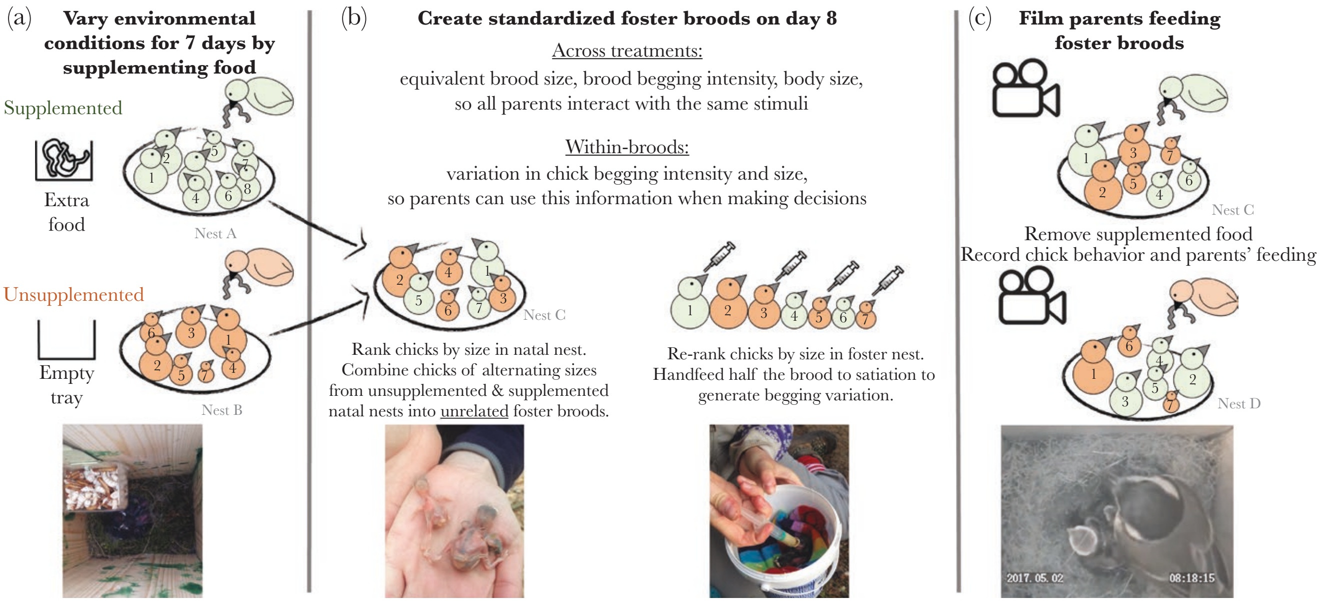

Fig. 1. Experimental design. (A) On hatching day, nests were randomly assigned to be in a good environment (supplemented, green, Nest A), or a poor environment (unsupplemented, orange, Nest B). Supplemented nests received a daily mix of meal worms and wax worms (approximating 20% of the brood's nutritional needs) for the week after hatching. Unsupplemented nests were visited daily to control for human disturbance. **(B)** After 1 week, we removed supplemented food and ranked chicks by size (weight) within natal nests. We created foster broods with chicks 1, 3, 5 and 7 from natal nest A, and chicks 2, 4, 6 from natal nest B. This accounted for potential differences in chick behavior based on their previous size rank; standardized size differences within broods; and standardized foster brood size to 7 or 6 chicks. We re-ranked chicks by size within foster nests (Nest C and Nest D). We handfed half of each foster brood to satiation in an alternating pattern by size rank; a mix of unsupplemented and supplemented chicks were fed in order to disentangle short-term and long-term need. This standardized brood-level begging intensity at the beginning of filming; ensured begging is variable enough across chicks to be a useable signal; and ensured begging intensity varied across size ranks. **(C)** We filmed adults feeding their fostered broods for 4.5 h, excluding first 0.5 h to ensure behavior had normalized (see Supplementary Movie 2 for an example). Fostered broods contained only unrelated chicks to ensure adult behavior was not influenced by familiarity to their own chicks. Photos by S. Caro.

Balen 1973; Eeva et al. 2009). We checked whether great tits were using the food by placing cameras into two nests during the supplementation period. We observed parents taking food from the trays and directly feeding their offspring (Supplementary Movie 1), and parents also ate the food themselves. Either outcome serves to improve environmental conditions as it simulates an increase in food abundance for the parents. Control nests were also visited each day so that all nests received comparable experimental disturbance, and an empty tray was placed in the nest box.

