

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

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2

3 **Abstract**

4 Different bird species have completely different parent-offspring interactions. When food is
5 plentiful, the chicks that are begging the loudest are fed the most. When food is scarce, bird species
6 instead feed the largest offspring. While this variation could be due to parents responding to
7 signalling differently based on food availability, it could equally be due to offspring adjusting their
8 behaviour, or to variation in information availability. We tested between these competing
9 explanations experimentally, by manipulating food availability in a population of wild great tits,
10 *Parus major*, while standardising offspring behaviour and size. We found that when food was
11 more plentiful, parents were: (1) more likely to preferentially feed the chicks that were begging
12 the most; and (2) less likely to preferentially feed larger chicks. In addition, we consistently found
13 these same patterns, in a meta-analysis across 57 bird species. Overall, our results suggest that
14 parents have more control over food distribution than offspring do, and that they flexibly adjust

15 how they respond to both offspring signals and cues of offspring quality in response to food
16 availability. Consequently, depending upon environmental conditions, predictably different
17 signalling systems are favoured.

18

Keywords: parent-offspring communication, signalling, plasticity, begging, meta-analysis,

Parus major

19 **Introduction**

20 In species where parents care for multiple offspring at the same time, families are constantly
21 negotiating how much parents will invest in each offspring. Yet the outcome of these negotiations
22 is completely different in different bird species (Caro et al. 2016). At one extreme, in some species,
23 the chicks in worse condition beg the most, and gain the most food from their parents. At the other
24 extreme, in other species, begging appears to be ignored, and the largest chicks obtain the most
25 food. Evolutionary theory and a comparative, across-species study have suggested that this pattern
26 reflects parents' adjusting their feeding strategy in response to environmental conditions and food
27 availability (Davis et al. 1999; Kilner 2002; Mock et al. 2011; Grodzinski and Johnstone 2012;
28 Caro et al. 2016; Koykka and Wild 2018). When food is plentiful, parents will be able to rear all
29 their offspring, and so should preferentially feed the offspring in greatest need, which can be
30 signalled by begging (Godfray 1995; Davis et al. 1999). In contrast, when food is scarce and only
31 a fraction of offspring can be raised, parents should preferentially feed the best quality offspring
32 based on size cues (Caro et al. 2016). This hypothesis posits that differences across species are
33 determined by parents adjusting their responses to signals in response to environmental conditions.
34

35 However, this hypothesis was based on observational data, and is open to alternative explanations.
36 First, changes in communication patterns could be controlled by either receivers (parents) or
37 signallers (offspring) (Kilner and Hinde 2008). If offspring control resource allocation via direct
38 competition, then the most competitive offspring should receive the most food. Consequently, in
39 situations where competitive ability shows greater variation, which could be when food is scarce,
40 we would expect signals of need to have less influence on food distribution (Royle et al. 2002;
41 Parker et al. 2002). Second, parents could have access to different information under different

42 environmental conditions, which would constrain their ability to respond to signals (Kilner and
43 Hinde 2008). For example, if all offspring beg at maximum intensity in worse environments,
44 parents cannot use begging to distinguish between offspring. Third, it is only known that across-
45 species differences are correlated with environmental conditions—it is not known whether
46 individuals are plastic in how they communicate based on local conditions. We might only expect
47 plasticity to evolve in species that experience variable ecological conditions within or between
48 breeding bouts (Forsman 2015). If parents could flexibly vary their decision rules according to the
49 environment, that would substantially increase the level of control that parents have within the
50 family (Kilner and Hinde 2008).

51

52 We used an experimental approach to directly test whether parents respond differently to begging
53 depending upon food availability in great tits, *Parus major*. This species lives in temperate regions
54 and is exposed to variable breeding conditions across years, and could therefore be expected to
55 evolve plasticity in response to offspring signals and cues. To distinguish between parental and
56 offspring responses to food availability, we both provided supplemental food to some parents and
57 cross-fostered offspring before observing behaviour. This allowed us to observe parents that had
58 and had not been supplemented, interacting with foster broods that were similar in begging
59 intensity, chick size cues, chick competitive asymmetry and supplementation history, as foster
60 broods comprised half supplemented, half unsupplemented chicks. Next, to investigate whether
61 plasticity is a general pattern across species, we conducted a phylogenetic meta-analysis,
62 examining the pattern of behaviour within 57 bird species. We assessed within-species plasticity
63 by quantifying each species' change in responsiveness to begging or chick size as environmental
64 quality improves.

