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## **LAY SUMMARY**

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

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

## **RUNNING TITLE**

Food distribution among offspring in black-throated tits

## **ABSTRACT**

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

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

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

## INTRODUCTION

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

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

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

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

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

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

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

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

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

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

## **MATERIALS AND METHODS**

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

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

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

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

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

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

## **Molecular sexing and paternity assignment**

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

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

### **Data collection from videos**

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

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

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

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

## **Statistical analysis**

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

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

To explore factors affecting nestling body mass we used a LMM with a Gaussian distribution, in which nestling mass was treated as the response variable, helper presence, brood size, brood age, brood age<sup>2</sup>, brood sex ratio, nestling sex, date and the two-way interactions of these variables as explanatory variables, and nest ID nested within year as random factors. The dataset for this analysis comprised 827 nestlings from 154 unhelped nests and 131 nestlings from 22 helped nests, measured between 2008 and 2017.

#### Factors affect adult food allocation among nestlings

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

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

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

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

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

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

## RESULTS

### Effect of helpers on nestling provisioning rates and body mass

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

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

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

### **Adult food allocation behaviors**

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

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

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

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

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

## DISCUSSION

We have shown that black-throated tit parents adopt a compensatory reduction strategy (Hatchwell 1999) when helped, reducing their own care relative to nests without helpers. The body mass of nestling black-throated tits increased faster in helped broods than in unhelped broods, as reported in other cooperatively breeding species (e.g. MacColl and Hatchwell 2002; Ren et al. 2016), suggesting that nestlings benefit from the care that helpers provide. The total provisioning rate at helped nests was higher than at unhelped nests, although not significantly, but it may be that adults with helpers were more able to satisfy the increasing need of nestlings with age because of their lower investment. In the congeneric long-tailed tit (*A. caudatus*), parents reduced investment when assisted by one helper, but maintained their investment with more helpers (Hatchwell and Russell 1996; MacColl and Hatchwell 2003). The majority (11 out of 13) of the helped nests in this study had only one helper, so our results are consistent with those for long-tailed tits. Intriguingly, our results also suggest that nestlings at nests with helpers were initially lighter but caught up with and exceeded the mass of nestlings at nests without helpers (Figure 4). Whether this is because helpers preferentially care for lighter broods, or because parents invest less in broods when care from helpers is anticipated (Russell et al. 2007) remains unknown and would warrant further investigation.

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

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

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

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

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

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

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

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

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

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

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

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

## CONCLUSIONS

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

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## FIGURE LEGENDS

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

Nestling mass at a given age were the predicted values by the model in Table 2 while setting other parameters to mean value. Differences in mass between nestlings from nests with and without helpers were assessed with *t*-tests, with asterisk (\*) and NS indicating significant and non-significant differences, respectively. Numbers in bars indicate sample sizes of nestlings and broods (in brackets).

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

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

**Figure 4** Comparisons of the interacting effects of begging position and brood size on 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	<i>F</i>	<i>P</i>	Estimate ± SE	df	<i>F</i>	<i>P</i>
Helper presence <sup>a</sup>	-8.841 ± 1.605	1,38	30.3	<b>&lt;0.001</b>		1,38	0.7	0.426
Brood size	2.346 ± 0.518	1,38	20.5	<b>&lt;0.001</b>	2.293 ± 0.603	1,39	14.4	<b>&lt;0.001</b>
Date	-0.266 ± 0.093	1,38	8.1	<b>0.007</b>	-0.273 ± 0.105	1,39	6.8	<b>0.013</b>
Brood age		1,37	1.0	0.327		1,38	0.5	0.489
Random effect	Estimate ± SE		<i>z</i>	<i>P</i>	Estimate ± SE		<i>z</i>	<i>P</i>
Year	16.148 ± 11.800		1.4	0.171	15.102 ± 13.081		1.2	0.248

714 <sup>a</sup>Helper 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.

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

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

Nestling mass is treated as the response variable in the analysis. Terms shown on the top of table and with estimates of coefficients are those retained in the final model. Reference levels of categorical factors are indicated by the symbol <sup>†</sup>. Significant *P*-values are shown in bold. Interactions of helper presence with nestling age<sup>2</sup>, nestling sex, brood size, brood sex ratio and date as well as interactions of brood size with nestling age, nestling age<sup>2</sup>, nestling sex, brood size, brood sex ratio and date were also tested and were all significant (all *P* > 0.07).

