Begging and feeding responses vary with relatedness and sex of provisioners in a cooperative breeder

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ARTICLE INFO

Begging behaviour can provide information on offspring hunger levels and be used by parents to adjust food provisioning efforts. In cooperative breeders, helpers also provide care by feeding the young. However, how helpers of different sex and relatedness to the offspring respond to begging behaviour has rarely been studied in cooperatively breeding species, which limits our understanding of the indirect and/or direct benefits that helpers may obtain by responding to offspring demand. Here, we used a cooperatively breeding bird, the sociable weaver, *Philetairus socius*, to investigate how nest intervisit intervals of breeders and different types of helpers, distinguished by sex and relatedness, varied with acoustic begging. Moreover, we tested whether these different classes of provisioners experienced distinct levels of begging. Our results show that only breeding males, but not breeding females or helpers of any sex and relatedness to the nestlings, returned faster to the nest to feed after experiencing more begging calls. When contrasted directly, we confirmed a statistically supported difference in responses to begging between male and female breeders. Surprisingly, second-order relatives experienced more begging calls than the other classes of more related helpers and breeders. These results show that we might find differences in how provisioners respond to begging levels when classifying group members according to their potential fitness gains. In sociable weavers, the benefits and costs of adjusting feeding efforts to begging seem to differ with sex and life history stage. Experimental and more detailed investigations on begging–feeding interactions are necessary to understand the origin and prevalence of these differences across cooperatively breeding systems.
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When offspring depend on food provisioning from breeders, parent–offspring communication signals are crucial to maximize the fitness of parents and their progeny (Trivers, 1974). Food demand through begging displays influences parental provisioning and thus it has been central in the study of parent–offspring interactions (Kilner & Johnstone, 1997). Begging has been described across taxa and usually involves the performance of visual and/or acoustic displays (e.g. birds: Wright and Leonard 2002; mammals:

Brotherton, 2001; insects: Mas and Kölliker 2008; amphibians: Yoshioka et al. 2016). In birds, nestlings extend their body and may display brightly coloured gapes, while repeatedly performing acoustic begging calls (Kilner, 2002b). Several studies have shown that begging can contain information about offspring hunger levels (Brotherton, 2001; Leonard & Horn, 2001a; Yoshioka et al., 2016). In food deprivation experiments, nestlings were seen to increase begging rate and duration (Leonard & Horn, 2001a; Ogawa et al., 2015; Sacchi, 2002). The relationship between begging intensity and hunger levels supports the hypothesis that begging is an honest signal of nestlings' need (Kilner and Johnstone 1997; Fresneau et al. 2018; but see Mock et al., 2011; Royle et al., 2002). In

addition, studies reporting growth and immunity costs associated with exaggerated begging suggest that these displays may be costly and condition dependent (Moreno-Rueda & Redondo, 2011, 2012).

Parents, accordingly, seem responsive to increases in offspring demand. Breeders were found to increase feeding behaviour in response to increased begging rate and duration in several biparental care systems (Bowers et al., 2019; Leonard & Horn, 1996, 2001b; Ottosson et al., 1997). Recognizing honest and condition-dependent signals of hunger may allow parents to provide care when it is most needed (Grodzinski & Lotem, 2007), while avoiding exploitation from the offspring (Godfray, 1991; Kilner & Johnstone, 1997).

Males and females can provide distinct levels of care and, in some species, only one sex is found to respond to begging (reviewed in Müller et al. 2007). For instance, in great tits, *Parus major*, male breeders increased feeding in response to begging while females did not (Tanner et al., 2008). In another study using begging playbacks in superb fairy-wrens, *Malurus cyaneus*, breeding males but not females increased food provisioning (MacGregor & Cockburn, 2002). In contrast, responses to begging intensity from breeding females but not males have been also been detected, for example in canaries, *Serinus canaria* (Kilner, 2002a) and in Manx shearwaters, *Puffinus puffinus* (Quillfeldt et al., 2004). These discrepancies between the sexes are often explained by the trade-off between parental care and other sex-specific costs of reproduction (e.g. gamete production or investing in attracting mates; Siefferman and Hill 2008). Therefore, the sexes may have different investment optimums, defined by the fitness benefits and costs of responding to begging stimuli.

In cooperatively breeding systems, 'helpers' cooperate with the breeders to provide food to the young. By providing care to offspring that are not their own, helpers can also experience different benefits and costs than breeders and may hence have evolved distinct food allocation strategies. When helpers share kin relationships with the offspring, the costs of helping may be compensated by indirect fitness gains (Green et al., 2016; Hamilton, 1964). Indirect benefits are greater for individuals with higher levels of relatedness to the recipients of help, which could explain why, in some cases, helpers that are more closely related to the offspring provision at higher rates than less related individuals (Barati et al., 2018; Green et al., 2016; Griffin & West, 2003; Nam et al., 2010; Wright et al., 2010; but see Kay et al. 2020). Breeders' and helpers' responses to offspring needs have been studied in several cooperatively breeding species, and most studies have found that helpers, like parents, increase their feeding effort when offspring demand is higher (see Table 1). Interestingly, experimental manipulations of begging caused parents and helpers to increase provisioning in Arabian babblers, *Turdoides squamiceps* (Wright, 1998), where most helpers are highly related to the offspring, but also in red-winged fairy wrens, *Malurus elegans* (MacLeod & Brouwer, 2018) and bell miners, *Manorina melanophrys* (McDonald et al., 2009), where groups often include less related individuals. It is often the case that these distinct types of helpers are present within species, which provides a good opportunity to understand which indirect and/or direct fitness benefits may explain helpers' responses to offspring demand for food. Specifically, helpers' response can be expected to vary proportionally to the degree of indirect fitness benefits they will obtain from maximizing their relatives' survival (Emlen & Wrege, 1988; Komdeur, 1994; Nam et al., 2010). Furthermore, in cooperative systems, different sexes usually have distinct

Table 1

Qualitative summary of results from studies on food provisioning adjustments to increasing food demand in cooperatively breeding species (measured as responses to begging behaviour, offspring age or offspring number)

Offspring demand measure	Breeders responded	Helpers responded	Helpers of both sexes responded	Helpers of different relatedness responded	Species	Source
Begging	**Yes**	**Yes**	**Yes**	–	Arabian babbler, *Turdoides squamiceps*	Wright (1998)
Begging	Only males	Yes	–	–	Superb fairy-wren, *Malurus cyaneus*	MacGregor and Cockburn (2002)
Begging	**Yes**	**Yes**	**Yes**	–	Meerkat, *Suricata suricatta*	English et al. (2008)
Begging	Yes[a]	**Yes**	–	–	Bell miner, *Manorina melanophrys*	McDonald et al. (2009)
Begging	Yes	Yes	Yes	Yes	Bell miner, *M. melanophrys*	Wright et al. (2010)
Begging	Yes	Yes	**Yes**	–	Red-winged fairy-wren, *Malurus elegans*	MacLeod and Brouwer (2018)
Begging	**Yes**	**B>H**	–	–	Black-throated tit, *Aegithalos concinnus*	Li et al. (2019)
Age	Yes	**B>H**	–	**Yes**	Bell miner, *M. melanophrys*	te Marvelde et al. (2009)
Age	Yes	Yes	–	–	Chestnut-crowned babbler, *Pomatostomus ruficeps*	Browning et al. (2012)
Age	**F>M**	**B>H**	–	–	Long-tailed tit, *Aegithalos caudatus*	MacColl and Hatchwell (2003)
Age	**F>M**	Yes	–	**Only related**[b]	Iberian magpie, *Cyanopica cooki*	Cruz et al. (2019)
Number nestlings	Yes	Yes	Yes	–	Acorn woodpecker, *Melanerpes formicivorus*	Koenig and Walters (2012)
Number nestlings	**Yes**	**Yes**	–	–	Long-tailed tit, *Aegithalos caudatus*	MacColl and Hatchwell (2003)
Number nestlings	Yes	Yes	–	**Yes**	Iberian magpie, *Cyanopica cooki*	Cruz et al. (2019)

Columns show whether individuals of different classes (breeders B versus helpers H) and, where available, sex (females F versus males M) and relatedness, responded to increasing food demand levels. Dashes represent untested variables. Values are in bold when differences within the class were statistically tested for and, when detected, differences are described (in the 'Helpers responded' column, values are bold if differences between breeders' and helpers' responses were tested for).

[a] Only breeding males were tested.

[b] Relatedness was not explicitly tested. Helpers were divided into 'first-option' or 'failed breeders' and relatedness was extrapolated (first-option usually related, failed breeders usually not).

reproductive strategies, with one sex dispersing to breed and the other being philopatric (Koenig & Haydock, 2004). The philopatric sex should benefit more from increasing the survival chances of the offspring, since young are often recruited as new group members (Clutton-Brock et al., 2002). Therefore, if helpers respond to offspring demand to obtain direct fitness benefits through group augmentation (group augmentation hypothesis; Kokko et al., 2001), we can expect philopatric helpers to match feeding effort to offspring demand more strongly than the dispersing sex. How helpers of different sex and relatedness respond to offspring demand, and specifically to begging behaviour, has rarely been assessed within species (see Table 1). Among these studies, even fewer have estimated whether food provisioning responses from the different group members differ statistically (see Table 1), which is essential if one wants to study whether and how the feeding rules of the distinct classes of individuals vary. This has resulted in scarce evidence for feeding adjustments among helpers of different sex and relatedness levels to the offspring (Table 1).