65 **Materials and Methods**

66 *Experimental study*

67 **Study area and species**

68 Great tits (*Parus major*) are a common passerine bird distributed across Eurasia. They are
69 primarily insectivorous while feeding young, with highly variable food availability both
70 geographically and temporally (van Balen 1973). This variation in ecological conditions within
71 and between breeding bouts makes great tits a prime candidate for studying the evolution of
72 flexibility in parental provisioning strategies. We studied a wild population of great tits living in a
73 mixed pine-deciduous forest (Boslust) covering approximately 75 ha in The Netherlands (5°85'E,
74 52°01'N). From March through June 2017, we monitored 130 nest boxes, and were able to include
75 34 broods in our study. We checked nest boxes every other day to determine the onset of egg
76 laying and clutch size. We began visiting nests daily the day before hatching was expected to
77 determine hatch date (day 0), brood size and mortality rates. Mean clutch size was 9.29 ± 0.23 SE
78 eggs, and mean brood size at hatching was 8.82 ± 0.26 SE in our study population. All of the study
79 broods hatched within 9 days of each other. Across all broods, 10.9% of chicks (33 of 302 chicks)
80 died in the first week after hatching.

81

82 **Experimental procedures**

83 In order to simulate variation in ecological conditions, we experimentally manipulated food
84 availability in an alternating pattern: half of the broods received supplemental food (mealworms
85 and wax worms), while the other half experienced natural conditions (see supplemental methods
86 for details).

87

88 We wanted all parents to be exposed to equivalent information from their broods during filming,
89 so that we could rule out the possibility that offspring are driving any differences in parental
90 provisioning preferences. We therefore standardized brood size and offspring supplementation
91 history across all broods immediately before filming. We cross-fostered chicks on the filming day
92 (8 days after hatching) to create experimental filming broods of 7 (27 broods) or 6 chicks (4
93 broods). Approximately half of the chicks in each filming brood came from a supplemented nest,
94 and the other half of the chicks came from an unsupplemented nest. Fostered chicks were the same
95 age as the parents' biological brood. Parents were not filmed with their own chicks. We also
96 wanted to ensure that there would be sufficient and equivalent variation in offspring size so that
97 parents could use this information during food allocation. To create an even distribution of weight
98 and prior weight ranks in filming broods, we ranked chicks by weight in their biological nests. We
99 assigned the heaviest chick to filming brood A, and the second heaviest to filming brood B, the
100 third heaviest to brood A, etc. We alternated this pattern at each nest. We wanted to ensure that
101 there would be enough variation in begging intensity and to ensure initial begging intensity would
102 vary across weight ranks. We hand-fed half of the chicks in each filming brood to satiation, in an
103 alternating pattern by weight rank (see supplemental methods for details). This ensured that not all
104 chicks begged maximally during filming and that not all small chicks begged at highest intensity
105 the whole time.

106

107 Thus, parents in both treatments were filmed at the same time of day, feeding broods of an
108 equivalent size and begging intensity, comprising unrelated supplemented and unsupplemented
109 chicks, half of which were satiated when the filming began.

110

111 **Details for great tit experimental supplementation**

112 To ensure only experimental broods received extra food, and to avoid changes to nest defense
113 associated with positioning the food near the nest box, we installed a small feeding tray inside each
114 nest box (Verhulst 1994; Grieco 2003; Eeva et al. 2009). This was done during incubation at all
115 nests. No broods were deserted after the introduction of the tray. Each day for the first week after
116 hatching, we provided a *c.* 20g mixture of live meal worms (*Tenebrio molitor*) and rehydrated wax
117 worm larvae (*Galleria mellonella*) cut into 0.25 cm pieces to supplemented nests. This represents
118 approximately 20% of the daily nutritional needs of the brood (van Balen 1973; Eeva et al. 2009).
119 We checked whether great tits were using the food by placing cameras into 2 nests during the
120 supplementation period. We observed parents taking food from the trays and directly feeding their
121 offspring (Supplementary Movie 2), and parents also ate the food themselves. Either outcome
122 serves to increase environmental conditions for the parents. Control nests were also visited each
123 day so that all nests received comparable experimental disturbance, and an empty tray was placed
124 in the nest box.