We alternated experimental treatments by assigning the first brood of the day that had hatchlings to the good environment (supplemented) treatment, and then the next brood the unsupplemented (control) treatment (Fig. 1A). We reversed this order each day. We did not pre-randomize because we wanted to equalize hatch date within each treatment. Supplemented and unsupplemented nests varied slightly in clutch size (supplemented 9.81 +/- 0.33se, unsupplemented 8.82 +/- 0.32, p = 0.038*), but not in brood size at day one (supplemented 9.18 +/- 0.36se, unsupplemented 8.59 +/- 0.36, p = 0.26) or hatch date (supplemented 25.29 +/- 0.58se, unsupplemented 25.18 +/- 0.57, p = 0.89). The difference in clutch size was driven by one unsupplemented nest with only 6 eggs; removing this nest or including clutch size as a control variable did not change the results of our parental response model. We confirmed that our supplemental feeding was successful in improving environmental conditions: 59% of supplemented nests had no brood reduction in the first week after hatching, compared to only 18% of unsupplemented control nests (z = 2.94, p = 0.0033**; n = 34 nests; Table S3). The total number of chicks that died per nest was also lower in supplemented nests (z = 2.10, p = 0.045*; Table S3). Chick mass of the surviving chicks on day 7 was not affected by supplementation (z = 1.58, p = 0.12; Table S3), perhaps because the smallest had already starved.

Details for cross-fostering treatment to standardize broods

We wanted all parents to be exposed to equivalent information from their broods during filming, so that we could rule out the possibility that offspring are driving any differences in parental provisioning preferences. We therefore standardized brood size and offspring supplementation history across all broods immediately before filming. We cross-fostered chicks on the filming day (8 d after hatching) to create experimental filming broods of 7 (27 broods) or 6 chicks (4 broods) if a seventh chick was not available from nearby, same-aged broods. This chick age was chosen for two main reasons: (1) it allowed us to provide supplemental food for long enough to impact chick survival, and (2) demand for food is extremely high since great tit chick growth rates in our population peak around this age. Approximately half of the chicks in each filming brood came from a food supplemented nest, and the other half of the chicks came from an unsupplemented nest. Fostered chicks were the same age as the parents' biological brood. Parents were not filmed with their own chicks. We also wanted to ensure that there would be sufficient and equivalent variation in offspring size so that parents could use this information during food allocation. To create an even distribution of weight and prior weight ranks in filming broods, we ranked chicks by weight in their biological nests. We assigned the heaviest chick to filming brood A, and the second heaviest to filming brood B, the third heaviest to brood A, etc. We alternated this pattern at each nest. We wanted to ensure that there would be enough variation in begging intensity and to ensure initial begging intensity would vary across weight ranks, decoupling size and initial begging intensity. In great tits, chicks that are in better condition, that are larger, and that are hungrier tend to beg more (Caro et al. 2016). We hand-fed half of the chicks in each filming brood to satiation, in an alternating pattern by weight rank (see supplemental methods for details). Satiated chicks do not beg at all for some time. This ensured that not all chicks begged maximally during filming and that not all small or large chicks begged at highest intensity the whole time.

During cross-fostering, chicks were removed from nests and placed into bird bags. We blocked the entrance to the nest box using another bird bag, which kept parents from reentering their nests and abandoning them. The bags containing chicks were kept under our shirts to ensure chicks stayed warm while being moved from one nest to another. Chicks were ringed, weighed, and handfed (if appropriate). We created foster broods by combining chicks as described above (Fig. 1), and then placed the whole foster brood in the new nest box. After the foster brood was put in the next box, we turned on the camera and removed the bird bag blocking the nest entrance. Chicks were typically moved to nearby nests, and so this whole process happened in under 30 min, usually faster. Parents typically reentered their nest box within 5 min of our removing the bird bag blocking its entrance, although we excluded the first 30 min of film to ensure adults had time to settle before we began recording data. All cross-fostering was done in the morning as soon as possible prior to filming, and all filming occurred between 7:00 and 15:00 (83% of feeding visits occurred between 9:00 and 13:00).

Thus, parents which had previously experienced both environmental treatments were filmed with no food supplementation, at the same time of day, feeding broods of an equivalent size and begging intensity, comprising unrelated supplemented and unsupplemented chicks, half of which were satiated when the filming began. We measured body size by weighing chicks during the cross-fostering, and measured begging intensity from our videos. Our cross-fostering treatment ensured that broods did not differ in their average begging intensity across treatments, removing the possibility that, for example, parents from poor environments respond less to begging simply because all chicks are begging maximally. Our study design can be considered as analogous to a neuroscience experiment where all study participants receive the same stimulus when making a decision.