Since breeders' and helpers' feeding rules can differ, begging behaviour may in turn vary according to the class and contributions of each individual (Bell, 2008b). In biparental care systems, begging is often preferentially directed towards the breeder that provides more food (Dickens et al., 2008; Kölliker et al., 1998; Paquet et al., 2018). In cooperative breeders, a study on bell miners reported that female breeders, which brought the largest food loads, experienced higher levels of brood begging than breeding males and helpers (Wright et al., 2010). Additional indication that the composition of breeding groups might affect begging behaviour was found in sociable weavers, *Philetairus socius*, where nestlings raised with more helpers were seen to beg less (Paquet, Covas, et al., 2015). Whether this effect was due to a larger number of individuals providing food or to lower begging rates towards helpers than towards breeders is unknown. Offspring could be saving energy by begging less towards individuals that bring less food or that respond less to this stimulus (Bell, 2008a; Kölliker et al., 1998; Paquet et al., 2018). Detailed studies on how begging behaviour varies in relation to male and female breeders, and among different types of helpers, are needed for a better understanding of the coevolution between offspring begging and adaptive food provisioning strategies in cooperative breeders.

Here, we investigated (1) how intervisit intervals of breeders and helpers, distinguished by sex and relatedness to the offspring, varied with brood begging. Furthermore, we quantified (2) the levels of acoustic begging experienced by the breeders and each class of helpers. Importantly, in both (1) and (2), we specifically tested for statistically supported differences between distinct classes of provisioners. Our study model is the sociable weaver, a cooperatively breeding passerine. In this species, there is no evidence of extrapair paternity (Paquet, Doutrelant, et al., 2015) and helpers are typically the offspring of one or both breeders (Covas et al., 2006). Other second-order relatives and distantly related/unrelated birds also provide help (Covas et al., 2006). Moreover, helpers are of both sexes, but males and females have different strategies to obtain a breeding position, as most females disperse to breed, whereas males typically remain in their natal colonies (Covas et al., 2006; Doutrelant et al., 2004; van Dijk et al., 2015). These life history traits lead to different predictions on begging–feeding interactions according to sex and kinship.

We expected (1a) breeders and male helpers to reduce the time between feeding events with increasing begging levels, and more strongly than female helpers which disperse to breed. (1b) For intervisit intervals of helpers distinguished by their relatedness

levels to the brood, we had different but nonmutually exclusive predictions according to the types of benefits that helpers can gain. If helpers benefit from responding to brood demand mostly through indirect fitness benefits, we expected full siblings ($r = 0.5$) to shorten intervisit intervals when brood demand is higher, and more so than second-order relatives ($r = 0.25$), and that unrelated individuals (or distant relatives, $r \leq 0.125$) would not respond. If individuals are feeding chicks exclusively as a 'payment' to be part of the group (Zöttl et al., 2013), we expected helpers to feed at rates that are independent of brood begging, as these direct benefits do not depend on maximizing offspring survival. However, if less related individuals provide care because they benefit as well from increasing offspring chances of survival (e.g. increasing group size; group augmentation hypothesis; Kokko et al., 2001), all relatedness classes of helpers are expected to adjust feeding efforts to begging intensity.

Accordingly, nestlings' begging was expected to be higher towards the individuals that respond the most to this stimulus. Since nest attendants produce calls before entering the nests, sociable weaver's chicks could use this information to distinguish their different care provisioners (Beer, 1971; Jacot et al., 2010; McDonald & Wright, 2011). Therefore, in line with our predictions on feeding adjustments, (2a) offspring should beg more towards breeders and male helpers than female helpers and (2b) when comparing differently related helpers, lower levels of begging were expected towards less related individuals.

METHODS

Study Species and Site

The sociable weaver is a colonial, cooperatively breeding passerine endemic to southern Africa (Maclean, 1973a). These weavers build massive communal nests, or 'colonies', with several chambers where they breed and roost throughout the year (Maclean, 1973b). Adults feed on both seeds and arthropods (Maclean, 1973d) but offspring are mainly fed with the latter (e.g. small insect larvae, termites, spiders and grasshoppers; Maclean, 1973d). Breeding seasons can last for several months (Mares et al., 2017) and sociable weavers may thus have numerous breeding attempts per season. Clutch size typically ranges between two and four eggs and females usually lay one egg per day (Covas & Du Plessis, 2005; Fortuna et al., 2021). The duration of the incubation period is around 15 days and both sexes incubate (Covas & Du Plessis, 2005; Maclean, 1973c). Nestlings normally hatch asynchronously and the subsequent nestling period lasts for 21–25 days (Covas & Du Plessis, 2005; Maclean, 1973c).

This work was conducted at Benfontein Nature Reserve in Northern Cape Province, South Africa (28°520S, 24°500E). Individuals have been captured once or twice per year at the colonies using mist nests since 1999 (Covas, 2002). Birds were ringed with a uniquely coded aluminium ring and a unique colour ring combination, allowing individual visual identification. Blood samples were collected for genetic sexing and determination of parentage relationships. In this population, most helpers are previous years' offspring of one or both breeders (Covas et al., 2006; this study) and assist with nestling feeding (Covas et al., 2008), nest building and sanitation (Ferreira, 2015). Males usually help until later in life than females, and are the most frequent helping sex (Covas et al., 2006; see below).

Data Collection

We sampled 14 different colonies in two breeding seasons, 2014/2015 and 2017/2018, between September and January. Brood

begging behaviour was recorded 4 and 9 days after the first nestling hatched (hereafter, day 4 and day 9, respectively), to study whether begging and/or provisioning adjustments changed throughout the nestling period (Leonard & Horn, 2006; Schwabl & Lipar, 2002).

Before each recording, chicks were weighed, a tie-clip microphone (Olympus ME15, frequency response = 100—12 000 Hz) was set at the nest entrance and a recorder (Olympus WS-750M) was placed outside the nest, attached to the colony structure. Calls were recorded at 44.1 kHz in uncompressed 32-bit PCM format.

To identify the birds entering the nests, and to score individual feeding intervals, a video camera (Sony Handycam HD) was placed on a tripod under the colony pointing to the entry of the target nest. Nests were recorded for 2—5 h.

Nestlings' head feathers were marked at hatching to enable individual recognition until day 9, when they were ringed with a unique numbered ring (Covas et al., 2008). Daily maximum temperature ($°C$) was collected at Kimberley Airport Station, 12 km from the centre of the study site.

Data Analyses

Number of begging calls

Acoustic begging levels were quantified as the number of begging calls during the first 20 s after a bird's arrival at the nest. This measure was extracted at day 4 for 22 broods in 2014/2015 and for 32 broods in 2017/2018. A 20 s duration was defined for each begging 'event' after visually assessing that acoustic begging tends to decline after this period. Begging was not quantified if another bird arrived during those 20 s, or if the provisioner spent less than 20 s inside the chamber ($N = 362$ excluded events, 17%). Begging was not quantified for nonfeeding visits (see below). The first begging event recorded for each nest was excluded from the analyses since hunger levels, and thus possibly begging behaviour, could have been influenced by the time necessary to set up the recorders. We only quantified begging when there was a sufficient signal-to-noise ratio to allow reliable counts (visually assessed; 12% of the events were not quantified because other birds or cicadas were calling too loudly or repeatedly in the background; $N = 255$ from 41 recordings).

Begging calls were counted manually in 2014/2015 and with a semiautomatic method in 2017/2018. The Pearson correlation coefficient of the counted number of begging calls between two people scoring manually was 0.98 (95% confidence interval, CI = [0.92,0.99]; $N = 12$ randomly chosen events from four different nests) and the correlation coefficient between manual scoring and semiautomatic scoring was 0.94 (95% CI = [0.81,0.98]; $N = 12$). The manual counting method consisted of visually marking and counting each begging call on spectrograms of the recordings (sampling frequency = 44.1 kHz, FFT length = 512 points, window = Hamming), using Avisoft-SASLab PRO v. 5.2.09 (Avisoft Bioacoustics, Berlin, Germany). A final sample of 688 begging events was quantified manually.

The semiautomatic counting method was performed in three steps. First, we removed background noise from the recordings, applying a high-pass filter that filtered frequencies below 2000 Hz, with a roll-off of 36 dB (see Fig. A1a, b) in Audacity v.2.3.2 (https://www.audacityteam.org/; Audacity Team, 2019). Moreover, on events with high background cicada noise, we band-pass filtered the recording, excluding frequencies between ca. 5000—6000 Hz (precise range defined after visual inspection; see Fig. A1c, d). Second, we cut recordings into short wave files, by only retaining sounds above a manually set amplitude threshold constant for all

wave files (using a custom-made software; Maat et al. 2014). This allowed us to separate each over-threshold sound (i.e. begging or other calls) and extract its onset time from the recording's start, enabling its posterior attribution to each bird visit. Third, each begging call contained in the short wave files was automatically identified in Sound Explorer (available at https://github.com/ornith; Maat et al., 2014). Since over-threshold sounds can include adult bird calls, and because begging calls that overlap can sometimes be cut together, all automatically selected sounds were visually assessed and excluded when needed. Finally, we counted the calls relative to each begging event, crossing the timing information of the video recording and the sound files. A final sample of 845 events were analysed with the semiautomatic method, making a total sample of 1533 begging events analysed with the two methods. All begging measurements were done blindly from the identity of the provisioning bird.

At day 9, the sample of recordings for which we could extract acoustic begging information was substantially smaller than at day 4. The acoustic features of older broods' begging did not allow us to distinguish single calls (see Fig. A1e) and thus to count them manually or automatically. We therefore used an alternative acoustic measure that was correlated with number of begging calls, the proportion of time spent begging (see Appendix). As this measure depended on amplitude envelopes, it could only be reliably quantified for 45% of the day 9 begging events (see Appendix). Consequently, we consider any findings for older broods only preliminary, owing to high uncertainty levels for the effect sizes, but all methods and results can be found in the Appendix.

Intervisit intervals and proxy of brood hunger

Intervisit intervals were used to measure birds' feeding responses and were defined as the time (s) each bird took to come back to the nest to feed again. This measure was scored from videos, for 1380 of the 1533 events for which number of begging calls was quantified (i.e. for the last recorded visit of each bird, begging was quantified but time to return after that event is unknown). To have a proxy of broods' hunger levels, we also estimated the time (s) between two feeding events ('interval last fed'), regardless of the birds' identity. Feeding visits were distinguished from visits for other purposes (such as building or sanitation) whenever possible. For each nest, group size was calculated as the number of different birds seen feeding the nestlings during each recording. Unringed birds were also included in group size estimates (found in two nests and counted as one more bird). Intervisit intervals and begging experienced by unringed birds were not analysed.

