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Article:

Li, J., Wang, Y., Lv, L. et al. (3 more authors) (2019) Context-dependent strategies of food allocation among offspring in a facultative cooperative breeder. Behavioral Ecology. ISSN 1045-2249

<https://doi.org/10.1093/beheco/arz037>

This is a pre-copyedited, author-produced version of an article accepted for publication in Behavioral Ecology following peer review. The version of record Jianqiang Li, Yong Wang, Lei Lv, Pengcheng Wang, Ben J Hatchwell, Zhengwang Zhang, Context-dependent strategies of food allocation among offspring in a facultative cooperative breeder, Behavioral Ecology, arz037 is available online at: <https://doi.org/10.1093/beheco/arz037>

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1 **LAY SUMMARY**

2 Parental allocation of care among offspring can be influenced by the availability of
3 resources. We show that when black-throated tit parents allocate food, they exhibit a
4 stronger preference for begging intensity (a proxy of nestling need) under better food
5 conditions (i.e. when a nest has helpers and for small broods) and a stronger preference
6 for begging position (a proxy of nestling competitive ability) under poor food
7 conditions (i.e. without helpers and with a large brood).

8 **Context-dependent strategies of food allocation among**
9 **offspring in a facultative cooperative breeder**

10 **RUNNING TITLE**

11 Food distribution among offspring in black-throated tits

12 **ABSTRACT**

13 Natural selection should favor adoption of parental strategies that maximize fitness
14 when allocating investment among offspring. In birds, begging displays often convey
15 information of nestling need and quality, allowing parents to make adaptive food
16 allocation decisions. We investigated how adults utilized cues likely to represent
17 nestling competitive ability (begging position) and need (begging intensity), and a cue
18 independent of nestling control (nestling sex) to distribute food among nestlings in a
19 facultative cooperative breeder, the black-throated tit (*Aegithalos concinnus*). We found

20 that parents reduced their efforts when helped, suggesting that parents of helped broods
21 would have the potential to satisfy nestling needs more than unhelped parents. This
22 suggestion was supported by the fact that nestling mass increased faster in helped than
23 in unhelped nests. We found no effect of nestling sex on food allocation, but, as
24 predicted, we found that adults responded differently to begging signals in relation to
25 the presence of helpers and brood size. First, helped parents were more responsive to
26 nestling begging intensity than parents without helpers. Second, female parents and
27 helpers had a stronger preference for nestling begging position in large than in small
28 broods. Third, the preference for nestling begging position was greater for unhelped
29 than for helped female parents. These results provide evidence that carers adjust their
30 preference for different offspring begging signals based on availability of food
31 resources.

32 **Key words:** black-throated tit, offspring begging, brood size, cooperative breeding,
33 food allocation, helper effect.

34 INTRODUCTION

35 In species where parents provision offspring, parental care is often one of the major
36 investments in an adult's life and must be traded off against other life history traits,
37 including personal survival and investment in other offspring (Stearns 1989; Royle et al.
38 2012). Selection should favor adults that adopt strategies that maximize their fitness, so
39 allocation of parental investment among offspring often involves complex conflicts
40 among family members (Parker et al. 2002; Houston et al. 2005). In birds and mammals,
41 studies have shown that adults may use cues under offspring control such as their
42 begging intensity (Manser et al. 2008; Shiao et al. 2009), position (Brotherton et al.
43 2001; Dickens and Hartley 2007; Shiao et al. 2009) and detectability (Heeb et al. 2003),
44 as well as cues independent of offspring control such as offspring size (Slagsvold 1997;
45 Dickens and Hartley 2007; Shiao et al. 2009) and gender (Ridley and Huyvaert 2007;
46 Mainwaring et al. 2011; Lees et al. 2018) to allocate care among offspring. Different
47 adults may even care for a specific subgroup of offspring with respect to such cues
48 (termed 'brood division'; Edwards 1985; Slagsvold 1997; Leedman and Magrath 2003;
49 Vega et al. 2007). Because differential allocation of care based on such cues is often
50 associated with the value of particular offspring (Slagsvold 1997; Lessells 2002),
51 investigation of the food allocation process may provide insights into how and why
52 selection has shaped parental investment strategies.

53 Cooperative breeding systems, in which more than two individuals care for young
54 (Jennions and Macdonald 1994; Koenig and Dickinson 2004), are expected to involve

55 more complex food distribution patterns than systems with uniparental and biparental
56 care. Many studies of avian cooperative breeders have investigated adult provisioning of
57 food in relation to factors such as brood sex ratio (McDonald et al. 2010; Nam et al.
58 2011), offspring sex and group size (Ridley and Huyvaert 2007), offspring size and food
59 abundance (Boland et al. 1997), and offspring size and breeding experience (Klauke et
60 al. 2014). In addition, several studies have examined whether adult provisioning effort
61 is correlated with nestling begging behavior (e.g. MacGregor and Cockburn 2002;
62 McDonald et al. 2009; MacLeod and Brouwer 2018). However, while these studies
63 have deepened our understanding of the factors influencing variation in adult
64 investment, most have failed to consider the effect of offspring behavior on adult
65 decisions about food allocation among offspring or variation in food allocation by
66 different adults. One exception is Brotherton et al. (2001)'s study of adult food
67 allocation preference in meerkats (*Suricata suricatta*), which considered offspring
68 begging behaviors and variation among adults. This study found that meerkat carers
69 followed a "feed the nearest begging pup" rule, and that female helpers fed female pups
70 significantly more than male pups, while male helpers fed pups of both sexes equally.

71 Furthermore, although many studies have investigated parental adjustment of
72 provisioning effort when assisted by helpers (e.g. Hatchwell and Russell 1996;
73 Hatchwell 1999; Valencia et al. 2006; Koenig and Walters 2011; Lu et al. 2011), the
74 question of whether the presence of helpers affects parental food allocation among
75 offspring has been neglected. Since helpers often increase food delivery to broods

76 (Wilkinson and Brown 1984; Doerr and Doerr 2007; Preston et al. 2016) and/or lighten
77 the load of parents (Hatchwell and Russell 1996; Caffrey 1999; Meade et al. 2010),
78 parents may be expected to adjust food allocation among offspring accordingly. For
79 example, they may be more concerned about nestling need when they are better able to
80 provide care (Caro et al. 2016).

81 In this study, we investigated adult-offspring interactions in the food allocation
82 process of a facultative cooperatively breeding bird, the black-throated tit (*Aegithalos*
83 *concinnus*) (Li et al. 2012). Our overall objectives were: (a) to explore how adults use
84 nestling begging displays (position in the nest and begging intensity) and a cue
85 independent of nestling control (nestling sex) to distribute food among nestlings; and (b)
86 whether food distribution differed among adults and between nests with and without
87 helpers. Following a description of the factors affecting nestling provisioning rates and
88 body mass, we tested the following hypotheses regarding parental allocation and
89 nestling begging behavior.