125

126 We alternated experimental treatments by assigning the first brood of the day that had hatchlings
127 to the supplemented treatment, and then the next brood the unsupplemented (control) treatment.
128 We reversed this order each day. We did not pre-randomize because we wanted to equalise hatch
129 date within each treatment. Supplemented and unsupplemented nests varied slightly in clutch size
130 (supplemented 9.81 +/- 0.33se, unsupplemented 8.82 +/- 0.32, $p = 0.038^*$), but not in brood size
131 (supplemented 9.18 +/- 0.36se, unsupplemented 8.59 +/- 0.36, $p = 0.26$) or hatch date
132 (supplemented 25.29 +/- 0.58se, unsupplemented 25.18 +/- 0.57, $p = 0.89$). The difference in clutch

133 size was driven by one unsupplemented nest with only 6 eggs; removing this nest or including
134 clutch size as a control variable did not change the results of our parental response model.

135

136 **Details of cross-fostering and hand-feeding**

137 All cross-fostering was done in the morning as soon as possible prior to filming, and all filming
138 occurred between 7:00 and 15:00 (83% of feeding visits occurred between 9:00 and 13:00).

139

140 Hand-feeding protocol: We ranked chicks by weight in their filming nests. We assigned chicks to
141 be handfed or not handfed in an alternating pattern by weight rank, which was reversed at each
142 nest. For example, in filming brood A, the heaviest chick was handfed and the second heaviest was
143 not, while in filming brood B the heaviest chick was not handfed. Immediately prior to filming,
144 we hand-fed chicks in an artificial nest containing a cloth wrapped hand-warmer. We fed the
145 selected chicks with Nutribird A 19 high energy bird food using a 5 mL syringe. We continued
146 feeding until begging had ceased and could no longer be induced by whistling and tapping the
147 sides of the bill with a syringe, indicating the chicks were probably satiated, as in (Kilner and
148 Davies 1998).

149

150 **Video data**

151 We filmed parents feeding their foster broods 8 days after hatching (see Supplementary Movie 1
152 for an example of video data). We installed an infrared camera inside the lid of a nest box the day
153 prior to filming in order to habituate parents. We paint-coded all chicks with a dot of red, non-
154 toxic acrylic paint on the head (Kate Lessells, pers. comm.) just prior to filming, so that we could
155 individually identify chicks in the videos. We excluded the first 30 minutes of filming to ensure

156 that parental and chick behaviour had enough time to return to normal after cross-fostering and to
157 give us enough time to leave the area. We did not provide supplemental food to the parents on the
158 filming day.

159

160 All videos were coded by the same observer, blind to the experimental treatment and to chick
161 weight ranks. The order in which the observer coded the videos was random with respect to
162 whether nests were supplemented and unsupplemented. Adult identity was determined by the
163 difference in crown feather glossiness of males and females, and confirmed by nest cleaning
164 behaviour, which only females perform (Christe et al. 1996). For each feeding visit, the observer
165 recorded the sex of parent, the identity of the fed chick, and the begging intensity of all chicks.
166 The observer recorded 20 feeding visits per parent or 4 hours of filming, whichever came first.

167

168 **Begging intensity**

169 Begging intensity was coded on a standard scale, following Hinde 2009, adapted from Kilner
170 (1995): *0 = non-gaping, 1 = gaping with a bent neck, 2 = gaping with neck stretched out, 3 =*
171 *gaping with raised body* (Kilner 1995; Hinde et al. 2009). We quantified relative begging intensity
172 by dividing the begging posture of each chick by the mean posture of all begging chicks on that
173 feeding visit. Values greater than 1 indicate that parents preferentially fed chicks with a higher
174 posture score than their nest mates. This relative measure accounts for differences in overall
175 begging intensity on different feeding visits, which could confound measures of food distribution
176 based on absolute begging intensity (Hinde et al. 2009).