Sex, role and relatedness category attribution

Sex was genetically determined from blood samples (Paquet, Doutrelant, et al., 2015). After group identification, we attributed breeder or helper roles to each individual. Breeding pairs were determined by a combination of genetic analyses from blood samples (Paquet, Doutrelant, et al., 2015) and field data (Silva et al., 2018; there is no evidence of extrapair paternity in this species; Covas et al., 2006; Paquet, Doutrelant, et al. 2015). Individual genotypes were used to genetically identify the parents of nestlings and nest attendants using full-likelihood parentage inference (Fortuna et al., 2021; Paquet, Doutrelant, et al., 2015). When no genetic data were available, we defined rules to determine parentage based on the birds' biology (e.g. the only birds in the group old enough to breed, etc.; for all details on parentage attribution see supporting information in Fortuna et al., 2021). All

individuals seen feeding that were not the breeders were considered helpers. In nests where one of the breeders was unknown, remaining birds could still be considered helpers if they were of the same sex as the known breeder.

We further categorized helpers by their level of relatedness to the brood: 0.5 (full siblings), 0.25 (half siblings/uncles/grandparents) or 0.125 or less (cousins, half uncles or more distantly/unrelated individuals). These kinship categories were attributed based on the parentage analyses described above, by identifying the helpers' and breeders' parents using an extensive database of individual genotypes and video recordings that allowed parentage inferences. Helpers with the same parents as the current brood (full siblings) were included in the $r = 0.5$ category and helpers with only one parent in common with the current brood (half siblings) were included in the $r = 0.25$ category. Helpers with the same parents as one of the target nest's breeders (i.e. uncles of the brood) and helpers that were parents of one of the target nest's breeders (grandparents) were also included in the $r = 0.25$ category. Helpers that shared only one parent with one of the target nest's breeders (half uncles) and helpers that were the offspring of siblings of one of the target nest's breeders (cousins of the chicks) were included in the $r \leq 0.125$ category. One helper with no known (close) relationship to the chicks was attributed to the $r \leq 0.125$ category after ruling out all possible relationships with $r \geq 0.25$, except being uncle from the mother's side since this type of helper has never been recorded in our population ($N = 474$ kin relationships; A.C. Ferreira, personal communication, 7 August 2021) as a result of female breeders being mostly immigrants and helpers mostly resident birds (Doutrelant et al., 2004).

Among the sample of helpers, there were previously cross-fostered birds that were placed as eggs into a new nest under experimental conditions (Paquet, Doutrelant, et al., 2015) during previous seasons and hatched in the presence of their foster parents. Some of them were found among our data as helpers of the breeding pairs ($N = 8$) and we attributed these to their social relatedness category. However, statistical analyses were also performed in a subset excluding these individuals, and estimates yield qualitatively similar results but with higher uncertainty for helper classes due to sample size reduction.

From the 54 nests sampled, 13% (seven nests) had no helpers. Cooperative groups included more male helpers than female helpers (71% males, 46 of 65 helpers). Around 59% of the helpers were attributed to the $r = 0.5$ category (38 of 64 helpers with known relatedness), 37.5% to the $r = 0.25$ category and only 3–5% of the helpers included in the analyses (depending on the data set) were attributed to the relatedness category of $r \leq 0.125$. The low sample of $r \leq 0.125$ helpers did not allow us to reliably compare the feeding response of these birds in relation to other bird classes, but all estimates are presented in the results.

Statistical Analysis

All statistical analyses were performed in a Bayesian framework using JAGS through the 'rjags' package v.4.10 (Plummer, 2019) in R v.4.0.4 (R Core Team, 2021).

To test whether some classes of birds came back faster than others after being exposed to more begging, we built linear mixed models with intervisit intervals (log scaled) as a response variable and estimated the slope between intervisit intervals and number of begging calls for each bird class. Comparisons between classes were calculated by computing the difference between their estimated slopes (see below). To define the classes, we included the

interaction between social role (breeder/helper) and sex (female/male) of each bird. For helpers only, we further tested the effect of their relatedness towards the brood (as categories: $r = 0.5$, $r = 0.25$ or $r \leq 0.125$). We expected sex to have a similar effect for all helpers independently of their relatedness, and we thus did not test for this interaction. Number of nestlings and mean brood mass were included to account for increased provisioning in larger broods and to control for nestlings' condition. To avoid excluding 26 data points (one nest) because of unknown values for mean brood mass, we estimated the missing information (with high uncertainty) within the model using brood mass as response variable following a normal distribution and the observed mean brood mass as mean prior (5.670 g) and a prior variance of 1000 (see Chapter 15 in McElreath, 2020 for more details). This was done for all models that included this variable. A similar step was done for all data sets with individuals with unknown role ($N = 7$) and/or unknown relatedness to the offspring ($N = 8$). We estimated the missing information on individual roles (breeder versus helper) using a Bernoulli distribution and a uniform prior bounded between 0 and 1. Relatedness class was estimated with a categorical distribution and the prior probabilities of belonging to each relatedness category were defined using a Dirichlet distribution, the joint distribution of independent gamma variables divided by their sum, to keep the probabilities bounded between 0 and 1 and summing to 1 (Kéry & Schaub, 2012). Here, we used the information on whether birds were known not to be full siblings of the brood, in which case their probability of being $r = 0.5$ was set to zero and the prior probability of belonging to the $r = 0.25$ class was set as a uniform distribution bounded between 0 and 1 and defined as 1 minus the probability of belonging to the $r \leq 0.125$ class. Daily maximum temperature (°C) and time since sunrise were also included in the models to account for weather effects on food availability and birds' foraging efficiency (du Plessis et al., 2012). We additionally included group size, as individuals' feeding effort may be reduced when breeding with more helpers (i.e. 'load lightening'; Johnstone, 2011; Brouwer et al. 2014; MacLeod and Brouwer 2018). However, additive care may instead be expected when the chances of nestling starvation are higher (Hatchwell, 1999; but see MacLeod and Brouwer 2018) and we thus predicted load lightening to occur at lower begging levels. Therefore, we included group size in interaction with number of begging calls. To control for repeated visits of the same birds and different feeding visits to the same nest, we added bird and nest identity, as well as colony identity, as crossed random effects. We treated breeding season as a fixed effect of two levels (2014/2015 and 2017/2018; results with season as random effect were nearly identical).

Similarly, to test whether birds of different classes experienced distinct begging levels, we built linear mixed models with number of begging calls as response variable and the interaction between social role and sex as a fixed effect. As before, for helpers, we tested the effect of their relatedness category towards the brood ($r = 0.5$, $r = 0.25$ or $r \leq 0.125$). We added number of chicks as covariate, because we expected more begging calls in nests with larger broods, and mean brood mass (g) as a proxy for offspring condition. We additionally accounted for group size effects on begging, which have been previously found in this species (Paquet, Covas, et al., 2015). Colony, nest and bird identity were added as random terms.

To further infer whether begging differences in relation to different classes of birds could be explained by nonrandom visits of birds when nestlings were hungrier, we built a second begging model adding the time interval since last fed (i.e. proxy of hunger)

and time since sunrise for each feeding event. In this model, to avoid excluding eight data points (from seven nests) due to unknown intervals between two feeding visits, we estimated the missing information (with high uncertainty) within the model using the observed mean (396.92 s) and a variance of 10 000 as priors. The estimates of both begging models are presented in the results.

Collinearity among predictors was assessed by calculating Spearman rank correlation coefficients (categorical variables were converted to numerical; all correlations below 0.45 except season and daily maximum temperature ($r = 0.63$) but both were kept in the models to account for remaining seasonal variation). All numerical variables were divided by their standard deviation (scaling), and numerical explanatory variables were additionally centred by subtracting their mean (Schielzeth, 2010). Intervisit intervals were first log transformed, then scaled.

We estimated parameters using vague priors (see scripts in https://osf.io/ds8vz/ for more details). Posterior samples (3000) from three Markov chain Monte Carlo (MCMC) chains were based on 150 000 iterations after an adaptation period of 5000, burn-in of 30 000 and thinning interval of 150 for each model. To assess models' goodness of fit, we performed postpredictive checks using the χ^2 discrepancy metric (Gelman et al., 1996). Bayesian *P* values were between 0.484 and 0.496, showing no evidence for lack of fit (values close to 0 or 1 indicate lack of fit). Model convergence was confirmed visually and through the 'R hat' Gelman−Rubin statistic (all parameters under 1.1; Gelman and Rubin 1992). For each estimate, we present mean and 95% credible interval (95% CrI) of the posterior samples. We report effects as credible when 95% CrIs do not overlap zero. When relevant, we also present '*P* (>0)', the proportion of the posterior samples that was higher than zero. Mean differences between bird classes (and 95% CrI of the differences) were calculated from the posteriors. No model simplification was performed. We computed mean marginal and conditional R^2 and their 95% CrIs, which reflect variance explained only by fixed effects and by both fixed and random effects, respectively (Gelman & Pardoe, 2006).

Ethical Note

This study was conducted under research permits from the Northern Cape Department of Environment and Nature Conservation (permits FAUNA 650/2014 and FAUNA 1338/2017) and the approval of the Ethics Committee of the University of Cape Town (2014/V1/RC) and it follows the ASAB/ABS Guidelines for the use of animals in research.

Any disturbance caused by the installation and removal of microphones, sound recorders and video cameras was comparable to that of routine monitoring procedures. Equipment was installed when no adult bird was at the nest by a team of two to three people to minimize time of disturbance. No nest was abandoned following installation of the recording devices. Nestlings were handled at their nest location and no chick suffered adverse effects after handling and routine blood sampling.