90 First, we hypothesized that adults would prefer a particular sex of nestlings. Males
91 exhibit natal philopatry (authors, unpublished data) and are the helping sex in this
92 species (Li et al. 2012), so under the repayment hypothesis (Emlen et al. 1986) parents
93 should favor male nestlings because they become helpers in the future, as found in some
94 cooperative breeders (e.g. Komdeur et al. 1997; Brotherton et al. 2001) although not in
95 others (Khwaja et al. 2017). Alternatively, the local competition hypothesis (Clark 1978)
96 predicts that female offspring would be favored because females exhibit greater natal

97 dispersal in our study population (authors, unpublished data).

98 Secondly, we hypothesized that adult responses to nestling begging position and
99 intensity would differ between cooperative and non-cooperative breeding groups.
100 Begging intensity and begging position are likely to provide adult birds with different
101 information. Begging intensity should reflect the need of an individual nestling
102 (Godfray 1991), and evidence shows that nestling begging intensity varies with hunger
103 (Redondo and Castro 1992; Mondloch 1995; Leonard and Horn 1998; Lichtenstein and
104 Dearborn 2004), body condition (Price et al. 1996), or both (Saino et al. 2000). In
105 contrast, begging position is more likely to reflect a nestling's competitive ability
106 (Budden and Wright 2001), a trait that relates to the nestling's future survival potential
107 (Whittingham et al. 2003). In many species, the probability of a nestling being fed
108 depends on the position it occupies (Kacelnik et al. 1995; Whittingham et al. 2003;
109 Rosivall et al. 2005; Tanner et al. 2008) and nestlings compete for the optimal position
110 (Gottlander 1987; McRae et al. 1993; Smiseth et al. 2003). Therefore, we predicted that
111 when parents had limited ability to raise the brood (i.e. when they had no helpers) they
112 should favor nestlings that are more likely to survive and thus the effect of begging
113 position on food allocation should be greater in the absence of helpers. On the other
114 hand, at nests with helpers where the need of nestlings is more easily satisfied, we
115 predicted that nestling need should be of more concern to parents and hence that food
116 allocation would be more influenced by nestling begging intensity than at nests without
117 helpers. The relative availability of food to nestlings should also vary with brood size,

118 so we also predicted that adult preference for nestling competitive ability should be
119 greater in large than in small broods and preference for nestling need be greater in small
120 than in large broods.

121 **MATERIALS AND METHODS**

122 **Study site, study population and field work**

123 The study was conducted in the Dongzhai National Nature Reserve (31.95°N, 114.25°E)
124 in the Dabieshan Mountains, Henan Province, central China. The black-throated tit is
125 resident at the study site and usually breeds from January to early June (Li et al. 2012).
126 Brood reduction through starvation is rare (1.6% of nestlings in 3.3% of broods; Li et al.
127 2012), but nesting success is low due to depredation of eggs or nestlings, so, typically,
128 less than one third of nests produces fledglings (Li et al. 2012). Most helpers are male
129 and they assist breeders at the nestling stage when c. 20% of nests have helpers (Li et al.
130 2012). The cause of helping in this species remains unknown, but some helpers are from
131 the same winter flock as helped parents (Li et al. 2012), while others are known to be
132 breeders whose own breeding attempts failed (authors, unpublished data).

133 Data for this study were collected from 42 nests between 2009 and 2017 (10 in 2009,
134 six in 2010, two in 2011, one in 2012, four in 2013, 11 in 2016 and eight in 2017). Each
135 year we searched for nests and monitored breeding behavior at each nest (usually every
136 1–3 days). Black-throated tits construct domed nests, with an entrance hole placed near
137 the top. Adult birds usually enter or reach into the nest to feed nestlings for the first few

138 days after hatching, but when nestlings are larger the adults feed them at the entrance
139 hole while perched outside the nest, enabling us to observe food allocation among
140 nestlings. Black-throated tit nestlings usually fledge when 14–16 days old, so we filmed
141 feeding behavior at nests with video cameras when nestlings were at least 10 days old.
142 The mean brood size of these nests was 6.0 ± 1.2 SD (range 3–8). To distinguish
143 nestlings within a brood during the food distribution process, each nestling was
144 color-marked on their forehead and throat using nontoxic color pens before filming,
145 with one or a combination of the following basic colors: blue, black, green, purple, red,
146 salmon pink, yellow and none (i.e. no color). Studies have shown that nestling
147 coloration, e.g. gape color, may influence parental feeding preference (Götmark and
148 Ahlström 1997; Dugas 2009). Therefore, although we marked nestlings on their throat
149 and forehead, and not on their gape the potential effect of marking on adult food
150 allocation was statistically accounted for (see Statistical analysis). The colors faded
151 away either before fledging or shortly after fledging and no apparent adverse effect was
152 observed on the nestlings. All but one of the broods monitored during this study fledged
153 successfully after the experiments; the reason for the failure of the nest was predation.
154 Black-throated tits are usually single-brooded (Li et al. 2012) and none of the adults we
155 observed in this study had repeated nests across years.

156 To film nests, cameras were fixed on tripods placed 0.5–2.5m from the nests; adults
157 became accustomed to cameras within 20 minutes, with little or no sign of nervousness
158 when feeding nestlings. Each nest was filmed for 9.85 ± 4.42 SD hours within $1.97 \pm$

159 0.81 SD days; observations were conducted in the morning and afternoon at 41 out of
160 42 nests. Adults were banded with unique color ring combinations before the breeding
161 season, or in some cases, were captured and banded after their nests were found. In one
162 nest, the female parent was not ringed but could be distinguished from the male parent
163 as the only unringed carer. Of the 42 observed nests, 13 (31%) had helpers (11 with one
164 helper, two with two helpers). All but one helper was male (the only female helper was
165 at a nest with two helpers). We distinguished helpers from parents based on the timing
166 of their appearance at the nest, as helpers typically appear only at the provisioning stage.
167 At two nests, the helpers were already present when we found the nests, so we
168 distinguished the father and helper using parentage analysis (see below); black-throated
169 tits have a relatively low rate of extra-pair paternity and helpers seldom sire offspring at
170 the nest they help (Li et al. 2014). Brood sizes of cooperative breeding nests (6.1 ± 1.4
171 SD) and non-cooperative breeding nests (6.0 ± 1.1 SD) did not differ significantly (t-test,
172 $df = 40$, $t = 0.2$, $P = 0.855$). Brood age at filming was also similar between cooperative
173 (12.4 ± 1.2 SD days old) and non-cooperative nests (12.3 ± 0.9 SD days old; t-test, $df =$
174 40 , $t = 0.3$, $P = 0.792$). Duration of filming was $11.9 \text{ h} \pm 5.6$ SD for cooperative nests
175 and $9.3 \text{ h} \pm 3.8$ SD for non-cooperative nests (t-test, $df = 40$, $t = 1.2$, $P = 0.227$).