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

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

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

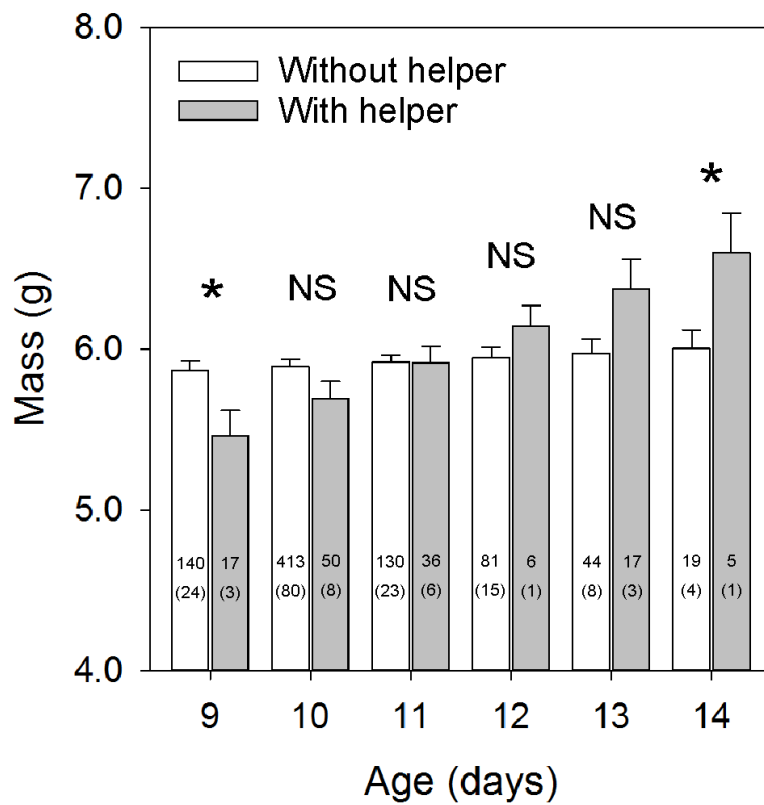
730 are indicated by the symbol †. Significant *P*-values are shown in bold.

731 **Table 4 Summary of the results of a generalized linear mixed model analysis of**  
732 **adult food allocation rule during each feeding event**

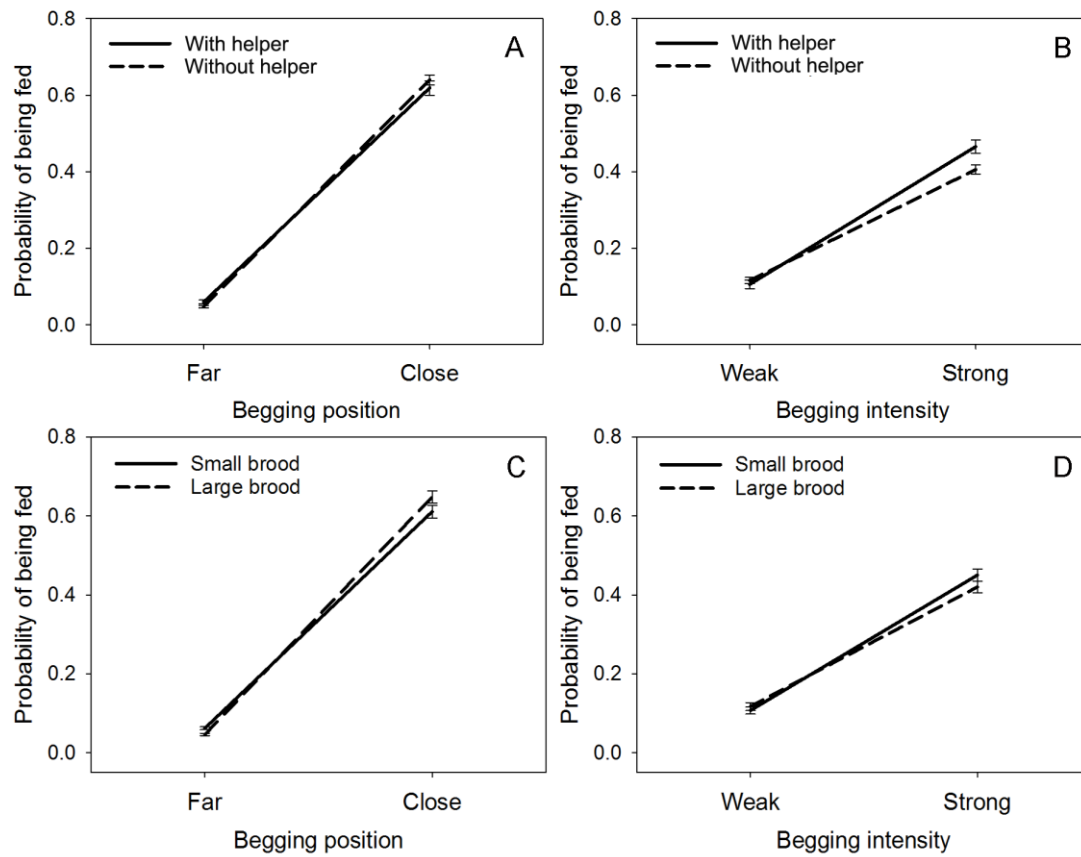
Fixed effects		Estimate $\pm$ SE	df	<i>F</i>	<i>P</i>
Begging position	Close	3.382 $\pm$ 0.158	1,16208	3226.1	<b>&lt;0.001</b>
	Far <sup>†</sup>				
Begging intensity	Strong	2.264 $\pm$ 0.195	1,16208	629.7	<b>&lt;0.001</b>
	Helped female <sup>†</sup>				
Adult type	Unhelped male	0.194 $\pm$ 0.239	4,2479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