Adult birds were annually captured outside the breeding season. Blood samples were collected only when necessary for sex and/or genotyping purposes. While queuing to be processed, birds rested in individual bird bags placed in a quiet, ventilated and shaded area. The blood volume collected (ca. 75 ml) was well below the threshold recommended for this passerine. Birds were given some recovering time after handling and were then released in small groups. Any bird that showed signs of fatigue or injury (1% of the birds captured) was taken to an indoor aviary and released once

recovered. To minimize handling times, a team of 8−12 experienced ringers were allocated to specific tasks to streamline the procedures conducted during the captures.

RESULTS

Intervisit Intervals

Individuals' intervisit intervals ranged between 28 s and over 3 h and 30 min (mean = 1190 s, SD = 1374 s, $N = 1371$ feeding visits to 54 broods; Fig. 1).

Breeding males returned faster to feed after experiencing a higher number of begging calls (Table 2, Fig. 1). This represents a decrease of over 1.5 min between feeding visits for each unit increase in begging (mean = 84 calls, SD = 43 calls). In contrast, breeding females did not return credibly faster after experiencing more calls (Table 2, Fig. 1) and clearly differed from male breeders (estimated difference = 0.142, 95% CrI = [0.009,0.273], $P(>0) = 0.98$; Table A1, Fig. 1). Among helpers, we found no evidence that males or females came back faster after experiencing a higher number of begging calls (Table 2, Fig. 1). Moreover, our results suggest that the response to begging of full-sibling male helpers ($r = 0.5$) was weaker than the response of breeding males, as indicated by the very low proportion of the posterior distribution that was higher than zero, even though credible intervals overlapped zero (estimated difference = −0.185, 95% CrI = [−0.383,0.01], $P(>0) = 0.03$; Table A1, Fig. 1). On the other hand, female helpers' responses did not seem to differ from those of the other classes of birds (Table A1). Lastly, we found no evidence that helpers more related to the brood returned faster than less related helpers after experiencing more begging (Tables 2, A1, Fig. 1).

Breeding males were also the class of birds with the shortest intervisit intervals on average. They returned faster than helpers of any sex or relatedness (Table A2, Fig. A2), and tended to return faster than breeding females, although this difference was not statistically credible (estimated difference = 0.12, 95% CrI = [−0.026,0.262], $P(>0) = 0.95$; Table A2, Fig. A2). These differences represented a mean difference of 3−7 min between breeding males and helpers, and around 1 min difference between the two breeders (see Fig. A2). Breeding females took less time between feeding visits than male helpers $r = 0.5$ and $r = 0.25$ and female helpers $r = 0.25$ (Table A2).

Individual birds in larger cooperative groups showed on average longer intervisit intervals than individuals in smaller groups, but only at high levels of begging (Table 2, Fig. A3). Intervisit intervals were longer in 2017/2018 than in 2014/2015 (Table 2), and birds returned faster to the nest later in the day (Table 2, Fig. A4). Mean brood mass and number of chicks were not credibly correlated with intervisit intervals (Table 2). Nest identity explained on average more random variation in intervisit intervals than colony or bird identity (Table 2). Additionally, there was a high proportion of unexplained variation in intervisit intervals, indicated by a high residual standard deviance (Table 2) and a conditional R^2 of 0.19 [0.128,0.267] (marginal $R^2 = 0.11$; 95% CrI = [0.078,0.156]).

Number of Begging Calls

Broods produced an average of 85 begging calls per 20 s event (SD = 43.5, range 0−230 calls, $N = 1519$ begging events from 54 broods; Fig. 2).

Among breeders, there were no credible differences between the number of begging calls experienced by males and females
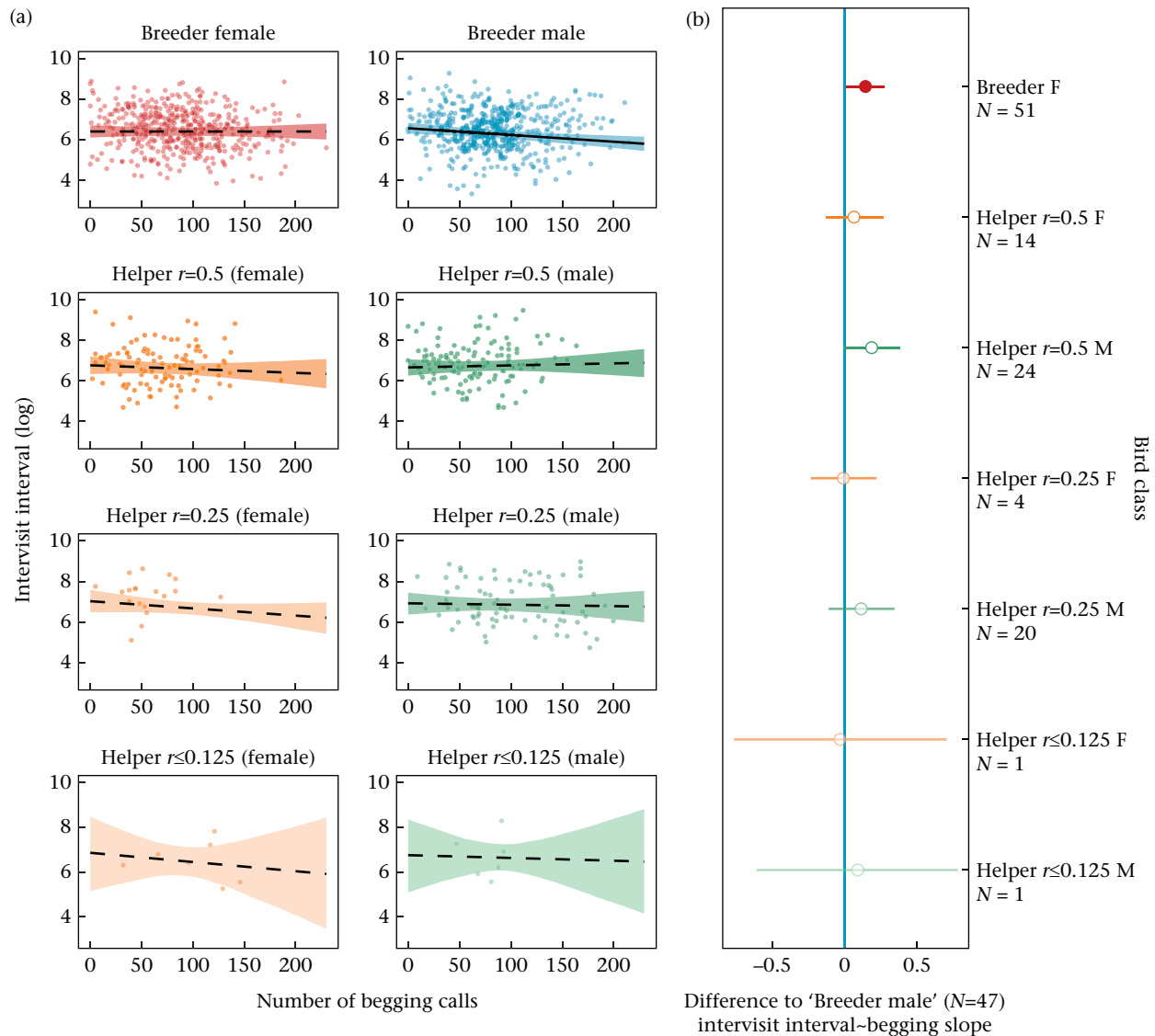
Figure 1. (a) Estimated slopes of intervisit intervals (s; log scale) of birds of different classes in relation to number of begging calls. Points show observed data and lines represent predicted slopes for each bird class. Bands show predicted credible intervals. Solid lines show intervisit intervals credibly correlated with number of begging calls. (b) Comparison between the breeding males' slope with the other bird classes. Circles represent mean differences and bars are the 95% credible intervals of the difference. Filled circles represent credible differences (see Table A1). Next to each class is the number of birds sampled for that category (N; total = 162 birds). F: females; M: males. The '*r*' values show helper relatedness to the brood.

(Table 3, Table A3). For helpers, there was a trend for female helpers to experience on average 6% fewer begging calls than male helpers (estimated difference = −0.125, 95% CrI = [−0.289,0.041], P(>0) = 0.07; Table A3) and breeding females (estimated difference between female helpers *r* = 0.5 and breeding females = 0.124, 95% CrI = [−0.037,0.282], P(>0) = 0.93; Table A3).

Helpers with relatedness levels equal to 0.25 (especially males) experienced the highest mean number of begging calls (mean = 100.7 calls, 95% CrI = [84.3,116.9]; Fig. 2, Table 3). These individuals experienced more begging calls than helpers with the highest relatedness (Fig. 2, Table A3), representing an average of 10−15 more calls per event (12−18% more calls). They also experienced more calls than breeding females, breeding males and more related female helpers (Fig. 2, Table A3). These differences were still clear when controlling for a brood hunger proxy

('interval last fed') and time since sunrise in the model (model 2; see Tables 3, A4), suggesting that helpers *r* = 0.25 did not experience more begging calls due to nonrandom visits to the nests when broods were hungrier, or when groups were feeding less. The number of begging calls produced when female helpers *r* = 0.25 visited the nests tended to be higher than in breeding males' visits (8% more calls on average; estimated difference = −0.164, 95% CrI = [−0.366,0.039], P(>0) = 0.05; Table A3), but differences with breeding females and more related male helpers were less clear (Table A3).