176 **Molecular sexing and paternity assignment**

177 Black-throated tits are sexually monomorphic (Li et al. 2010), so the sex of adults and
178 nestlings was determined using primers *sex1*'/ *sex2* (Wang et al. 2010) with blood
179 samples collected through venipuncture of the brachial vein. For the two nests at which

180 the helper and male parent could not be distinguished, we determined their identity
181 through parentage analysis using a panel of microsatellite markers: Ase18, Ase37,
182 Ase64, Escu6, Man13, Pca3, PmaD22 (Simeoni et al. 2007) and TG01040, TG03031,
183 TG04004, TG04041, TG01147 (Dawson et al. 2010). All loci were amplified with
184 polymerase chain reactions (PCR) in three independent multiplex reactions (see Li et al.
185 2014 for reaction conditions). Fragment lengths were analyzed using ABI 3730xl
186 96-capillary DNA analyzer, LIZ500 as an internal standard. Electropherograms were
187 analyzed using GeneMapper version 4.0. As maternity was known, we assigned
188 paternity by comparing the genotype of male adults to that of the nestlings. The male
189 whose genotype matched that of the nestlings was identified as the male parent. In these
190 two nests, helpers did not sire a nestling. The male parent of one nest had sired all the
191 nestlings, while the male parent of another nest sired four of eight nestlings of the brood
192 (the remaining nestlings were sired by an unsampled male).

193 **Data collection from videos**

194 A total of 8695 feeding events were recorded at 42 nests (207.0 ± 109.5 SD feeding
195 events per nest). From each feeding event, we recorded the type of adult (mother, father
196 or helper) and the identities of the begging and fed nestlings (using color code).
197 According to our earlier observations that black-throated tits prefer to feed either the
198 nestlings closest to the adults or those with the strongest begging intensity (Li 2010), we
199 recorded nestling begging intensity and position, classifying each into one of two
200 categories: if a nestling's begging intensity was the strongest (based on overall

201 judgments of whether a nestling had a more opened mouth, a more stretched neck
202 and/or was first to beg), it was categorized “1”, otherwise, “0”; if a nestling’s position
203 was the closest to the feeding adult, then it was given “1”, otherwise, “0”; in cases
204 where it was hard to discriminate between the levels of begging intensity and position
205 of two nestlings (i.e. they had similar begging intensity or position), we placed them in
206 the same category. The method for classifying nestling begging intensity neglected
207 differences in begging behaviors between, for example, a nestling begging first and a
208 nestling having a more opened mouth (i.e. they were both treated as having begging
209 intensity of “1”). Because they are both reflections of nestling need for food, our
210 treatment simplified the data recording process while not hindering answering our
211 questions regarding whether nestling need was under consideration by adults when
212 making the feeding decisions. All begging behaviors in the videos were scored by one
213 observer to reduce bias. Repeatability of nestling behavior scoring was 0.98 ± 0.02 SD
214 for begging position and 0.95 ± 0.03 SD for begging intensity based on re-scoring 257
215 feeding events from eight randomly selected nests (32.1 ± 5.6 SD events per nest).
216 Black-throated tits provision nestlings with spiders and insects such as Lepidoptera,
217 Orthoptera, Diptera and Ephemeroptera (Li et al. 2012). The sizes of food items
218 delivered by different types of adult do not differ significantly (Li 2010), so the food
219 size in each feeding event was not considered in our analyses and the number of feeds
220 should be a reasonable estimation of the biomass delivered to a nestling.

221 Adults usually fed only one nestling during each feeding event. If more than one

222 nestling was fed (in less than 5% of the total of feeding events), the first nestling only
223 was recorded as fed by the adult because this decision was the parent's primary choice
224 of which offspring to invest in (Rosivall et al. 2005; Dickens and Hartley 2007).
225 Feeding events for which the identities of either the adult or the begging nestlings could
226 not be identified were excluded from analyses. Furthermore, as we were interested in
227 adults' food allocation decisions when they had a choice, we omitted cases where only
228 one nestling begged for food (Rosivall et al. 2005). Therefore, the final data set included
229 only those feeding events for which we knew the exact identities of the feeding adult
230 and all begging nestlings, as well as those with at least two begging nestlings (n = 5599
231 feeds in total and 133.3 ± 82.0 SD feeds per nest).

232 **Statistical analysis**

233 **Effect of helpers on nestling provisioning rates and body mass**

234 The effects of helping behavior on provisioning rates were analyzed using linear mixed
235 models (LMMs) with a Gaussian distribution. In the analyses, total (all adults) and
236 parental provisioning rates to the nests were set as response variables to investigate the
237 effect of helping behavior on total and parental investment in provisioning nestlings,
238 respectively. Helper presence (helped vs. unhelped), brood age (days since hatching),
239 brood size (number of nestlings) and date (calculated as the number of days after the
240 date on which the first brood of the population hatched each year) were treated as
241 explanatory variables and year as a random factor to control for the non-independence
242 of data collected in the same year.

243 To explore factors affecting nestling body mass we used a LMM with a Gaussian
244 distribution, in which nestling mass was treated as the response variable, helper
245 presence, brood size, brood age, brood age², brood sex ratio, nestling sex, date and the
246 two-way interactions of these variables as explanatory variables, and nest ID nested
247 within year as random factors. The dataset for this analysis comprised 827 nestlings
248 from 154 unhelped nests and 131 nestlings from 22 helped nests, measured between
249 2008 and 2017.

250 Factors affect adult food allocation among nestlings

251 We first analyzed whether adults' food allocation rules were affected by a nestling's sex,
252 begging position and begging intensity and whether the rules were related to helper
253 presence and brood size using a generalized linear mixed model (GLMM) with a
254 binomial distribution and a logit link. The response variable was whether a nestling was
255 fed (1) or not (0) and the explanatory variables were helper presence, nestling sex,
256 nestling begging position (1/0) and intensity (1/0), brood size type (small if a brood had
257 ≤ 6 nestlings and large if a brood had > 6 nestlings) and their two-way interactions. We
258 checked whether it was appropriate to include begging position and intensity in a same
259 model while avoiding the problem of collinearity by calculating for each nestling a phi
260 coefficient, a measure of the degree of association between two binary variables. The
261 phi coefficient ranges from -1 to +1 and a strong association is assumed when the
262 absolute value of phi is > 0.7 (Kruska-Miller 2014). The mean of the absolute values of
263 phi coefficients across the nestlings ($n = 254$) was 0.374 ± 0.168 SD, suggesting that the

264 correlation between nestling begging position and intensity was acceptable. In addition
265 to the above explanatory variables, the number of begging nestlings during a feeding
266 event and brood age were also included as explanatory variables. Filming date,
267 calculated as the number of days after the date on which the first brood of the
268 population hatched each year, was also included as an explanatory variable to control
269 for any seasonal variation in food availability. Nestling ID nested within nest ID, which
270 was further nested in year, were included as random factors to control for the
271 non-independence of data collected from the same nestling, the same nest and the same
272 year. Note that sample size in some years was small. We report the result with year
273 included in the random effects because excluding year did not qualitatively change the
274 results while including it can account for the structure of our data. Each feeding event
275 was also initially included as a random factor to control for the non-independence of
276 nestling begging behavior during a feeding event, but was removed from the analyses
277 because it explained zero variance. To control for the potential effect on parental food
278 allocation of color marks on chicks, nestling color was included as a random factor.