Video data

We filmed parents feeding their foster broods 8 d after hatching (Fig. 1C, see Supplementary Movie 2 for an example of video data). We installed an infrared camera inside the lid of a nest box the day prior to filming in order to habituate parents. We paint-coded all chicks with a dot of red, nontoxic acrylic paint on the head just prior to filming, so that we could individually identify chicks in the videos (Kate Lessells, pers. comm.). We excluded the first 30 min of filming to ensure that parental and chick behavior had enough time to return to normal after cross-fostering and to give us enough time to leave the area. We did not provide supplemental food to the parents on the filming day.

All videos were coded by the same observer, blind to the experimental treatment and to chick weight ranks. The order in which the observer coded the videos was random with respect to whether parents were supplemented and unsupplemented. Adult identity was determined by the difference in crown feather glossiness of males and females, and confirmed by nest cleaning behavior, which only females perform (Christe et al. 1996). Adult identity was recorded as the nest plus sex (eg 307_M) since only the mother and father feed chicks in great tits. For each feeding visit, the observer recorded the sex of parent, the identity of the fed chick, and the begging intensity of all chicks. The observer recorded 20 feeding visits per parent or 4 h of filming, whichever came first.

Begging intensity

Begging intensity was coded on a standard scale, following Hinde 2009, adapted from Kilner (1995): *0 = non-gaping, 1 = gaping with a bent neck, 2 = gaping with neck stretched out, 3 = gaping with raised body* (Kilner 1995; Hinde et al. 2009). We quantified relative begging intensity by dividing the begging posture of each chick by the mean posture of all begging chicks on that feeding visit. This relative measure accounts for differences in overall begging intensity on different feeding visits, which could confound measures of food distribution based on absolute begging intensity (Hinde et al. 2009).

Chick size

We ranked chicks by weight in their filming brood, with chick 1 being the heaviest and chick 7 being the lightest. Using weight rank as opposed to absolute weight makes nests more directly comparable—parents may always prefer feeding the largest chick, whether the largest chick weighs 12g or 10g. A priori, we assumed that weight rank would not have a linear effect. Parents may treat small differently than large and medium sized chicks, since the smallest chicks are most vulnerable to starvation (Magrath 1990; Forbes et al. 1997; Theofanellis et al. 2008; Podlas and Richner 2013). We therefore categorized chicks as either being the smallest chick in the brood, or not the smallest chick in the brood. We also recorded chick mass in grams to assess the impact of absolute weight and relative weight rank on postural begging intensity. The mean mass and standard error for each weight rank was: Chick 1 11.50 ± 0.19g, Chick 2 10.52 ± 0.19g, Chick 3 9.8 ± 0.21g, Chick 4 9.20 ± 0.18g, Chick 5 8.57 ± 0.18g, Chick 6 7.83 ± 0.24g, and Chick 7 7.03 ± 0.23g. The largest size difference was between the largest and second largest chick.

Statistical analysis

We checked whether our environmental quality treatment was biologically relevant by investigating its effect on the likelihood of brood reduction (whether at least one chick died) in the first week after hatching before any cross-fostering took place. The effect of environmental quality via food supplementation to parents on brood reduction likelihood was assessed using a binomial linear model in lme4 in R, while controlling for clutch size, brood size, and hatch date (Bates et al. 2015; R Core Team 2023). The extent of brood reduction was assessed using a quasi-Poisson linear model to account for zero-inflated count data, while controlling for clutch size, brood size, and hatch date. Chick mass 1 wk after hatching was assessed using a linear mixed model, while controlling for clutch size, hatch date, and nest ID. We standardized and centered continuous variables (Cohen et al. 2013).

We analyzed parental provisioning and offspring begging using a Bayesian logistic mixed model (MCMCglmm) in R (Hadfield 2010; R Core Team 2023). We used uninformative priors, ran the model for 700,000 iterations with a burn-in of 150,000 and a thinning interval of 10. We assessed the convergence of the MCMCglmm model by visual inspection of convergence plots and geweke plots (Hadfield 2010). In parental response models, the response variable was whether a chick was fed or not. We included nest ID, parent ID, chick ID, and feeding visit ID as random effects. In this model, we analyzed a three-way interaction between parental environmental quality treatment (ie supplementation), relative begging intensity, and weight category as the fixed effects. We were interested in this interaction because our flexibility hypothesis was about the effect of environmental condition on how parents respond to offspring information, and because parents may respond differently to the begging of different offspring (Van Heezik and Seddon 1996). Our criterion for statistical significance for the interactions was a conservative $p < 0.007$, given a Bonferroni correction for seven tests in our model. We also used DIC values to determine whether a simplified model without a three-way interaction was better, but found the simple model was worse (Δ DIC = +6). For the offspring begging model, the response variable was whether a chick begged or not. We analyzed the effects of handfeeding, being from a supplemented nest (natal supplementation), being in a foster nest with adults who had been supplemented (foster supplementation), weight category, mass, and the mean begging intensity of the chick's nestmates on that feeding visit. The model would not converge if we included both nestmates' mean begging intensity on that feeding visit and the unique ID of the feeding visit, and so we included natal nest ID, foster nest ID, parent ID, and chick ID as random effects, but not feeding visit ID. We also ran a glmer model with a Poisson distribution on the response variable of postural begging intensity (0, 1, 2 or 3), which found the same significance patterns.