Broods with more nestlings produced more begging calls (Table 3, Fig. A5), showing an average increase to the mean number of begging calls of 20 calls for each extra chick (or 1 more call/s). There was an indication, but noncredible, that broods being fed by larger groups (with more helpers) begged less (Table 3), with an average decrease of four begging calls (5% fewer calls) per

Table 2
Mean estimates and 95% credible intervals (CrI) from model with intervisit intervals as response variable in relation to number of begging calls

Response	Explanatory variable	Level	Mean	95% CrI	P(>0)
Intervisit Interval	(Intercept)	(Breeder female)	6.409	[6.199,6.609]	
	Role*Sex				
		Breeder male	−0.12	[−0.262,0.026]	0.05
		Helper female	0.196	[−0.026,0.422]	0.96
		Helper male	**0.332**	**[0.132,0.533]**	**1**
	Relatedness				
		Helper r=0.25	0.13	[−0.142,0.398]	0.83
		Helper r≤0.125	−0.099	[−0.709,0.505]	0.38
	Season				
		2017/2018	**0.394**	**[0.155,0.658]**	**1**
	Role*Sex*No. of begging calls				
		Breeder female	0	[−0.106,0.106]	0.5
		Breeder male	**−0.142**	**[−0.232,−0.056]**	**0**
		Helper female	−0.08	[−0.263,0.11]	0.2
		Helper male	0.043	[−0.141,0.221]	0.68
	Relatedness*No. of begging calls				
		Helper r=0.25	−0.073	[−0.308,0.167]	0.27
		Helper r≤0.125	−0.096	[−0.817,0.633]	0.39
	No. of chicks		0.005	[−0.104,0.108]	0.54
	Mean mass of chicks		0.043	[−0.065,0.157]	0.78
	Group size*No. of begging calls		**0.083**	**[0.007,0.16]**	**0.98**
	Group size		−0.053	[−0.163,0.055]	0.17
	Maximum temperature day		−0.086	[−0.196,0.025]	0.06
	Time since sunrise		**−0.177**	**[−0.249,−0.107]**	**0**
	Random terms	Standard deviance			
	Residuals	0.936		[0.902,0.973]	
	Nest ID	0.224		[0.122,0.328]	
	Bird ID	0.079		[0.002,0.199]	
	Colony ID	0.101		[0.004,0.298]	

Reference for 'Role*Sex' is Breeder female (intercept), reference for 'Relatedness' is Helper r=0.5 (for each sex) and reference for 'Season' is 2014/2015. The 'r' values show helper relatedness to the brood. Credible effects are in bold. 'P(>0)' shows the proportion of the posterior samples that was higher than zero. Marginal R^2 of 0.114 [0.078;0.156] and conditional R^2 of 0.187 [0.128; 0.267].

additional helper. Mean brood mass was not credibly correlated with the number of begging calls produced (Table 3). Results from the model including our proxy of brood hunger (model 2) showed that broods produced more begging calls when intervals between feeding visits were longer (Table 3, Fig. A6) and that begging increased later in the day (Table 3, Fig. A7). All estimates from model 2 were consistent with model 1 results (Tables 3, A3, A4) and both models explained a large proportion of variation in the number of begging calls produced (model 1: marginal $R^2 = 0.201$, 95% CrI = [0.097;0.315]; conditional $R^2 = 0.547$, 95% CrI = [0.452; 0.649]; model 2: marginal $R^2 = 0.257$, 95% CrI = [0.161;0.361]; conditional $R^2 = 0.589$, 95% CrI = [0.504; 0.678]). Still, the residual random variation was high (Table 3) and nest identity explained on average over five times more variation in number of begging calls than the identity of the feeding bird or the breeding colony (Table 3).

DISCUSSION

In this study, we investigated how intervisit intervals of breeders and helpers, distinguished by their sex and relatedness, vary in relation to acoustic begging. Our aim was to test whether individuals of different classes showed different feeding responses and experienced distinct levels of begging, to better understand the rules of nestling feeding behaviour in cooperatively breeding systems. The number of begging calls produced by the broods correlated with our proxy of hunger, confirming that acoustic begging is likely to signal hunger levels in this species. While breeding males returned faster to the nest to feed when experiencing more begging calls, there was no evidence that breeding females or helpers (independently of their sex or

relatedness) adjusted food provisioning to brood begging levels. Specifically, we found statistically supported differences between the response to begging of male breeders and female breeders, and an indication that the feeding response of full-sibling male helpers differed as well from breeding males. Surprisingly, second-order relatives (half siblings, uncles and grandparents) experienced more begging calls than breeders and more related helpers, while there were no credible differences in the begging experienced by the two latter classes.

Sex Differences in Parental Responses

Breeding males returned faster with food after experiencing more begging calls while breeding females showed, on average, no response to begging. Sex-specific responses to brood demand have been described in several biparental care systems (reviewed in Müller et al., 2007) and in a few cooperative systems, but the direction of these differences seems to vary across studies (Table 1; see Müller et al., 2007). Since sociable weavers are both socially and genetically monogamous (Covas et al., 2006), both breeders should have similar fitness returns from brood survival. Thus, a plausible explanation for a male-only response in this species is that female breeders are responding to begging behaviour through other mechanisms that we did not identify here or are responding to other needs of the brood.

First, when nestlings are young (i.e. at day 4 chicks can be between 1 and 4 days old), breeding females could respond to the need of brooding the nestlings, which could thus weaken the correlation between begging and their feeding response. Indeed, in the two cooperative systems where differences between breeders were found (Table 1; MacColl & Hatchwell, 2003; Cruz
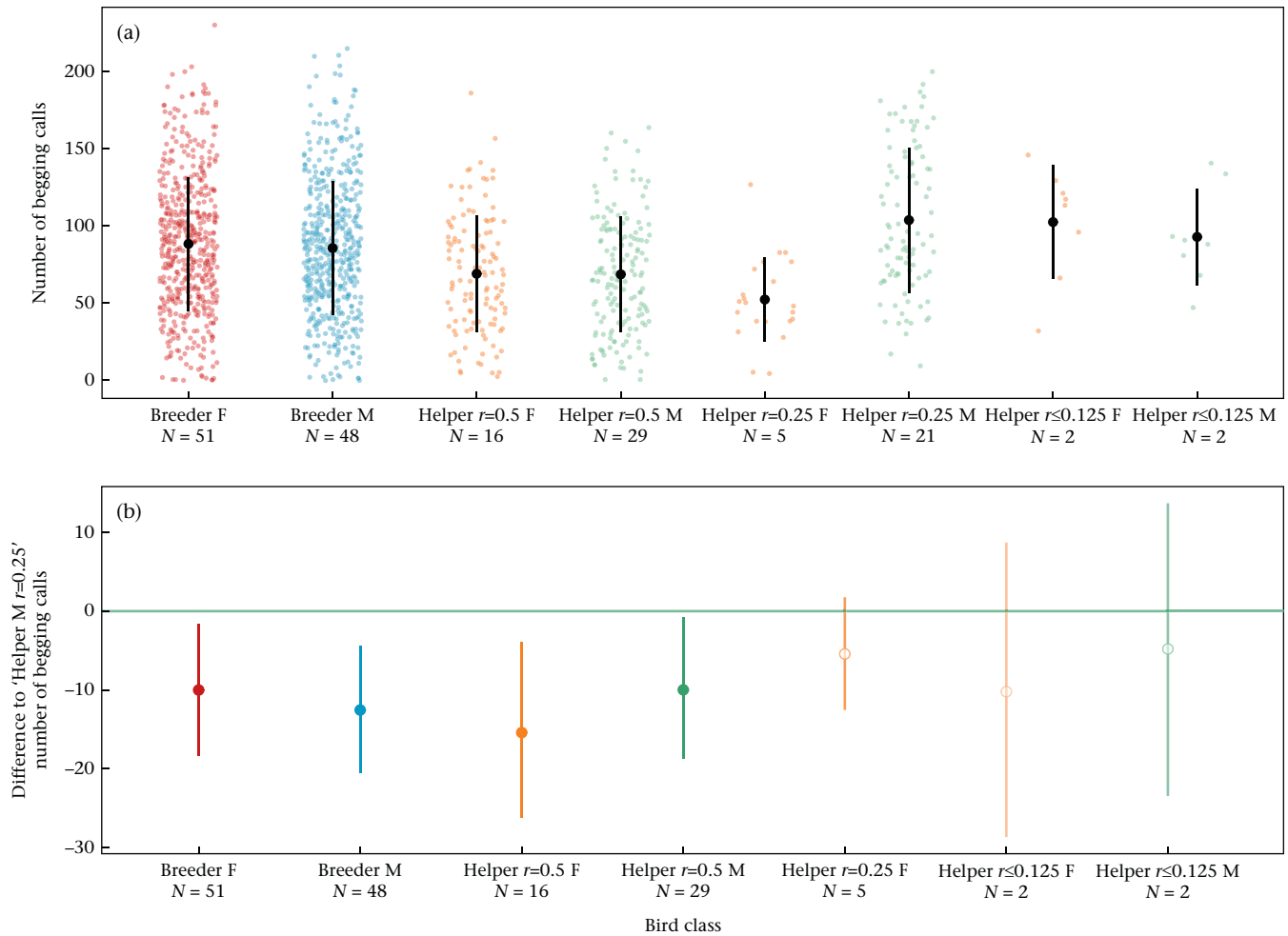
Figure 2. (a) Observed data, mean and SD of number of begging calls experienced by birds of each class, at each feeding event. Points show observations (*N* = 1519), circles show mean number of begging calls and bars show SD. (b) Predicted estimated differences in number of begging calls experienced by different bird classes in relation to 'Helper male *r* = 0.25' (*N* = 21 birds; estimated from model 1; model 2 showed nearly identical results). Circles show posterior means and bars show 95% credible intervals. Filled circles show differences credibly different from zero (Table A3). Below each class is the number of birds sampled in each category (*N*; total = 174 birds). The '*r*' values show helper relatedness to the brood.

et al. 2019), females increased feeding responses more strongly than males as nestlings aged, probably because of the decreased need to brood the chicks. However, our data do not support this explanation, as we looked at the time spent inside the nest and found no difference according to breeders' sex (see Fig. A8, Table A5; see also Maclean, 1973d). Second, females could be adjusting the quality of prey brought to the nest in response to begging (Browning et al., 2012), given that breeding females have been observed to bring larger prey than other birds in this population (Ferreira, 2015). Yet, nestlings 4 days old or younger are not able to consume large prey and thus little prey size variation is expected at this age. Female breeders could still be responding to nestling begging by bringing small prey with higher nutritional quality or by feeding the hungriest chick (Kölliker et al., 1998). Alternatively, although not responding specifically to begging, mothers could still be adjusting provisioning behaviour by paying more attention to cues of long-term need, such as gape coloration or offspring size (Kilner, 2002b). Responding to different signals of need could allow breeders to increase the survival chances of more young, by promoting a more balanced food distribution (Kölliker et al., 1998; McRae et al., 1993), which could otherwise be monopolized by the chick that begs more or the heaviest chick (especially when

offspring are born asynchronously, as in sociable weavers). Future studies in this system should focus on begging−feeding interactions within broods, to detect which nestling is being fed and better understand whether female breeders are responding to other cues of need or condition.