279 Secondly, we analyzed whether different types of adults (i.e. helped female parent,
280 helped male parent, helper, unhelped female parent and unhelped male parent) differed
281 in their food allocation rules by replacing helper presence in the model obtained above
282 with adult type.

283 Finally, because a significant interaction between brood size and begging position
284 was found (see results), we further explored whether the interacting effects of brood size

285 and begging position on food allocation differed among adults by conducting analyses
286 for each type of adult separately.

287 In all analyses, simplification of initial models was conducted through stepwise
288 backward elimination of the least significant terms starting from the interactions first,
289 and the P-values of removed terms shown in the results were obtained by re-fitting them
290 individually to the minimal model (Russell et al. 2003; Baglione et al. 2006).
291 Denominator degrees of freedom of the mixed model analyses were obtained by
292 Satterthwaite approximation as the data were unbalanced (Heck et al. 2012). All
293 analyses were conducted in SPSS 25.0 (IBM SPSS, Chicago, Illinois) and tests were
294 two-tailed with an alpha level of 0.05.

295 **RESULTS**

296 **Effect of helpers on nestling provisioning rates and body mass**

297 The presence of helpers did not significantly affect total provisioning rates (helped vs.
298 unhelped, 23.7 ± 5.8 SD vs. 20.1 ± 5.9 SD feeds/h; Table 1), but parental provisioning
299 rates were significantly reduced when they were helped (helped vs. unhelped, 14.6 ± 4.5
300 SD vs. 20.1 ± 5.9 SD feeds/h; Table 1). In addition, both total and parental provisioning
301 rates were positively related to brood size, negatively related to date, and unrelated to
302 brood age (Table 1).

303 Nestling body mass increased with age, and there was a significant interaction
304 between age and helper presence, showing that the increase of nestling mass with age
305 was faster in helped broods (Table 2). Interestingly, nestling mass in helped nests was

306 lower than in unhelped nests at younger ages, but this situation reversed when nestlings
307 were older, helped nestlings becoming heavier (Figure 1). Male nestlings were
308 significantly heavier than female nestlings, but brood size, brood sex ratio and date had
309 no effect on nestling mass (Table 2).

310 **Adult food allocation behaviors**

311 Both begging position and begging intensity had significant effects on the probability
312 that a nestling was fed (Figure 2; Table 3). Begging position was more important than
313 intensity for food allocation, because nestlings occupying a close position had about 1.5
314 times probability of being fed than those showing strong begging intensity (c. 60% vs.
315 40%; Figure 2). Among the other factors tested, the number of begging nestlings in each
316 feeding event had a significant negative effect on the probability of an individual
317 nestling being fed; all other factors, including nestling sex, brood age and filming date,
318 did not affect food allocation (Table 3).

319 Helper presence interacted significantly with begging position and intensity when
320 determining whether a nestling would be fed (Table 3), with the effect of begging
321 position being smaller (Figure 2A) and the effect of begging intensity being greater
322 (Figure 2B) at helped than at unhelped nests. Brood size also interacted significantly
323 with begging position (Table 3), with the effect of position being greater in larger
324 broods (Figure 2C). There was also a trend for the effects of begging intensity to be
325 greater in smaller broods (Figure 2D), but this interaction between brood size and
326 begging intensity was not significant (Table 3).

327 To examine whether responses to nestling begging position and intensity differed
328 among different types of adults, we replaced helper presence in the final model of Table
329 3 with adult type. We found a significant interaction between adult type and nestling
330 begging position and intensity (Table 4). Begging position had a significantly greater
331 effect on food allocation decisions of unhelped female parents than of helped female
332 parents, but there was no significant difference between other adult types and helped
333 female parents (Table 4; Figure 3A). This result implies that only female parents
334 adjusted their food allocation strategies in relation to the presence of helpers. In contrast,
335 begging intensity had a significantly smaller effect on food allocation by unhelped
336 female parents, unhelped male parents and helpers than for helped female parents; there
337 was no significant difference in the responses between helped female and male parents
338 (Table 4; Figure 3B), suggesting that unhelped parents and the helpers were less
339 concerned about nestling begging intensity than helped parents.

340 Food allocation by adults was affected by a significant interaction between begging
341 position and brood size (Tables 3 and 4); we conducted separate analyses for each type
342 of adult to investigate this relationship further. Begging position had a significantly
343 greater effect on food allocation in large than in small broods for unhelped female
344 parents (GLMM, estimate \pm SE = 0.591 ± 0.189 , df = 1,5685, F = 9.8, P = 0.002; Figure
345 4A), helped female parents (GLMM, estimate \pm SE = 0.935 ± 0.307 , df = 1,1747, F =
346 9.3, P = 0.002; Figure 4C), and helpers (GLMM, estimate \pm SE = 0.909 ± 0.332 , df =
347 1,1412, F = 7.5, P = 0.006; Figure 4E), but not for either unhelped (GLMM, estimate \pm

348 SE = 0.310 ± 0.180 , $df = 1,5545$, $F = 3.0$, $P = 0.085$; Figure 4B) or helped male parents
349 (GLMM, estimate \pm SE = -0.238 ± 0.282 , $df = 1,1907$, $F = 0.7$, $P = 0.400$; Figure 4D).

350 **DISCUSSION**

351 We have shown that black-throated tit parents adopt a compensatory reduction strategy
352 (Hatchwell 1999) when helped, reducing their own care relative to nests without helpers.

353 The body mass of nestling black-throated tits increased faster in helped broods than in
354 unhelped broods, as reported in other cooperatively breeding species (e.g. MacColl and
355 Hatchwell 2002; Ren et al. 2016), suggesting that nestlings benefit from the care that
356 helpers provide. The total provisioning rate at helped nests was higher than at unhelped
357 nests, although not significantly, but it may be that adults with helpers were more able
358 to satisfy the increasing need of nestlings with age because of their lower investment. In
359 the congeneric long-tailed tit (*A. caudatus*), parents reduced investment when assisted
360 by one helper, but maintained their investment with more helpers (Hatchwell and
361 Russell 1996; MacColl and Hatchwell 2003). The majority (11 out of 13) of the helped
362 nests in this study had only one helper, so our results are consistent with those for
363 long-tailed tits. Intriguingly, our results also suggest that nestlings at nests with helpers
364 were initially lighter but caught up with and exceeded the mass of nestlings at nests
365 without helpers (Figure 4). Whether this is because helpers preferentially care for lighter
366 broods, or because parents invest less in broods when care from helpers is anticipated
367 (Russell et al. 2007) remains unknown and would warrant further investigation.