To check for the robustness of our categorical measure of chick size (smallest vs not-smallest chick), we also ran a model where we investigated all weight ranks (1 through 7). We included the quadratic effects of weight rank, as we wanted to investigate whether weight rank had a linear effect or not (Table S1). After finding a three-way interaction between environmental treatment, weight rank and begging intensity, we investigated whether, within each weight rank, the interaction between environmental treatment and chick begging intensity was significant. We only found a significant three-way interaction for the smallest chicks (weight rank 7, Table S2, $p < 0.01$), supporting our categorical factor of smallest or not smallest chick.

Of the 34 broods filmed for our study, we excluded one brood because the parents abandoned during filming (n = 1 good environment nest). We excluded two broods that had fewer than 20 feeding visits total within 4 h, since these broods received significantly less food than the other broods, which could have influenced their behavior (n = 1 good environment and 1 poor environment nest). We excluded data from four parents with fewer than 15 observed feeding visits, in order to make sure we had enough observations per individual. We excluded six feeding visits where the begging posture of more than two chicks was unknown. Our final sample size for the analysis of parental provisioning was 14 good environment (supplemented) nests, 15 poor environment (unsupplemented) nests (54 adults, 199 chicks, 1121 feeding visits). We analyzed the full data set as well, and there were no qualitative differences in the results or in their statistical significance.

Results

We found that parental provisioning rules were flexible in response to previously experienced food abundance—parents responded differently to offspring begging and size, depending upon whether parents had received supplemental food in the previous week (interaction between environmental treatment, weight rank and relative begging intensity: 95% CI 3.40 to –0.48, pMCMC = 0.0034**; Fig. 2; Table 1). In all nests and for all chicks, the likelihood of being fed increased with higher relative begging intensity (95% CI 2.26 to 2.97, pMCMC < 0.0001***; Table 1), but chick size mediated how much begging increased the likelihood of being fed. Parents that had received supplemental food responded primarily to begging signals, responding equally to the begging of all chicks regardless of size (Fig. 2a). However, parents that had experienced worse environmental conditions, the control treatment with no extra food, responded more to size by responding more to the begging of larger chicks than to the begging of the smallest chick (Fig. 2b). The random effects of chick identity, nest identity and parental identity also explained portions of the variance in a chick's likelihood of being fed (Table 1).

We confirmed that this difference in offspring provisioning based on food abundance could not be explained by differences in offspring behavior or size cues, but instead by differences in parental behavior. Since we cross-fostered chicks between nests directly before filming, parents in both environmental treatments received equivalent stimuli from their foster broods. During filming, there was no difference in mean begging posture or in chick weights between foster broods for parents in either environmental treatment (mean of begging posture: $t_{27} = 0.63$, $p = 0.53$; SD of begging: $t_{27} = 0.15$, $p = 0.88$; mean of weight: $t_{27} = -0.90$, $p = 0.38$; SD of weight: $t_{27} = -0.64$, $p = 0.53$). Chick begging likelihood was only influenced by whether the chick had been hand fed to satiation immediately prior to filming (95% CI 0.61 to 1.28, pMCMC < 0.0001***) and by the mean begging intensity of its nestmates on that feeding visit (95% CI 0.23 to 0.38, pMCMC < 0.0001***; Table 2). There were no significant interactions with food supplementation or size on the likelihood of begging. Not only were they more likely to beg, but chicks begged at a higher intensity level when their nestmates were begging more intensely ($z = 9.07$, $p < 0.001$***, Fig. 3). Individual chick ID explained a larger portion of the variance in feeding likelihood than parent ID (Table 1), and chick ID had a strong impact on begging likelihood (Table 2). Individual differences in offspring behavior may impact parents' decisions.