177

178 **Chick size**

179 We ranked chicks by weight in their filming brood, with chick 1 being the heaviest and chick 7
180 being the lightest. Using weight rank as opposed to absolute weight makes nests more directly
181 comparable—parents may always prefer feeding the largest chick, whether the largest chick
182 weighs 12g or 10g. A priori, we assumed that weight rank need not have a linear effect. Parents
183 may treat large and medium sized chicks differently than they treat small chicks, since the smallest
184 chicks may be most vulnerable to starvation (Magrath 1990; Forbes et al. 1997; Amundsen and
185 Slagsvold 1998; Theofanellis et al. 2008; Podlas et al. 2013). Furthermore, the difference in
186 absolute weight between ranks was lower in the middle of hierarchy (0.68g) than at either end
187 (1.05g). We therefore included the quadratic term for weight rank in analyses.

188

189 **Statistical analysis**

190 We checked whether our supplementation treatment was biologically relevant by investigating its
191 effect on the likelihood of brood reduction (whether at least one chick died) in the first week after
192 hatching before any cross-fostering took place. The effect of supplementation on likelihood of
193 brood reduction likelihood was assessed using a binomial linear model in lme4 in R, while
194 controlling for clutch size, brood size, and hatch date (Bates et al. 2015). The extent of brood
195 reduction was assessed using a quasi-poisson linear model to account for zero-inflated count data,
196 while controlling for clutch size, brood size, and hatch date (Bates et al. 2015). Chick mass one
197 week after hatching was assessed using a linear mixed model, while controlling for clutch size,
198 hatch date, and nest ID (Bates et al. 2015). We standardised and centered control variables (Cohen
199 et al. 2003).

200

201 We analysed parental provisioning using a Bayesian logistic mixed model (MCMCglmm) in R
202 (Hadfield 2010; R Core Team 2013). We used uninformative priors, ran the model for 700,000
203 iterations with a burn-in of 150,000 and a thinning interval of 10. We assessed the convergence of
204 the MCMCglmm model by visual inspection of convergence plots and geweke plots (Hadfield
205 2010; 2012). The response variable was whether a chick was fed or not. We included nest ID,
206 parent ID, chick ID, and feeding visit ID as random effects. We analysed a three-way interaction
207 between supplementation treatment, relative begging intensity, and weight rank as the fixed effect.
208 We were interested in this interaction because our main hypothesis was about the moderating effect
209 of supplementation, and because parents may respond differently to begging of different offspring
210 (van Heezik and Seddon 1996). We tested whether weight rank had a non-linear effect. We
211 included both the linear and quadratic 3-way interaction terms in the same model, along with all
212 possible 2-way interactions using both the linear and quadratic terms (Ganzach 1997). If the
213 quadratic interactions were not significant, we would have removed them. Including polynomial
214 terms in interactions can lead to false positives or negatives due to collinearity (Ganzach 1997).
215 Centering variables reduces this collinearity between polynomials, and so we scaled and centred
216 begging and weight rank (Cohen et al. 2003; Dalal and Zickar 2011).

217

218 Of the 34 broods filmed for our study, we excluded one brood because the parents abandoned
219 during filming, and two broods that had fewer than 20 feeding visits. We excluded data from four
220 parents with fewer than 15 observed feeding visits. We excluded six feeding visits where the
221 begging posture of more than two chicks was unknown. Our final sample size for the analysis of
222 parental provisioning was 14 supplemented nests, 15 unsupplemented nests (54 adults, 199 chicks,

223 1121 feeding visits). We analysed the full data set as well, and there were no qualitative differences
224 in the results or in their statistical significance.