368 Lightening of the reproductive load (Crick 1992) for black-throated tit parents is

369 likely to change their reproductive pay-offs and hence allow parents to adjust their food
370 allocation strategies. Here, we showed that food distribution among nestlings by
371 black-throated tit adults was influenced by nestling begging position and intensity, and
372 the magnitude of the effects of begging position and intensity were dependent on the
373 presence of helpers, as well as adult type and brood size. Food distribution according to
374 nestling begging position and intensity is common in birds (e.g. Whittingham et al. 2003;
375 Rosivall et al. 2005; Shiao et al. 2009). If begging position and intensity represent
376 nestling competitive ability and need, respectively, our results suggest that both the
377 competitive ability and need of black-throated tit nestlings affected parental feeding
378 decisions. We predicted that the preference for nestling need should be greater for
379 helped parents while the preference for nestling competitive ability should be greater for
380 unhelped parents. The first of these predictions was fully supported because the effect of
381 begging intensity on food allocation was greater for both female and male parents when
382 they were helped (Table 4; Figure 3B). The second prediction was partially supported
383 because female, but not male, parents preferred nestling position when they were not
384 helped (Table 4; Figure 3A). The latter result also suggests that the different effect of
385 begging position on food allocation by adults at nests with and without helpers (Table 3;
386 Figure 2A) resulted primarily from differences in female parents' food distribution.

387 Following the same reasoning, we also predicted that the preference for nestling need
388 should be greater in small broods, and the preference for competitive ability should be
389 greater in large broods. The effect of begging intensity on food allocation did indeed

390 tend to be greater in small broods, although the difference was not significant (Table 3;
391 Figure 2D), but, as predicted, nestling position had a bigger effect on food allocation in
392 large than in small broods (Table 3; Figure 3C). Separate analyses of the interacting
393 effects of brood size and begging position for each type of adult suggest that the greater
394 influence of begging position in large compared to small broods was because female
395 parents and helpers (but not male parents) showed greater preference for nestling
396 begging position in larger broods.

397 Overall, our results indicate that black-throated tits adjust food allocation strategies
398 based on helper presence and brood size. Similar adjustment of parental investment in
399 relation to resource availability has been reported in other species. For example, in
400 cooperatively breeding white-winged chough (*Corcorax melanorhamphos*), adults
401 prefer larger nestlings under conditions of food limitation, but increase their
402 provisioning rate and favor smaller nestlings when food is plentiful (Boland et al. 1997).
403 Similarly, adult bluethroats (*Luscinia svecica*) differentially allocate food according to
404 food availability, biasing food distribution to disfavor junior nestlings when food was
405 limited (Smiseth et al. 2003). In a recent meta-analysis of parent-offspring
406 communication across bird species, Caro et al. (2016) found that parents prefer to feed
407 needy nestlings in good environments and pay less attention to offspring need but more
408 to offspring quality in poor environments. In facultative cooperative breeders, such as
409 the black-throated tit, nests with helpers and/or small broods may represent a situation
410 of relative food abundance, while the nests without helpers and/or a large brood size

411 represent a situation of food-limitation. Thus, our results are consistent with other
412 studies that reported condition-dependent preferences for nestling need and quality.
413 Moreover, the results imply that the condition-dependent preferences can be tested more
414 widely in non-cooperative species that have variable brood size, in which parents may
415 vary in their ability to satisfy the need of a brood.

416 Our results also suggest that only female black-throated tit parents were sensitive to
417 nestling begging position because significant differences in the effect of position on
418 food distribution in relation to helper presence and brood size were found only in
419 female parents. Sex-specific parental food distribution strategies have been found in
420 several bird species. For example, in the zebra finch (*Taeniopygia guttata*) female but
421 not male parents preferred to feed a particular sex, in this case female nestlings
422 (Mainwaring et al. 2011), while in the green-backed tit (*Parus monticolus*), only male
423 parents preferred a particular size of nestling (Shiao et al. 2009). Dickens and Hartley
424 (2007) found that blue tit (*Cyanistes caeruleus*) males had a stronger preference than
425 females for feeding the closest nestlings regardless of their size, whereas female parents
426 were more likely to feed small and hungry nestlings when they were at intermediate
427 distances from her. In cases of post-fledging brood division, for example in toc-toc
428 (*Foudia sechellarum*), female parents exclusively provision female fledging, whereas
429 male parents provision male fledglings (Vega et al. 2007). Thus, there seems to be no
430 general pattern of which sex is choosy across species, nor in the nestling characteristics
431 chosen. The absence of a general inter-specific pattern suggests that a better

432 understanding of black-throated tits' and any other species' parental food allocation
433 strategies requires a detailed understanding of all aspects of a species' life history that
434 may affect individual reproductive investment.

435 Another notable result is that at helped nests, the effect of nestling begging intensity
436 on helpers' food distribution was smaller than that of the parents, implying that helpers
437 were less concerned by nestling need than parents. This result is of interest for two
438 reasons. First, helpers in some cooperative breeding species invest less in a brood than
439 parents do by having lower provisioning rates (Green et al. 2016) or by giving 'false
440 feeds' (a behavior where helpers arrive at nests but refrain from delivering foods to the
441 young; Canestrari et al. 2010). Our results indicate a more cryptic form of reduced
442 helper investment, i.e. by paying less attention to nestling need. However, this behavior
443 is hard to detect, so future studies of cooperatively breeding species may need to pay
444 particular attention to food allocation among offspring when comparing the investment
445 of parents and helpers.

446 Second, if helpers are less concerned than parents by nestlings' need for food, this
447 may shed light on the fitness benefits derived by helpers from their cooperative behavior.
448 Helping should confer direct and/or indirect benefits that outweigh the costs of helping
449 (Emlen 1982; Cockburn 1998; Heinsohn and Legge 1999), and in the congeneric
450 long-tailed tit helping is known to be driven by kin-selected indirect fitness benefits
451 from the increased productivity of relatives (Russell and Hatchwell 2001; Nam et al.
452 2010; Hatchwell et al. 2014). The benefits that black-throated tit helpers receive from

453 helping are currently uncertain, but if the cooperative system is similar to that of
454 long-tailed tits (i.e. helping normally occurs between closely related individuals), the
455 relatedness between helpers and the nestlings they care for would be less than half of
456 that between the parents and their offspring, so helpers should not necessarily put
457 similar investment into caring for nestlings.