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

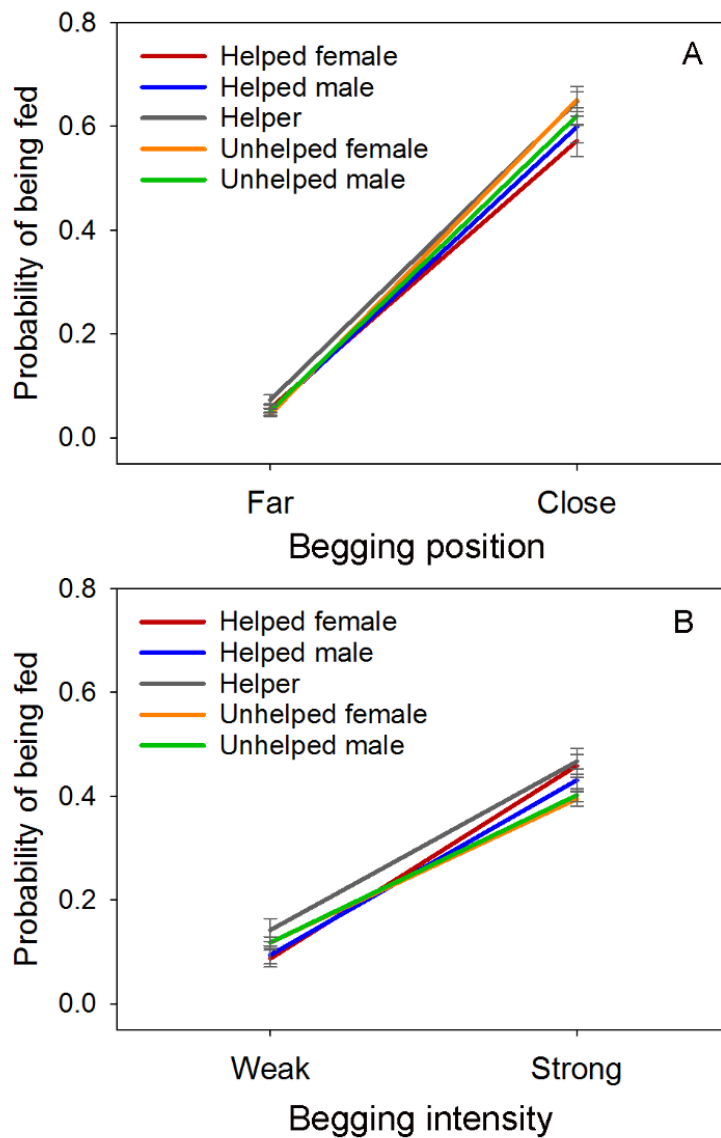
735 model of Table 3 with adult type. Significant *P*-values are shown in bold. Reference  
736 levels of categorical factors are indicated by the symbol †. The asterisk (\*) following a  
737 category of adult indicates that the category is significantly different from the reference  
738 level (i.e.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



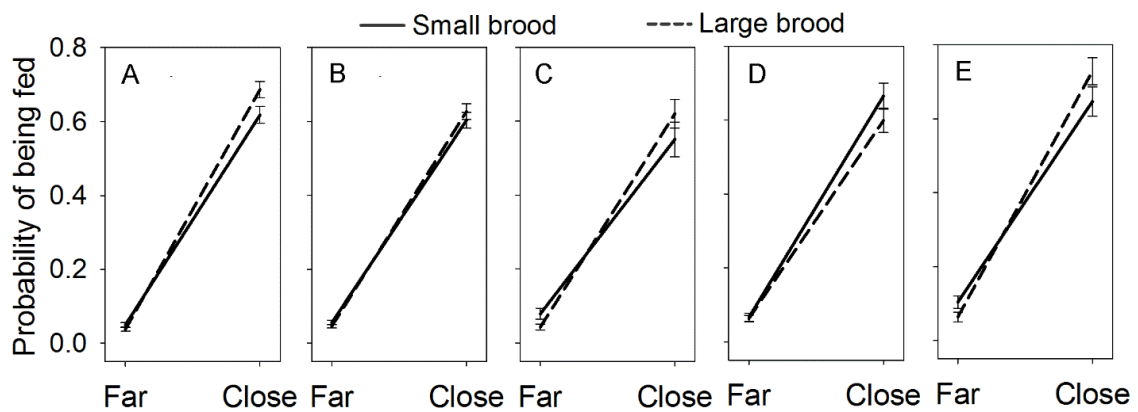
**Figure 1** The relationship of nestling mass ( $\pm$  SE) with age and helper presence. Nestling mass at a given age were the predicted values by the model in Table 2 while setting other parameters to mean value. Differences in mass between nestlings from nests with and without helpers were assessed with *t*-tests, with asterisk (\*) and NS indicating significant and non-significant differences, respectively. Numbers in bars indicate sample sizes of nestlings and broods (in brackets).



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



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



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