Discussion

Our experimental results show that parents conditionally adjust how they respond to signaling, depending upon environmental conditions (food abundance). Parents did not simply feed the chicks that were the largest or that begged the most. Instead, they have evolved to adjust their sensitivity to multiple sources of information depending on local conditions, in a sophisticated manner. When they have recently experienced that food is more plentiful, great tit parents respond equitably to all their offspring's postural begging, but when food is scarcer, parents selectively respond less to the begging of the smallest chick (Fig. 2). Offspring begging likelihood, on the other hand, depended only on whether a chick had been hand fed to satiation immediately prior to filming and on how intensely its nestmates were begging on that feeding visit. These results show how variation in environmental quality can lead to different forms of communication, even within species, and that receivers rather than signalers are driving that change in parent-offspring communication.

Parent-offspring communication models

Our experimental findings support our hypothesis that parents flexibly shift how they respond to begging signals, and that this change is caused by environmental conditions, specifically food

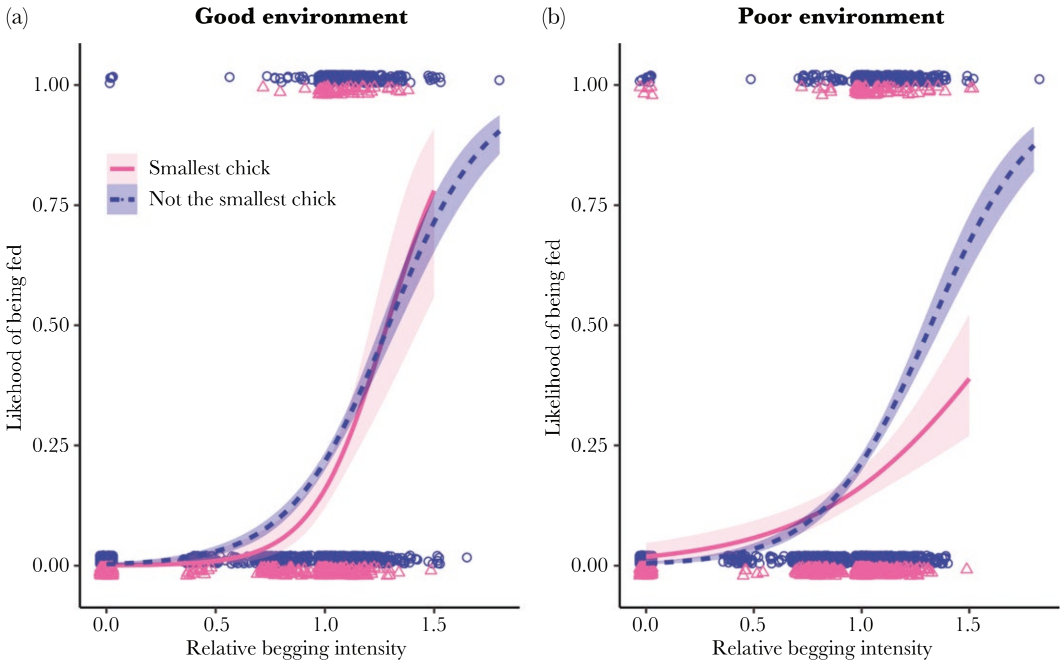

Fig. 2. A chick's likelihood of being fed depends on its relative begging intensity, size rank, and whether its parents had experienced a good or poor environment. In supplemented nests where parents had experienced good environmental conditions based on receiving supplemental food (A), higher relative begging intensity led to a greater likelihood of being fed for all chicks equally. In unsupplemented nests where parents had experienced worse conditions (B), smaller chicks showed less of an increase in their likelihood of being fed based on begging intensity than larger chicks did (95% CI of the interaction = −3.40 to −0.48, p = 0.0034, MCMCglmm). The smallest chick in the nest (the "runt," ranks 7 or 6, depending on brood size) are shown in pink with a solid line and triangles, while the rest of the brood is shown in blue with a dashed line and circles. A relative begging intensity of 1 indicates a chick is begging the same as its nest mates on average, while > 1 means it begged at a higher intensity. Each data point is one chick in a feeding visit, vertically jittered to show overlapping points (n = 14 supplemented nests, 15 unsupplemented nests, 1121 feeding visits).

Table 1. The effect of environmental treatment, begging and size on a chick's likelihood of being fed on a given visit.