458 In our analysis of parental food distribution in relation to nestling sex, we found no
459 evidence to support predictions of the repayment hypothesis (Emlen et al. 1986) or local
460 competition hypothesis (Clark 1978). Previous studies of biased food allocation
461 according to nestling sex have yielded inconsistent results. For example, Ridley and
462 Huyvaert (2007) found that within broods of Arabian babblers (*Turdoides squamiceps*),
463 parents preferentially fed male offspring (the philopatric sex) when group size was
464 relatively small and female offspring (the dispersive sex) when group size was large,
465 while helpers consistently favored young of opposite sex to themselves. In contrast,
466 there was no evidence of preferentially allocated care in relation to offspring sex in
467 either long-tailed tits (Nam et al. 2011) or rifleman (*Acanthisitta chloris*; Khwaja et al.
468 2018). Our results are consistent with the latter studies, and also with the more general
469 finding that support for the repayment hypothesis is equivocal (Khwaja et al. 2017).
470 Potential reasons for an absence of biased investment in relation to nestling sex have
471 been discussed extensively (Nam et al. 2011; Khwaja et al. 2017), and it is likely that
472 the unpredictable nature of helping in species with redirected care (i.e. where helpers
473 are typically failed breeders) is particularly relevant for black-throated tits.

474 **CONCLUSIONS**

475 Cooperative breeding systems provide fertile ground for investigations of adult
476 investment strategies. Our study of black-throated tits indicates that nestling begging
477 position and intensity, but not nestling sex, influence adult food distribution among
478 nestlings. More importantly, if begging position and intensity represent nestling
479 competitive ability and need, respectively, the results suggest that black-throated tit
480 adults adjust their preference for nestling competitive ability and need in relation to
481 their ability to provide food, which, in turn, depends on the presence of helpers and
482 brood size. The findings demonstrate the value of cooperative breeders as model
483 systems to investigate adaptive food allocation strategies, and also show that
484 context-specific food allocation strategies should be tested more widely in
485 non-cooperative species with variable brood size and hence variation in the need and
486 competition that individual nestlings experience.

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488 **submission)**

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687

688 **FIGURE LEGENDS**

689 **Figure 1** The relationship of nestling mass (\pm SE) with age and helper presence.

690 Nestling mass at a given age were the predicted values by the model in Table 2 while

691 setting other parameters to mean value. Differences in mass between nestlings from

692 nests with and without helpers were assessed with t-tests, with asterisk (*) and NS

693 indicating significant and non-significant differences, respectively. Numbers in bars

694 indicate sample sizes of nestlings and broods (in brackets).

695 **Figure 2** Comparisons of the effects of begging behaviors on predicted probability (\pm

696 SE) of a nestling being fed during each feeding event at nests with and without helpers

697 (A and B) and in large and small broods (C and D). Predicted values in A–C are from

698 the simplified model in Table 2 and those in D are obtained by re-adding the interaction

699 between begging intensity and brood size to the simplified model in Table 2; all other

700 explanatory variables in the model set to mean values. Lines depict the change of

701 relative preference for different begging position and intensity.

702 **Figure 3** Comparisons of the effects of nestling begging position (A) and intensity (B)

703 on predicted probability (\pm SE) of a nestling being fed during each feeding event by

704 different types of adults. Predicted values are from the model in Table 4 with all other

705 explanatory variables set to mean values. Lines depict the change of adults' relative

706 preference for different begging position and intensity.

707 **Figure 4** Comparisons of the interacting effects of begging position and brood size on

708 predicted probability (\pm SE) of a nestling being fed during each feeding event by

709 unhelped female parents (A), unhelped male parents (B), helped female parents (C),
710 helped male parents (D) and helpers (E). Lines depict the change of adults' relative
711 preference for different begging position in relation to brood size.

712 **Table 1 Summary of the results of linear mixed model analyses of factors affecting**
 713 **total and parental provisioning rates to the brood**

Response variable	Parental provisioning rates				Total provisioning rates			
Fixed effect	Estimate ± SE	df	F	P	Estimate ± SE	df	F	P
Helper presence ^a	-8.841 ± 1.605	1,38	30.3	<0.001		1,38	0.7	0.426
Brood size	2.346 ± 0.518	1,38	20.5	<0.001	2.293 ± 0.603	1,39	14.4	<0.001
Date	-0.266 ± 0.093	1,38	8.1	0.007	-0.273 ± 0.105	1,39	6.8	0.013
Brood age		1,37	1.0	0.327		1,38	0.5	0.489
Random effect	Estimate ± SE		z	P	Estimate ± SE		z	P
Year	16.148 ± 11.800		1.4	0.171	15.102 ± 13.081		1.2	0.248

714 ^aHelper absence is considered as the reference level. Estimates of coefficients are shown

715 for terms retained in the final model. Significant P-values are shown in bold.

716 **Table 2 Summary of the results of a linear mixed model analysis of factors**
 717 **affecting nestling mass**

Fixed effects		Estimate ± SE	df	F	P
Helper presence	Present	-2.223 ± 0.840	1,171	7.0	0.009
	Not [†]				
Nestling sex	Male	0.331 ± 0.026	1,814	164.1	<0.001
	Female [†]				
Nestling age		0.229 ± 0.071	1,171	10.9	0.001
Helper presence × nestling age	Present	0.202 ± 0.078	1,171	6.8	0.010
	Not [†]				
Brood size			1,181	0.9	0.358
Brood sex ratio			1,187	0.5	0.461
Nestling age ²			1,179	3.3	0.070
Date			1,180	1.8	0.183
Random effects		Estimate ± SE		z	P
Nest ID (year)		0.182 ± 0.023		8.0	<0.001

718 Nestling mass is treated as the response variable in the analysis. Terms shown on the
 719 top of table and with estimates of coefficients are those retained in the final model.
 720 Reference levels of categorical factors are indicated by the symbol †. Significant
 721 P-values are shown in bold. Interactions of helper presence with nestling age², nestling
 722 sex, brood size, brood sex ratio and date as well as interactions of brood size with
 723 nestling age, nestling age², nestling sex, brood size, brood sex ratio and date were also
 724 tested and were all significant (all P > 0.07).

725 **Table 3 Summary of the results of generalized linear mixed model analyses of**
 726 **factors affecting food allocation by black-throated tits**

Fixed effects		Estimate ± SE	df	F	P
Begging position	Close	3.002 ± 0.104	1,16217	3845.8	<0.001
	Far [†]				
Begging intensity	Strong	1.993 ± 0.112	1,16217	720.6	<0.001
	Weak [†]				
Helper presence	Present	0.194 ± 0.239	1,373	0.778	0.378
	Not [†]				
Brood size	Small	-0.157 ± 0.078	1,237	1.2	0.267
	Large [†]				
Helper presence × begging position	Present	-0.330 ± 0.110	1,16217	9.0	0.003
	Not [†]				
Helper presence × begging intensity	Present	0.342 ± 0.135	1,16217	6.4	0.011
	Not [†]				
Brood size × begging position	Small	-0.468 ± 0.105	1,16217	19.9	<0.001
	Large [†]				
Number of begging nestlings		-0.365 ± 0.027	1,10945	184.6	<0.001
Date			1,225	0.7	0.397
Brood age			1,673	0.2	0.653
Nestling sex			1,208	0.0	0.925
Nestling sex × begging position			1,16215	0.0	0.979
Nestling sex × begging intensity			1,16215	1.4	0.229
Nestling sex × helper presence			2,204	0.4	0.644
Nestling sex × brood size			1,204	0.8	0.359
Brood size × begging intensity			1,16216	3.2	0.074
Brood size × helper presence			1,206	0.9	0.340
Begging position × intensity			1,16216	3.1	0.076
Random effects		Estimate ± SE		z	P
Color mark		0.006 ± 0.009		0.7	0.472
Nestling ID (nest ID (year))		0.104 ± 0.024		4.3	<0.001

727 Whether a nestling was fed (1/0) during each feeding event is treated as the response
 728 variable in the analysis. Terms shown on the top of the table and with estimates of
 729 coefficients are those retained in the final model. Reference levels of categorical factors

730 are indicated by the symbol †. Significant P-values are shown in bold.