On the other hand, discrepancies in parental responses are often attributed to trade-offs between parental care and other sex-specific reproductive behaviours (Siefferman & Hill, 2008). The lack of evidence for female breeders' adjustments in sociable weavers may indicate that mothers cannot adjust their feeding responses, possibly because they are already feeding close to their maximum, due, for instance, to recent energetic costs with egg laying (Monaghan & Nager, 1997; Visser & Lessells, 2001). These costs may be exacerbated in this species, since female breeders often produce multiple clutches per season, from which 60−70% normally fail (Covas et al., 2008; Fortuna et al., 2021). Breeding females are thus expected to spend considerable amounts of resources in egg laying every season, which could explain why they respond less to begging than males.

Furthermore, since begging behaviour at young ages can be partially regulated by hormones of maternal origin that are deposited in the eggs, mothers could also use this as a mechanism to shift food provisioning efforts towards their partner (Moreno-

Table 3
Mean estimates and 95% credible intervals (CrI) from models with number of begging calls as response variable

Response	Explanatory variable	Level	Mean	95% CrI	P(>0)
No. of begging calls (model 1)	(Intercept) Role*Sex	(Breeder female)	2.083	[1.738,2.428]	
		Breeder male	−0.058	[−0.178,0.061]	0.18
		Helper female	−0.124	[−0.282,0.037]	0.07
		Helper male	0	[−0.15,0.152]	0.5
	Relatedness				
		Helper r=0.25	**0.23**	**[0.019,0.43]**	**0.99**
		Helper $r \leq 0.125$	0.119	[−0.274,0.53]	0.72
	Season				
		2017/2018	−0.148	[−0.623,0.342]	0.26
	No. of chicks		**0.301**	**[0.114,0.492]**	**1**
	Mean mass of chicks		−0.09	[−0.279,0.099]	0.17
	Group size		−0.174	[−0.364,0.02]	0.04
	Maximum temperature day		0.166	[−0.067,0.387]	0.93
	Random terms	Standard deviance			
	Residuals	0.728		[0.702,0.756]	
	Nest ID	0.61		[0.489,0.767]	
	Bird ID	0.056		[0.002,0.137]	
	Colony ID	0.14		[0.006,0.39]	
No. of begging calls (model 2)	(Intercept) Role*Sex	(Breeder female)	2.13	[1.772,2.47]	
		Breeder male	−0.068	[−0.183,0.049]	0.12
		Helper female	−0.111	[−0.272,0.05]	0.08
		Helper male	0.006	[−0.139,0.155]	0.53
	Relatedness				
		Helper r=0.25	**0.214**	**[0.006,0.409]**	**0.98**
		Helper $r \leq 0.125$	0.035	[−0.353,0.443]	0.56
	Season				
		2017/2018	−0.197	[−0.664,0.292]	0.21
	No. of chicks		**0.295**	**[0.107,0.479]**	**1**
	Mean mass of chicks		−0.128	[−0.323,0.062]	0.1
	Group size		−0.137	[−0.325,0.038]	0.07
	Maximum temperature day		0.165	[−0.056,0.387]	0.93
	Interval last fed		**0.096**	**[0.059,0.134]**	**1**
	Time since sunrise		**0.264**	**[0.212,0.317]**	**1**
	Random terms	Standard deviance			
	Residuals	0.701		[0.675,0.727]	
	Nest ID	0.589		[0.468,0.74]	
	Bird ID	0.065		[0.003,0.148]	
	Colony ID	0.179		[0.011,0.451]	

Reference for 'Role*Sex' is Breeder female (intercept), reference for 'Relatedness' is Helper r=0.5 (for each sex) and reference for 'Season' is 2014/2015. The 'r' values show helper relatedness to the nestlings. Models are similar but second model includes hunger proxies. Credible effects are in bold. 'P (>0)' shows the proportion of the posterior samples that was higher than zero. Model 1: marginal R^2 = 0.201 [0.097;0.315] and conditional R^2 of 0.547 [0.452; 0.649]. Model 2: marginal R^2 = 0.257 [0.161;0.361] and conditional R^2 of 0.589 [0.504; 0.678].

Rueda, 2007; Paquet & Smiseth, 2016; Smiseth et al., 2011), and therefore not respond themselves. There is evidence that in sociable weavers mothers without helpers produce eggs with a higher concentration of androgens (Paquet et al., 2013). Additionally, we found some indication that offspring with fewer helpers beg more, and a previous cross-fostering experiment on the same system suggests that this pattern is partly mediated by prenatal effects (Paquet, Covas, et al., 2015). Thus, it is possible that mothers influence offspring begging through strategically varying egg hormonal levels according to their number of helpers (Moreno-Rueda, 2007), which, together with our result that only breeding males respond to begging, further suggests that female breeders may be manipulating their partners to feed more when the pair has less help. This hypothesis could be tested by manipulating females' prenatal environmental conditions (e.g. modifying the size of their groups) and measuring behavioural and fitness consequences for the parents and their offspring (Paquet & Smiseth, 2016).

No Evidence of Response from Helpers

In contrast to all the previous studies that investigated provisioners' responses to brood demand in cooperative breeders (Table 1), we found no evidence that helpers, of any sex or relatedness, adjusted feeding behaviour to begging levels in sociable weavers. We predicted that female helpers would respond less than breeders and male helpers, as they should not benefit as much from maximizing brood survival and subsequent group augmentation (Kokko et al., 2001), since they disperse to other colonies to breed (Doutrelant et al., 2004). Our results showed instead that neither male nor female helpers seem to adjust feeding intervals to brood begging. This suggests that helping benefits may not depend on how helpers respond to brood demand, and thus on increasing the chances of offspring survival, or that helpers, like breeding females, are under energetic constraints that do not allow them to increase their feeding efforts. The difference between breeding males and full-sibling male helpers is especially interesting, since these individuals share comparable levels of kinship to the brood and are of the same sex. Contrary to expectations, only breeding males seem to respond to begging, and our comparison tests suggested low similarity between their response and that of the full-sibling male helpers. This finding reinforces the idea that, besides sex and genetic relationships, differences in life history stages may regulate feeding rules by affecting the costs of responding to brood demand. Full-sibling helpers may incur higher energetic costs because they are not as dominant as breeders, which restricts their access to food and increases their chances of

engaging in aggressive interactions (Rat et al., 2015). Increasing feeding efforts may also be costlier for these helpers due to poorer foraging skills, as these are typically younger individuals than breeders (Covas et al., 2006).

We also expected the association between feeding effort and begging to be stronger for helpers more closely related to the brood, since closer relatives have been predicted to gain the highest indirect fitness benefits from brood survival (Emlen & Wrege, 1988; Komdeur, 1994; Nam et al., 2010; but see ; Kay et al., 2020). In contrast, sociable weaver helpers' feeding rules did not appear to depend on offspring begging, and no differences were found according to their genetic relationship to the brood. Similarly, a previous study conducted in bell miners found no difference between relatedness classes, although both related and unrelated helpers adjusted provisioning effort to increasing brood needs (McDonald et al., 2009; te Marvelde et al., 2009). In spite of the major role of inclusive fitness in the evolution of cooperative care in family-based systems like sociable weavers (Hamilton, 1964; Kay et al., 2020), our results indicate that indirect benefits from helping relatives may not be maximized via adjusting feeding effort to begging levels.

Finally, note that helpers, as well as breeding females, may still adjust feeding intervals to begging once nestlings are older. At later stages, helpers may learn how to respond to begging stimuli (especially the younger, less experienced, individuals) or start increasing their feeding effort because older broods have a higher reproductive value. Even though our analyses from older broods' begging (day 9) showed no evidence for feeding adjustments from breeders or any class of helpers (see Appendix and Table A6), we consider these findings only preliminary as we used a substantially smaller sample and a different begging measure. Further information is necessary to understand how consistent feeding responses to begging are across the nestling dependence period.

Half Siblings Experience More Begging Calls

We expected nestlings to adjust begging levels according to the responsiveness of nest attendants to this signal. Sociable weavers produce calls when entering the nest, which could allow chicks to individually identify food provisioners (Beer, 1971; Jacot et al., 2010; McDonald & Wright, 2011). Our results showed that breeding males returned faster to feed after experiencing more begging, but these were not the individuals experiencing the highest mean number of begging calls per visit. Contrary to our predictions, $r = 0.25$ helpers (especially males) experienced higher begging levels than breeders and more closely related helpers. This group of helpers mostly included half siblings of the brood (79%; but also, uncles, 17%, and grandparents, 4%), which were estimated to experience an average of 101 begging calls per 20 s event, around 10–15 more begging calls than full-sibling helpers. To our knowledge, this is the first report of begging intensity differences according to helper relatedness in birds. A previous study on banded mongoose, *Mungos mungo*, found that pups begged less towards helpers that were less responsive to begging (Bell, 2008b). Offspring have also been found to beg more towards female breeders, both in biparental care systems when mothers seem to be a more reliable food source (Kölliker et al., 1998; Paquet et al., 2018; Roulin & Bersier, 2007), and in a cooperative system (Wright et al., 2010), probably because mothers are more often present when offspring are hungry. Here, we found no evidence that half siblings are responsive to begging levels, or that they provide food more often. Therefore, it is unlikely that nestlings are begging preferentially towards second-order helpers, and we propose two other explanations for the high begging levels

they experienced. First, these helpers could have been visiting the nests more often when offspring are hungrier. However, when we included a proxy of brood hunger and time since sunrise in the models, we still detected the same effect of helper relatedness on begging levels, suggesting that these helpers do not specifically visit the broods when their levels of hunger are the highest or when feeding activity is generally lower. Alternatively, the food provisioning behaviour of second-order relatives may differ from the other group members. For example, they could elicit more begging by bringing smaller prey or taking longer to deliver it to the brood (Doutrelant & Covas, 2007). Moreover, this class of helpers could exhibit more false-feeds by consuming the food they bring to the nest (Boland et al., 1997; McDonald et al., 2007), which would explain the estimated number of extra begging calls experienced due to no nestling being fed. This finding raises interesting questions about the quality and purpose of feeding visits of different helpers in this cooperatively breeding system, which could be investigated in future studies by recording feeding behaviour from inside the nest cavities.