225

226 *Comparative study*

227 **Data collection for the meta-analysis**

228 To determine whether birds show a consistent adjustment of feeding rules based on local
229 conditions across species, we collected data on within-species changes in the strength of the
230 relationship (correlation coefficient) between feeding and begging in 17 species, and feeding and
231 size cues in 52 species (719 effect sizes from 145 studies; Data S1; Fig. S1). We conducted a
232 literature search on Web of Science and Google Scholar using the keywords ‘beg’, ‘parent-
233 offspring’, ‘bird’, ‘begging’, ‘communication’ and ‘provision’ (see Fig. S1 for PRISMA flowchart
234 detailing data collection and exclusion criteria). We included all papers with any measure relating
235 to the relationship between parental food allocation and offspring behavioural begging or size cues.
236 We excluded species that did not have data on these relationships in more than one environment
237 condition, since we were interested in the change in the strength of these relationships over
238 different ecological conditions. We excluded studies if it was impossible to determine whether
239 parents were responding to begging or to size cues. We excluded studies where offspring signals
240 were structural (such as mouth colour), rather than behavioural (such as begging postures), as these
241 may represent different signalling systems (Caro et al. 2016). There was not enough within-species
242 data on structural signals in different environments include them. We only included effect sizes
243 for the relationship of begging on within-brood food allocation, rather than on increases in overall
244 parental feeding effort, as these represent fundamentally different aspects of parental care. We
245 excluded data on species that lay only one egg per brood, as selective pressures on these species

246 are likely to differ from species laying multiple eggs per brood. If relevant data were given in
247 papers without statistical tests, such as raw means and standard errors, we estimated effect sizes
248 (Borenstein et al. 2011). This resulted in a dataset of 719 effect sizes from 145 studies on 57 species
249 (Data S1).

250

251 ***Environmental quality***

252 We categorized populations as experiencing normal, better than normal, or worse than normal
253 environments, based on experimental manipulations of long-term chick condition (parents were
254 fed reduced or supplemented diets, or chick demand was artificially increased or decreased),
255 ecological measures (such as prey density, date or rainfall), or average offspring mortality across
256 different years in long-term observational studies (Caro et al. 2016). These measures were not
257 always directly related to food availability, but they likely captured variation in some ecological
258 aspect relevant to offspring condition. If no information on environmental quality was available,
259 data were classified as normal conditions.

260

261 **Measures of feeding, begging and size cues**

262 Many aspects of behavioural begging were reported in the literature, such as begging amplitude,
263 duration, latency, likelihood, call structure, and begging postures. Different measures of food
264 allocation were also presented, such as weight gain over a short time period, actual food intake,
265 number of food items received, likelihood of being fed, growth rate, and mortality. We assumed
266 all measures of begging intensity and feeding preferences were functionally equivalent, and so
267 included all reported statistics in our analyses. Because test statistics were converted to a
268 standardized scale, differences between the various measures of begging intensity or feeding

269 preferences should not influence the overall trends seen. A previous comparative analysis, using a
270 more comprehensive dataset, found no impact of study methodology, such as which measure of
271 feeding preference was used or whether studies were experimental or observational, on the effect
272 size of begging or size cues on feeding preferences (Caro et al. 2016).

273

274 **Statistical analyses**

275 We transformed any test statistic measuring either an effect of begging or size cues on feeding into
276 a standardized effect size (Fisher's Z-transformed correlation coefficient) (Borenstein et al. 2011;
277 Grissom and Kim 2011; Koricheva et al. 2013). These correlation coefficients follow a normal
278 distribution, account for different scales in their original measurements, are well suited to the
279 ordered nature of the data, and are more straightforward to interpret than standardized differences
280 in means (Borenstein et al. 2011; Grissom and Kim 2011; Koricheva et al. 2013). Fisher's Z-
281 transformed correlation coefficients were analysed using the MCMCglmm package in R, which
282 implements Bayesian generalized linear mixed models with Markov chain Monte Carlo methods
283 (Hadfield 2010; R Core Team 2013). We ran bivariate response models so we could measure
284 phylogenetic covariance between responsiveness to begging and responsiveness to size cues. We
285 weighted models by sample size, and controlled for phylogeny and repeated measures on the same
286 study and species. Our measure of sample size was the number of broods used to generate the
287 original test statistic, because this is a standard measure across studies, and conservatively avoids
288 pseudoreplication if chick number or number of observations were used as the sample size. We
289 treated environmental quality as a three-level ordered categorical variable. To control for
290 phylogeny, we obtained phylogenies from Birdtree.org, ran models on 4 random phylogenetic trees
291 with Ericson and Hackett backbones, and then averaged model results (Jetz et al. 2014).