731 **Table 4 Summary of the results of a generalized linear mixed model analysis of**

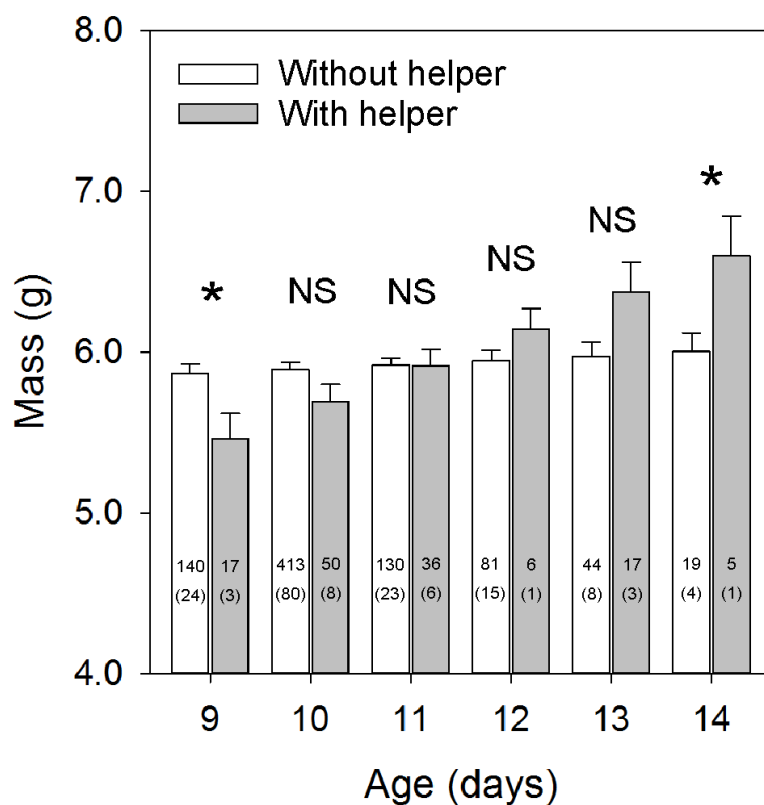
732 **adult food allocation rule during each feeding event**

Fixed effects		Estimate ± SE	df	F	P
Begging position	Close	3.382 ± 0.158	1,16208	3226.1	< 0.001
	Far [†]				
Begging intensity	Strong	2.264 ± 0.195	1,16208	629.7	< 0.001
	Helped female [†]				
Adult type	Unhelped male	0.194 ± 0.239	4,2479	1.3	0.257
	Unhelped female	0.026 ± 0.240			
	Helper	0.518 ± 0.277			
	Helped male	0.017 ± 0.288			
	Helped female [†]				
Brood size	Small	0.309 ± 0.096	1,237	1.2	0.271
	Large [†]				
Adult type × begging position	Unhelped male	0.260 ± 0.175	4,16208	4.0	0.003
	Unhelped female [*]	0.576 ± 0.177			
	Helper	0.038 ± 0.220			
	Helped male	0.216 ± 0.209			
	Helped female [†]				
Adult type × begging intensity	Unhelped male [*]	-0.602 ± 0.224	4,16208	2.7	0.031
	Unhelped female [*]	-0.620 ± 0.223			
	Helper [*]	-0.570 ± 0.269			
	Helped male	-0.228 ± 0.275			
	Helped female [†]				
Brood size × begging position	Small	-0.466 ± 0.105	1,16208	19.6	< 0.001
	Large [†]				
Number of begging nestlings		-0.365 ± 0.027	1,11451	183.6	< 0.001
Random effects		Estimate ± SE		z	P
Color mark		0.006 ± 0.009		0.7	0.460
Nestling ID (nest ID (year))		0.103 ± 0.024		4.2	< 0.001

733 Whether a nestling was fed (1/0) during each feeding event is treated as the response

734 variable in the analysis. The model was obtained by replacing breeding type in the final

735 model of Table 3 with adult type. Significant P-values are shown in bold. Reference
736 levels of categorical factors are indicated by the symbol †. The asterisk (*) following a
737 category of adult indicates that the category is significantly different from the reference
738 level (i.e. helped female parent) assessed by a t-test.



739

740 **Figure 1** The relationship of nestling mass (\pm SE) with age and helper presence.

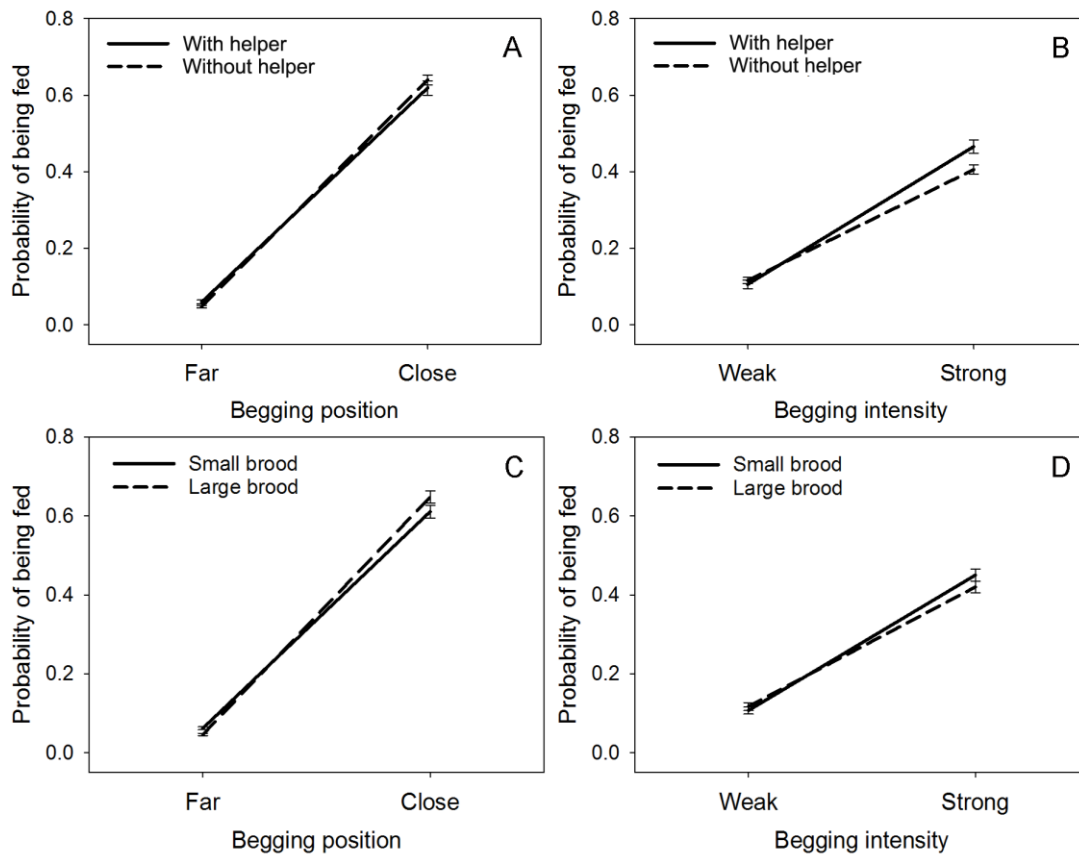
741 Nestling mass at a given age were the predicted values by the model in Table 2 while