Conclusion

We observed clear differences in how breeding males and females adjust provisioning effort to offspring demand. Furthermore, we found no evidence of helpers' responses to increasing begging levels. Relatedness did not seem to explain helpers' feeding adjustments, indicating that indirect fitness benefits may not play a role in how helpers regulate their feeding contributions. Interestingly, breeding females and full-sibling male helpers, which are among the classes of individuals that should benefit the most from maximizing brood survival, did not appear to match feeding responses to begging. This suggests that the costs of increasing feeding effort are distinct for the different members of the group, and that sexual (i.e. reproductive) and life history stage constraints may regulate feeding strategies in this system. Experimental manipulations of acoustic begging levels, and further tests of other phenotypic cues that may signal hunger, such as visual signals, would be necessary to confirm causality and assess the nature of these differences. Moreover, we encourage further investigations on the begging–feeding interplay in cooperative breeders, to understand whether in most species all individuals respond to increases in brood demand, or whether different responses to begging should be expected when individuals vary in sex, relatedness and other life history-related traits.

Author Contributions

Data Availability

Analyses and plots in this manuscript can be fully reproduced using the code and data provided in https://osf.io/ds8vz/.

Acknowledgments

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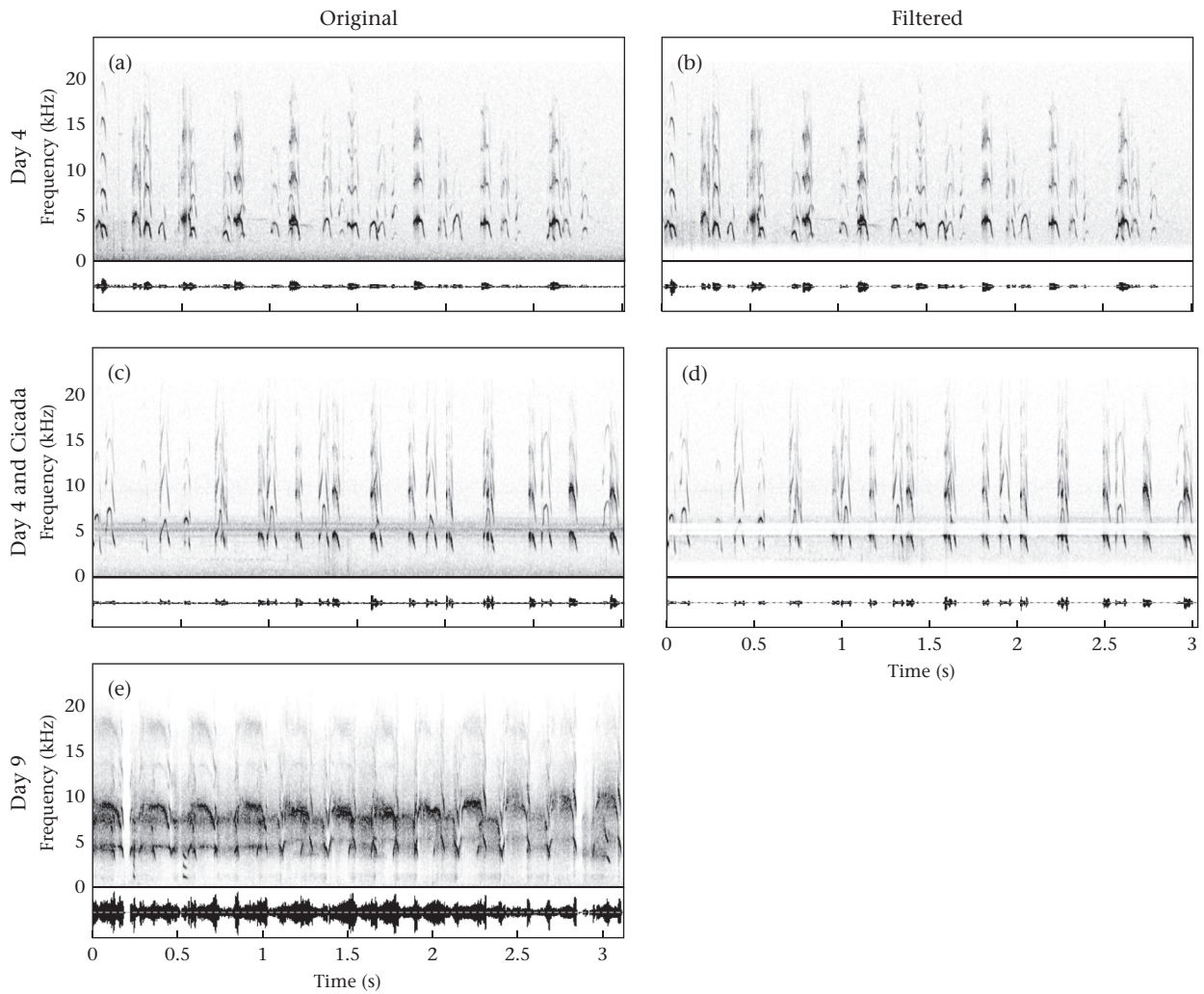
Appendix

Figure A1. Spectrograms illustrating raw data and the first steps of noise removal (see main text). (a) Typical begging at day 4: it is possible to distinguish each individual call even when they overlap. (b) Same recording as (a) after 2 kHz high-pass filter (36 dB roll-off) to decrease background noise level. (c) Typical begging at day 4 with cicada(s) calling in the background. Cicadas' calls have a stereotyped fixed frequency that can be erased using (d) a band pass excluding frequencies between ca. 5 and 6 kHz, improving substantially the signal-to-noise ratio. (e) Typical begging at day 9: nestlings' vocalizations develop into noisy calls not visually distinguishable from each other. Spectrograms were generated with the 'soundgen' R package (Anikin, 2019), using the original audio files with sampling rate of 44.1 kHz, window type Gaussian, length of (fast Fourier transforms) FFT windows 50 ms, and 70% overlap between successive FFT frames. Oscillograms below each spectrogram represent the non-normalized amplitude envelopes.
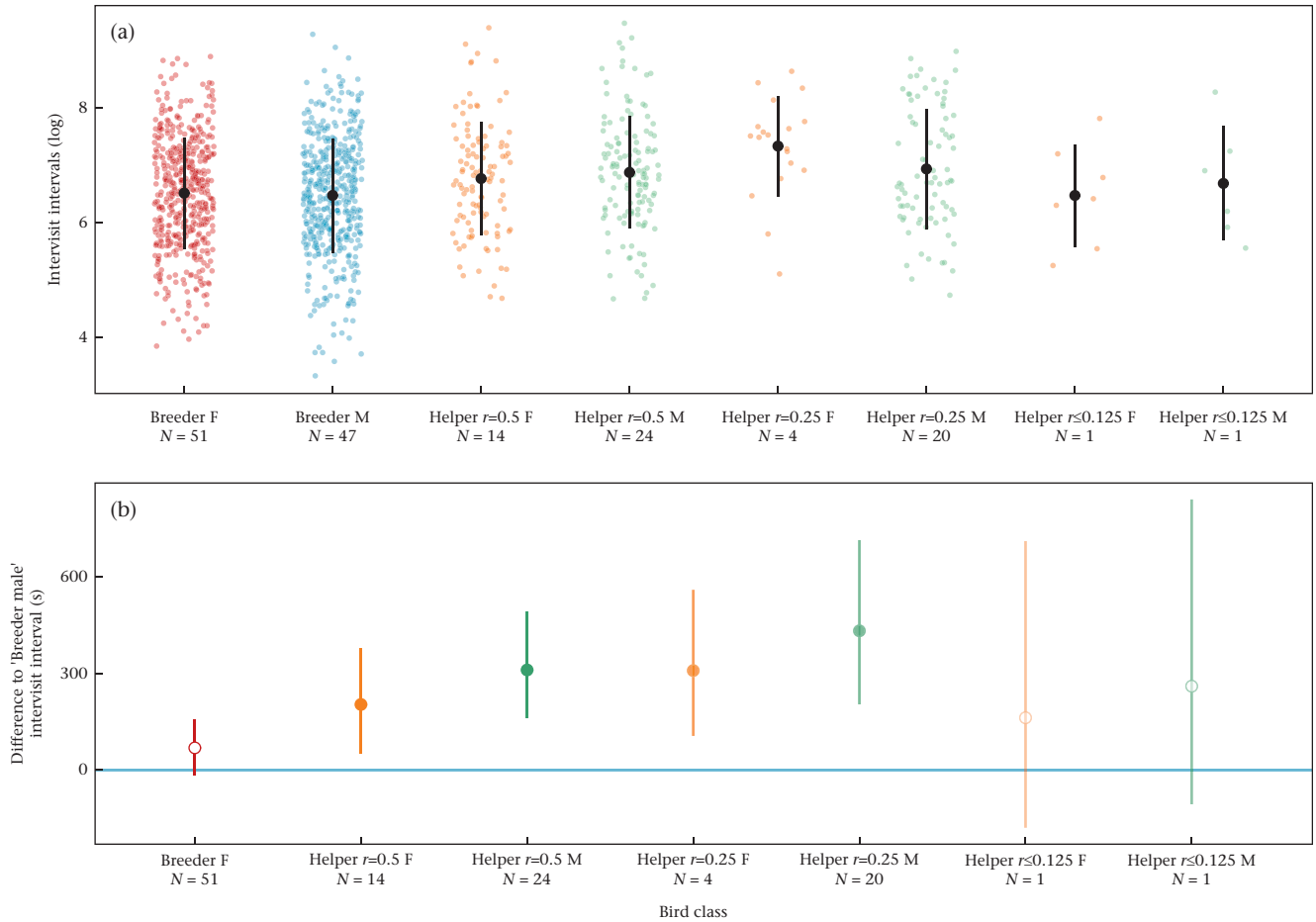
Figure A2. (a) Observed data, mean and SD of intervisit intervals (s; log) of birds of distinct classes. Points show observations (*N* = 1371), filled circles show mean and bars show SD. (b) Estimated differences in intervisit intervals (s) of different bird classes in relation to 'Breeder male' (*N* = 47). Below each class is the number of birds sampled in each category (total = 162 birds). Circles show posterior means and bars show 95% credible intervals. Filled circles show differences credibly different from zero (Table A2). F: females; M: males. The '*r*' values show helper relatedness to the brood.
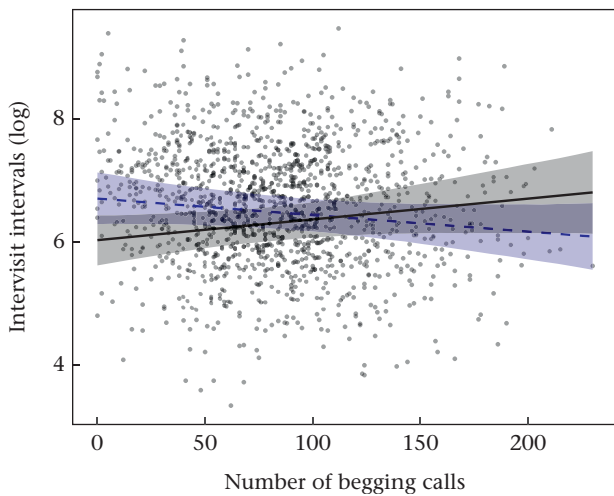