292

293 **Results**

294 *Great tit experiment*

295 We found that parental provisioning rules were flexible in response to environmental conditions –
296 parents responded differently to offspring begging and size, depending upon whether parents had
297 received supplemental food in the previous week (interaction between supplementation, quadratic
298 weight rank and relative begging intensity: 95% CI -1.09 to -0.03, pMCMC = 0.041*; Fig. 1; Table
299 S2). In all nests and for all chicks, the likelihood of being fed increased with higher relative
300 begging intensity (95% CI 1.91 to 2.87, pMCMC < 0.0001***; Table S2), but chick size mediated
301 how much begging increased the likelihood of being fed. In nests that had been supplemented (Fig.
302 1a), parents responded primarily to begging signals, responding equally to the begging of all chicks
303 regardless of size. However, in unsupplemented nests (Fig. 1b), parents responded more to size by
304 responding more to the begging of larger chicks than to the begging of the smallest chicks.

305

306 We confirmed that this difference in food allocation could not be explained by differences in
307 offspring behaviour or size cues. Since we swapped chicks between nests directly before filming,
308 there was no difference in relative begging posture or in chick weights between supplemented and
309 unsupplemented foster broods (mean of begging: $t_{27} = 0.63$, $p = 0.53$; SD of begging: $t_{27} = 0.15$, p
310 $= 0.88$; mean of weight: $t_{27} = -0.90$, $p = 0.38$; SD of weight: $t_{27} = -0.64$, $p = 0.53$). Since we handfed
311 a subset of chicks across the weight hierarchy, relative begging posture also did not vary by chick
312 weight rank ($t_{167.8} = 0.40$, $p = 0.69$) or quadratic weight rank ($t_{174.2} = -0.62$, $p = 0.54$). We also
313 confirmed that our supplemental feeding was successful in improving environmental conditions:
314 59% of supplemented nests had no brood reduction in the first week after hatching, compared to

315 only 18% of unsupplemented control nests ($z = 2.94$, $p = 0.0033^{**}$; $n = 34$ nests; Table S1). The
316 total number of chicks that died per nest was also lower in supplemented nests ($z = 2.10$, $p =$
317 0.045^{*} ; Table S1). Chick mass of the surviving chicks on day 7 was not affected by
318 supplementation ($z = 1.58$, $p = 0.12$; Table S1).

319

320 *Comparative study*

321 Next, to explore whether plasticity is a general trend across birds, we conducted a phylogenetic
322 meta-analysis on 57 bird species. Species were included if they had data on parental responsiveness
323 to begging or chick size in multiple environmental conditions (poor, normal or good). We
324 quantified responsiveness as the correlation coefficient (effect size) between feeding and (a)
325 begging or (b) size. These two coefficients vary between ± 1 , with higher values indicating that
326 either (a) begging or (b) size has a stronger effect on the likelihood that a chick is fed. We estimated
327 plasticity by calculating each species' change in responsiveness as environmental quality varies,
328 i.e. the within-species slope of correlation coefficients over environmental quality. A positive slope
329 would indicate that parents become more responsive in better environments, a slope of 0 would
330 indicate no plasticity based on the environment, and a negative slope would indicate that parents
331 become less responsive in better environments. If other species adjust their behaviour in the way
332 that we have observed with great tits, then we would observe a consistent within-species pattern,
333 with parents becoming more responsive to begging (positive slopes), and less responsive to size
334 (negative slopes), in better environments.

335

336 We found this predicted pattern, with parents became more responsive to begging, and less
337 responsive to size, in better environments. Specifically, we found a stronger correlation between

338 begging and feeding in better environmental conditions (95% CI of the slope = 0.13 to 0.67,
339 $p_{MCMC}=0.0037$; Fig. 2a). Across 17 species with available data on responsiveness to begging in
340 more than one environmental condition, 14 species showed the predicted increase in correlation
341 strength (82%), and three species showed a decrease (18%).