Fixed effects	Estimate	95% CI	pMCMC
Environmental treatment	0.21	−0.36 to −0.72	0.44
Weight rank (smallest or not smallest chick)	−1.16	−2.49 to −0.10	0.039
Relative begging posture	**2.60**	**2.26 to 2.97**	**$<0.001^{***}$**
Environmental treatment: weight category	1.45	0.15 to 2.85	0.019
Environmental treatment: begging posture	−0.28	−0.73 to 0.20	0.25
Relative begging posture: weight category	0.92	−0.33 to 2.31	0.18
Environmental treatment: begging posture: weight category	**−1.94**	**−3.40 to −0.48**	**0.0034^{**}**
Random effects			
Nest	0.13	0.05 to 0.22	
Parent ID	0.08	0.04 to 0.12	
Chick ID	0.30	0.17 to 0.45	
Feeding visit	0.05	0.03 to 0.07	

MCMCglmm logistic regression, N = 29 nests, 54 adults, 199 chicks, 1121 feeding visits. The Bonferroni corrected cutoff for significance was 0.007, and significant terms are in bold.

abundance. These signals may be a signal of need, quality or hunger (Kilner 2002; Royle et al. 2002; Mock et al. 2011; Grodzinski and Johnstone 2012; Caro et al. 2016). In great tits, receiving or not receiving extra food for the week after chicks hatched changed which offspring parents prefer to feed, and what information parents pay attention to (Fig. 2). We know this change occurred regardless of any effect of offspring behavior, since we standardized offspring behavior on the filming day by creating mixed cross-fostered broods to act as the consistent stimulus for parents (Fig. 1). We also did not see any effect of food supplementation for the week after hatching on offspring postural begging behavior (Table 2). While we initially expected that parents' switching would be a dramatic change from feeding based on begging signals to feeding solely or mostly based on size cues, instead we found a more subtle shift. Parents only responded less to the begging of the smallest chicks, the "runts" of the brood, when food was scarcer (Fig. 2) (Forbes et al. 1997). This effect of body size corresponds with prior research indicating that body size may have a non-linear effect on starvation likelihood and begging behavior, affecting the lowest ranking offspring much more than the "core" brood (Magrath 1990; Forbes et al. 1997;

Table 2. The effect of environmental treatment, handfeeding, size and sibling competition on a chick's begging posture.

Fixed effects	Estimate	95% CI	pMCMC
Mass (g)	−0.02	−0.25 to 0.24	0.93
Weight rank (smallest or not smallest chick)	0.01	−0.60 to 0.58	0.98
Natal nest supplemented with food	0.07	−0.41 to 0.56	0.78
Foster nest supplemented with food	0.05	−0.43 to 0.53	0.85
Handfed to satiation before filming	**0.91**	**0.61 to 1.28**	**<0.001********
Mean begging intensity of nestmates	**0.31**	**0.23 to 0.38**	**<0.001*****
Random effects			
Natal Nest	0.26	0.08 to 0.49	
Foster Nest	0.23	0.07 to 0.44	
Parent ID	0.11	0.04 to 0.17	
Chick ID	1.23	0.93 to 1.58	

MCMCglmm logistic regression, N = 29 nests, 54 adults, 199 chicks, 1121 feeding visits. The Bonferroni corrected cutoff for significance was 0.007, and significant terms are in bold.

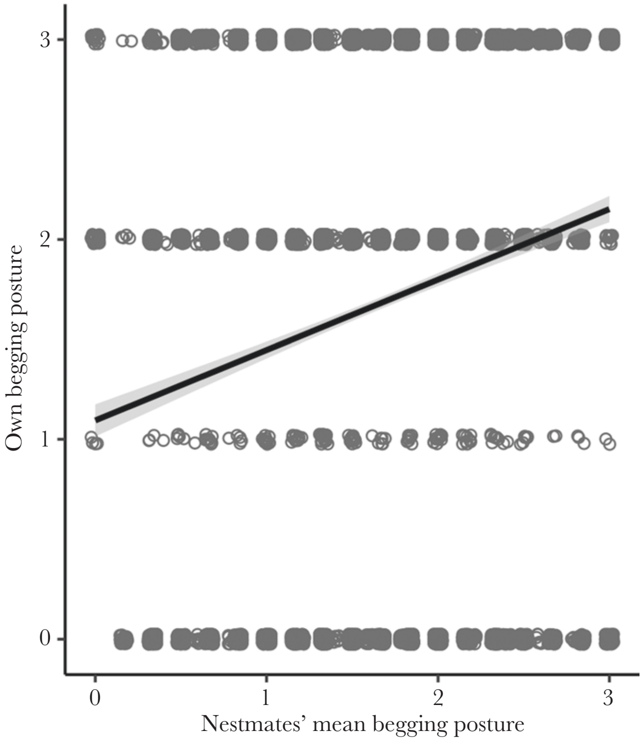

Fig. 3. Chicks begged at a higher intensity when their nestmates begged more. A chick's begging posture increased as the mean begging posture of its nestmates, excluding that chick, increased ($z = 9.07$, $p < 0.001^{***}$). Each data point is one chick in a feeding visit, vertically jittered to show overlapping points (n = 199 chicks, 1121 feeding visits).