742 setting other parameters to mean value. Differences in mass between nestlings from

743 nests with and without helpers were assessed with t-tests, with asterisk (*) and NS

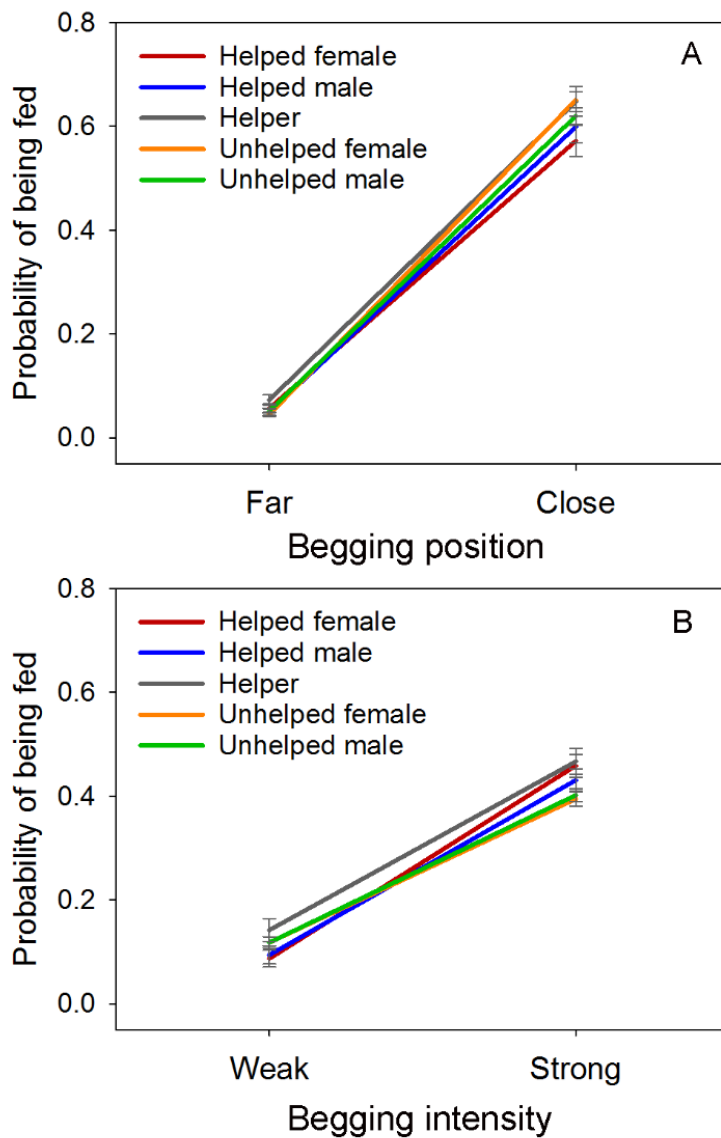
744 indicating significant and non-significant differences, respectively. Numbers in bars

745 indicate sample sizes of nestlings and broods (in brackets).

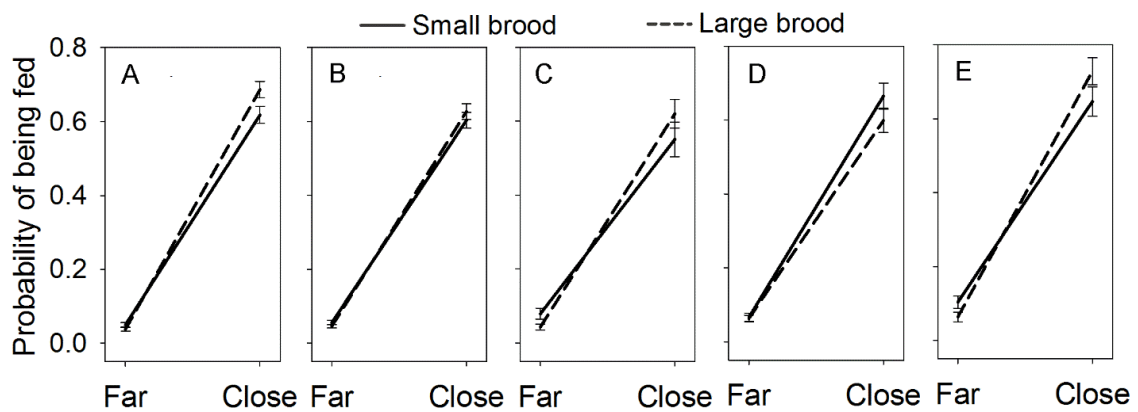


746

747 **Figure 2** Comparisons of the effects of begging behaviors on predicted probability (\pm
748 SE) of a nestling being fed during each feeding event at nests with and without helpers
749 (A and B) and in large and small broods (C and D). Predicted values in A–C are from
750 the simplified model in Table 3 and those in D are obtained by re-adding the interaction
751 between begging intensity and brood size to the simplified model in Table 3; all other
752 explanatory variables in the model set to mean values. Lines depict the change of
753 relative preference for different begging position and intensity.



754 **Figure 3** Comparisons of the effects of nestling begging position (A) and intensity (B)
 755 on predicted probability (\pm SE) of a nestling being fed during each feeding event by
 756 different types of adults. Predicted values are from the model in Table 4 with all other
 757 explanatory variables set to mean values. Lines depict the change of adults' relative
 758 preference for different begging position and intensity.



759 **Figure 4** Comparisons of the interacting effects of begging position and brood size on
 760 predicted probability (\pm SE) of a nestling being fed during each feeding event by
 761 unhelped female parents (A), unhelped male parents (B), helped female parents (C),
 762 helped male parents (D) and helpers (E). Lines depict the change of adults' relative
 763 preference for different begging position in relation to brood size.