342

343 Also, as predicted, we found the opposite pattern in parental response to size cues. Within species,
344 there was a weaker correlation between chick size and feeding in better environmental conditions
345 (95% CI of the slope = -0.23 to -0.05, $p_{MCMC} = 0.0016$; Fig. 2b). Across 52 species with available
346 data on responsiveness to size cues in more than one environmental condition, 32 species showed
347 the predicted decrease in correlation strength (62%), and 20 had an increase (38%). There was no
348 species-level correlation between how responsive parents are to begging and how responsive they
349 are to size cues (95% CI -0.54 to 0.52). These results suggest that the pattern we observed in great
350 tits, where parents facultatively adjusted their responsiveness in reaction to local conditions, occurs
351 consistently across a range of different bird species.

352

353 **Discussion**

354 Our experimental and comparative results show that parents conditionally adjust how they respond
355 to signalling, depending upon environmental conditions (food availability). Parents did not simply
356 feed the chicks that were the largest or that begged the most. Instead, they have evolved to adjust
357 their sensitivity to multiple sources of information depending on local conditions, in a
358 sophisticated manner. When food is more plentiful, great tit parents respond equitably to all their
359 offspring's begging, but when food is more scarce, parents selectively respond more to the begging
360 of larger chicks (Fig. 1a,b). Likewise in our meta-analysis, we found the same consistent pattern,

361 across 57 species (Fig. 2a,b). These results show how variation in environmental quality can lead
362 to different forms of communication, even within species.

363

364 The degree to which parents actively control food allocation as opposed to passively respond to
365 the greatest stimulus or cede to the winner of sibling competition has been contentious (Clutton-
366 Brock 1991; Kacelnik et al. 1995; Parker et al. 2002; Heeb et al. 2003; Ploger and Medeiros 2004).

367 Since our cross-fostering experiment ensured there was minimal variation in brood size,
368 competitive asymmetry and begging behaviour, changes in allocation patterns can definitively be

369 attributed to changes in great tit parental response strategies, rather than differences in offspring
370 behaviour or information constraints. It should be noted, however, that we examined provisioning

371 at one point midway through the nestling period. It is possible that older chicks may be able to
372 exert more control via scramble competition. Furthermore, given that species differed in the degree

373 of their plasticity (Fig. 2a,b), it is probable that species vary in the actual balance of power between
374 parents and offspring, so that in some species offspring behaviour drives changes in food

375 distribution patterns. It may be also that some species flexibly determine their investment strategies
376 in other ways and at other times; for example, 1) during incubation by varying the amount of

377 hatching asynchrony (e.g. blackbirds (Magrath 1992) and European rollers (Parejo et al. 2015));
378 2) during different points in the breeding season by varying how parents respond to UV signals

379 (e.g. alpine swifts and European starlings (Bize et al. 2006)); or 3) during different times within a
380 single breeding attempt by varying aggression towards offspring (e.g. American coots (Shizuka

381 and Lyon 2012)). Recent work on genetic covariance and plasticity in canaries found that both
382 offspring and parental signalling strategies varied plastically across different hunger levels

383 (Fresneau and Müller 2019). This indicates that even if parents are plastic in their behavior and

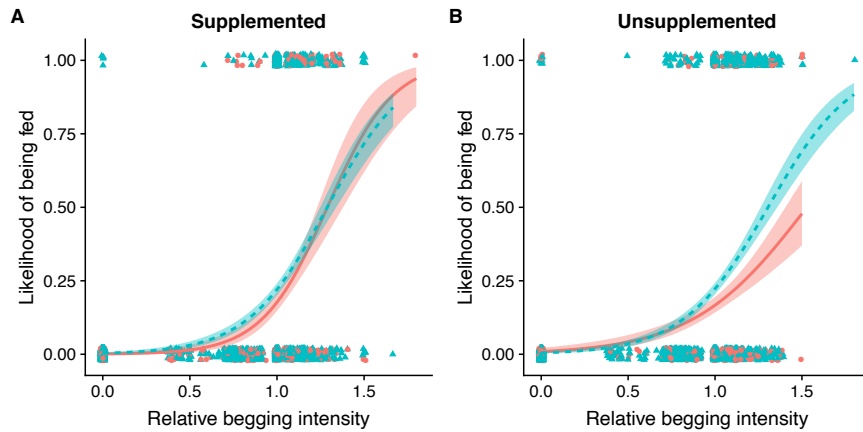
384 control provisioning, they may still be influenced by changes in their offspring's behavior. Future
385 research could continue disentangling what is driven by parental preference, by parents' reactions
386 to offspring signals, or by offspring directly.