Theofanellis et al. 2008; Podlas and Richner 2013). Brood reduction, the starvation or killing of a subset of brood, most frequently happens to only the smallest offspring, while the rest of the brood is safe (Morandini and Ferrer 2015). Depending on the species and brood, runts could encompass just the smallest offspring or the two smallest offspring. Given that parents stop responding to the begging only of the smallest chicks in unsupplemented nests, this may imply that begging is functioning as a signal of need, and that parents are avoiding feeding the neediest chicks in food-limited conditions.

Our finding that parents still respond to begging when food is scarce can support the Signal of Quality model, since some aspects of begging may indicate offspring quality in great tits, rather than offspring need. Our study only found relationships between postural begging intensity and recent feeding history rather than other aspects of chick quality such as body size or size rank. However, we only assessed postural begging, and we intentionally manipulated begging intensity through our handfeeding protocol. Our study cannot rule out the possibility that in an unmanipulated state, great tit chicks signal their quality through begging vocalizations, color or other behaviors. Our results should be interpreted cautiously, as our sample size was restricted to 29 broods. Additional studies should be done, both in great tits and in other species, to investigate how consistent and widespread the flexible shift between Signal of Need and Signal of Quality modes of food allocation are.

We found additional support for the Signal of Hunger model, that posits that begging is primarily an indicator of hunger rather than long-term need (Mock et al. 2011). Whether a chick had been fed to satiation immediately prior to filming was one of the best predictors of its postural begging intensity, rather than its mass or weight rank (Table 2). Since we recorded only postural begging, and not begging vocalizations or other aspects of begging displays, we cannot preclude the possibility that those modes of begging do contain information about a chicks' long-term need. Begging may contain information about multiple aspects of offspring condition simultaneously, including hunger, cryptic need, cryptic quality, health status, and even obvious competitive ability or body size (Wright and Leonard 2002; Wild et al. 2017). This aligns with previous studies; for example, puffin chicks make two separate vocalizations to indicate body condition and time since their last feeding (Rector et al. 2014), and European starling chicks indicate their lipid reserves and body size through different components of begging signals respectively (Jacob et al. 2011). Since begging typically comprises multiple modes (behavioral posturing, vocalizations, mouth coloration and more) in addition to more obvious cues of offspring quality (such as body size), it is reasonable to assume parents can make use of all of these sources of information when deciding how to allocate food amongst their offspring (Wright and Leonard 2002). It is also possible that parents feed different kinds or sizes of food to offspring that beg differently or are different sizes; for example, offspring with brightly coloured mouths but that make quiet begging calls may receive different resources, such as more spiders, than offspring with dull mouths but loud calls, who might receive more caterpillars. Subtle aspects of parental feeding decisions, such as resource types given to different offspring, should be investigated.

The degree to which parents actively control food allocation as opposed to passively responding to the greatest stimulus or cede to the winner of sibling competition has been contentious (Kacelnik et al. 1995; Kilner and Johnstone 1997; Parker et al. 2002; Heeb et al. 2003; Ploger and Medeiros 2004; Soler et al. 2022; Ferrer-Pereira et al. 2023; Parejo-Pulido et al. 2023). Our cross-fostering experiment ensured there was minimal variation in brood size, competitive asymmetry and begging behavior across broods. Our cross-fostering design of filming broods with half chicks from a food-limited and half chicks from a food-supplemented background reduced the likelihood that our results are due to differences in offspring jostling or physical competition. This aligns with prior work on food limitation and scramble competition in birds; for instance, under food limitation, bluethroat parents change their provisioning strategies while offspring did not show much difference in scramble competition behavior (Smiseth 2003). Thus, changes in allocation patterns can definitively be attributed to changes in great tit parental response strategies, rather than differences in offspring behavior or information constraints. Our study therefore supports a signaling, rather than a scramble competition, explanation for begging behavior. These results support other recent experimental work on parental shifts in provisioning strategies with differences in food availability (Smiseth 2003; Soler et al. 2022; Ferrer-Pereira et al. 2023). It should be noted, however, that we examined provisioning at one point midway through the nestling period. It is possible that older chicks may be able to exert more control via scramble competition. It is probable that species vary in the actual balance of power between parents and offspring, so that in some species offspring behavior does drive changes in food distribution patterns. It may be also that some species flexibly determine their investment strategies in other ways and at other times; for example, 1) during incubation by varying the amount of hatching asynchrony (eg blackbirds (Magrath 1992) and European rollers (Parejo et al. 2015)); 2) during different points in the breeding season by varying how parents respond to UV signals (eg alpine swifts and European starlings (Bize et al. 2006)); or 3) during different times within a single breeding attempt by varying aggression towards offspring (eg American coots (Shizuka and Lyon 2013)). Still, if parents could flexibly vary their decision rules according to the environment, that would substantially increase the level of control that parents have within the family (Kilner and Hinde 2008; Soler et al. 2022; Ferrer-Pereira et al. 2023).