387

388 What explains diversity in signalling systems is a fundamental question in signalling theory. Our
389 results suggest that receivers control the outcome of parent-offspring communication and assess
390 multiple sources of information from signallers. This is analogous to how females respond to
391 multiple signals of quality in sexual signalling (Bro-Jørgensen 2010), and may be similar to
392 aggressive signalling and other forms of communication as well. Our results highlight the need for
393 dynamic signalling models that allow for flexibility in responsiveness based on environmental
394 conditions, and that incorporate multiple signals and cues (Mangel and Clark 1988; Wild 2011).

395

396 **Figures and legends**



397

398 **Fig. 1. A chick's likelihood of being fed depends on its relative begging intensity, size rank,**

399 **and whether its parents were supplemented.** In supplemented nests (a), higher relative begging

400 intensity led to a greater likelihood of being fed for all chicks equally. In unsupplemented nests

401 (b), smaller chicks showed less of an increase in their likelihood of being fed based on begging

402 intensity than larger chicks did (95% CI of the interaction = -1.09 to -0.03, MCMCglmm). Weight

403 ranks 1-5 are shown in blue, while the smallest two chicks in the nest (ranks 6-7) are shown in red.

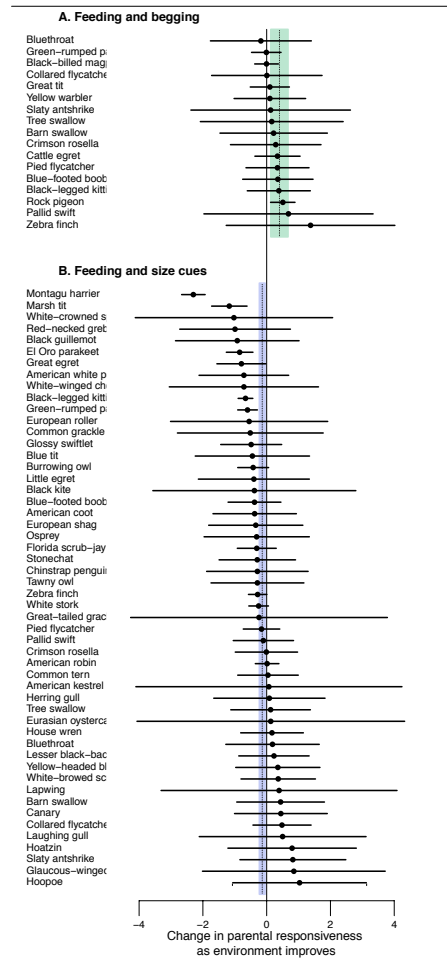
404 We show weight categories for graphical clarity; statistical analyses report the non-linear effect of

405 weight rank as a continuous variable. A relative begging intensity of 1 indicates a chick is begging

406 the same as its nest mates on average, while >1 means it begged at a higher intensity. Each data

407 point is one chick in a feeding visit, vertically jittered to show overlapping points (n = 14

408 supplemented nests, 15 unsupplemented nests, 1121 feeding visits).



409

410 **Fig. 2. Environmental quality and parental response to offspring begging and size.** Circles
 411 represent each species' slope for the correlation coefficient between feeding and (a) begging, and
 412 (b) size cues, over environmental quality. Lines represent the 95% CI of the slope within each
 413 species. The shaded region shows the 95% CI across all species, controlling for phylogeny and
 414 weighted by sample size. Positive values indicate that parents respond more in better environments
 415 (green). Negative values indicate parents respond less in better environments (purple). Species
 416 respond more to begging (95% CI = 0.13 to 0.67, MCMCglmm, n=17 species), and less to size
 417 cues (95% CI = -0.23 to -0.05, MCMCglmm, n=52 species), in better environments. This pattern
 418 is more consistent for changes in responsiveness to begging, but is also significant for changes in
 419 responsiveness to size.

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