Plasticity in parent-offspring communication

Additionally, whether different species, or individuals within a species, are equally flexible remains an open question. It is likely that the predictability of environmental variation, the timescale of environmental fluctuation, and the reliability of cues will impact the likelihood of the evolution of parental behavioral plasticity (Chenard and Duckworth 2021; Snell-Rood and Ehlman 2021). In general, we could expect more flexibility in species that live in environments that vary substantially and that vary over short time scales, since the nestling dependency period in birds is usually measured in weeks. Future work could delve more deeply within populations to study the same individuals across multiple breeding bouts to assess whether there are between-individual differences in parental flexibility (Dingemanse and Wolf 2013).

Offspring and parents in the same species may or may not both be flexible. Our study found no evidence that overall environmental conditions (natal nest food supplementation) had an impact on great tit offspring postural begging (Table 2). Instead, only whether a chick had been recently fed to satiation and how much its nestmates were currently begging impacted postural begging. However, there is some evidence for offspring flexibility in other species. For example, recent work on genetic covariance and plasticity in canaries found that both offspring and parental signaling strategies varied plastically across different hunger levels (Fresneau and Müller 2019). However, in general parents may shift strategies more readily than offspring, because they have access to more information or because their evolutionary incentives change more as the environment changes. Parents can directly assess environmental conditions as they forage. Dependent chicks in a nest, however, do not know what the overall food abundance is in the environment; they only know how much food they themselves have been given. This information asymmetry may constrain dependent chicks' flexibility. When information asymmetry related to communication has been considered previously, it typically refers to the signaler's information about their own cryptic condition or motivation (Kilner and Hinde 2008; Leimar and McNamara 2023) and not to environmental conditions or the receivers' motivations. Additionally, while parents may benefit from shifting towards or away from brood reduction as food abundance changes, each individual offspring might always benefit most from being the one to survive and not starve. The inclusive fitness gains of flexibility might therefore differ for parents and offspring, but formal theory is needed to fully explore this. Future empirical studies can also investigate the extent to which offspring also flexibly shift begging strategies based on the environment or based on changes in their parents' behavior. Additionally, we assessed only one aspect of offspring behavior, postural begging, and offspring may have changed other aspects of their begging displays or engaged in more direct jostling and competition with siblings. More research is needed on the variety of ways in which offspring may display phenotypic plasticity in begging based on environmental conditions.

Conclusion

What explains diversity in signaling systems is a fundamental question in signaling theory. Our results suggest that receivers are plastic in how they respond to offspring, that receivers control the outcome of parent-offspring communication and that they assess multiple sources of information from signalers. This is analogous to how females respond to multiple signals of quality in sexual signaling (Bro-Jørgensen 2010), and may be similar to aggressive signaling and other forms of communication as well. Our results highlight the need for dynamic signalling models that allow for flexibility in responsivenss based on environmental conditions, and that incorporate multiple signals and cues (Wild 2011).

Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

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Author Contributions

Shana Caro (Conceptualization [lead], Data curation [lead], Formal analysis [lead], Funding acquisition [equal], Investigation [equal], Methodology [equal], Project administration [equal], Resources [equal], Supervision [equal], Writing - original draft [lead], Writing - review & editing [equal]), Adara Contreras Velasco (Data curation [equal], Methodology [equal], Writing - review & editing [equal]), Tjomme van Mastrigt (Data curation [equal], Methodology [equal], Writing - review & editing [equal]), Kees van Oers (Funding acquisition [equal], Investigation [equal], Methodology [equal], Supervision [equal], Writing - review & editing [equal]), Ashleigh S Griffin (Conceptualization [equal], Writing - review & editing [equal]), Stuart A West (Conceptualization [equal], Writing - review & editing [equal]), and Camilla A Hinde (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Project administration [equal], Resources [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing - original draft [equal], Writing - review & editing [equal])

Conflict of interest

The authors confirm they have no conflicts of interest.

Data Availability

Analyses reported in this article can be reproduced using the data provided by Caro et al. (2025).

Ethics

Permission to do fieldwork in the Boslust forest was granted by 'Stichting Geldersch Landschap en Kasteelen'. Permission for animal experiments was granted by Central Authority for Scientific Procedures on Animals (CCD) of The Netherlands under project number AVD-801002017831 to KVO.

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