Figure A3. Effect of the interaction between number of begging calls and group size on intervisit intervals (s; log). The solid line represents predicted values for pairs with four helpers (above average) and the dashed line represents predicted values for pairs without helpers (below average). Bands show the predicted 95% credible intervals. Breeder females were used as reference level.
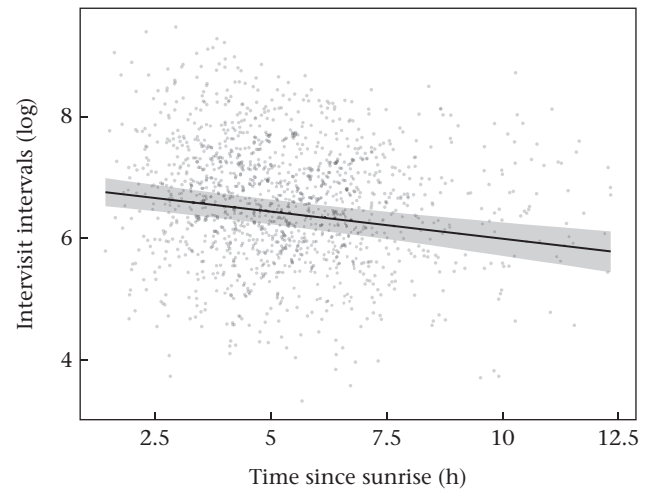

Figure A4. Effect of time since sunrise (h) on intervisit intervals (s; log). Points show observed data and the line represents the predicted slope. Bands show the predicted 95% credible intervals.
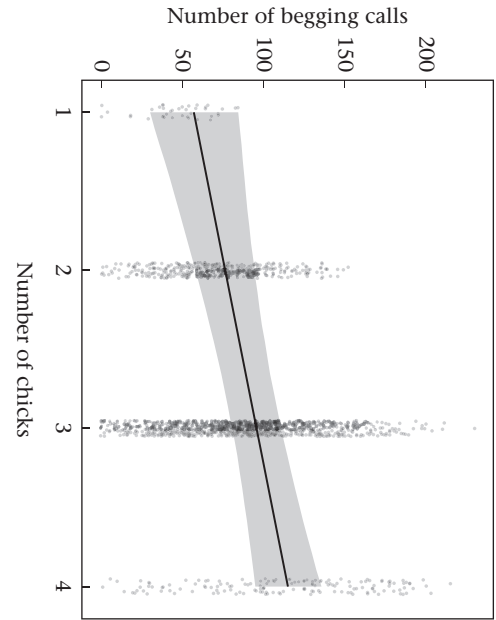
Figure A5. Effect of number of chicks on number of begging calls produced over a 20 s event. Points show observed data and the line represents the predicted slope from model 1. Bands show the predicted 95% credible intervals.

Figure A6. Effect of interval since last time fed (h; i.e. proxy of hunger) on the number of begging calls produced over a 20 s event. Points show observed data and the line represents the predicted slope from model 2. Bands show the predicted 95% credible intervals.

Figure A7. Effect of time since sunrise (h) on the number of begging calls produced over a 20 s event. Points show observed data and the line represents the predicted slope from model 2. Bands show the predicted 95% credible intervals.
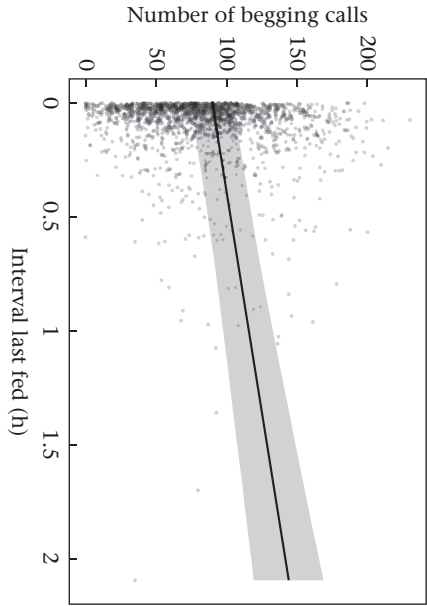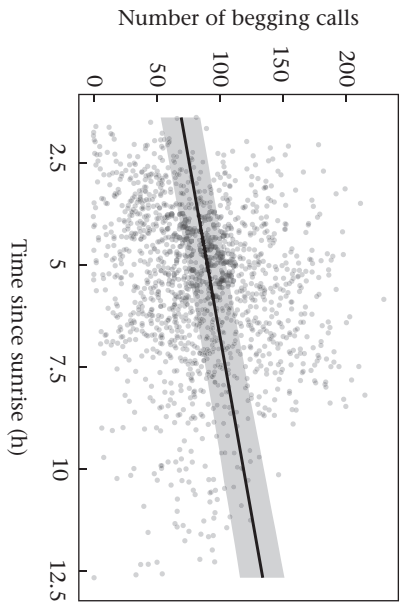
Table A1
Comparison of intervisit intervals of different bird classes in relation to number of begging calls

	Breeder female	Breeder male	Helper female r=0.5	Helper male r=0.5	Helper female r=0.25	Helper male r=0.25	Helper female $r \leq 0.125$
Breeder male	**0.142 [0.009,0.273] P=0.98**						
Helper female r=0.5	0.08 [−0.127,0.286] P=0.78	−0.062 [−0.267,0.13] P=0.28					
Helper male r=0.5	−0.043 [−0.242,0.163] P=0.33	−0.185 [−0.383,0.01] P=0.03	−0.123 [−0.339,0.094] P=0.13				
Helper female r=0.25	0.153 [−0.087,0.385] P=0.9	0.01 [−0.219,0.235] P=0.54	0.073 [−0.167,0.308] P=0.73	0.196 [−0.132,0.51] P=0.89			
Helper male r=0.25	0.03 [−0.213,0.263] P=0.6	−0.112 [−0.343,0.113] P=0.17	−0.05 [−0.375,0.273] P=0.38	0.073 [−0.167,0.308] P=0.73	−0.123 [−0.339,0.094] P=0.13		
Helper female $r \leq 0.125$	0.176 [−0.572,0.918] P=0.68	0.033 [−0.705,0.767] P=0.54	0.096 [−0.633,0.817] P=0.61	0.219 [−0.568,0.966] P=0.71	0.023 [−0.716,0.743] P=0.53	0.146 [−0.668,0.922] P=0.64	
Helper male $r \leq 0.125$	0.053 [−0.664,0.766] P=0.57	−0.089 [−0.779,0.609] P=0.41	−0.027 [−0.744,0.719] P=0.48	0.096 [−0.633,0.817] P=0.61	−0.1 [−0.82,0.622] P=0.4	0.023 [−0.716,0.743] P=0.53	−0.123 [−0.339,0.094] P=0.13

For each comparison, we estimated mean difference, 95% credible intervals and P (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the posteriors of classes on top of the matrix by those of classes on the left (e.g. top left= Breeder female − Breeder male). Credible differences are in bold.

Table A2
Comparison of mean intervisit intervals of different bird classes

	Breeder female	Breeder Male	Helper female r=0.5	Helper male r=0.5	Helper female r=0.25	Helper male r=0.25	Helper female r≤0.125
Breeder male	0.12 [−0.026,0.262] P=0.95						
Helper female r=0.5	−0.196 [−0.422,0.026] P=0.04	**−0.315** **[−0.537,−0.091]** **P=0**					
Helper male r=0.5	**−0.332** **[−0.533,−0.132]** **P=0**	**−0.452** **[−0.643,−0.255]** **P=0**	−0.136 [−0.361,0.098] P=0.13				
Helper female r=0.25	**−0.326** **[−0.605,−0.045]** **P=0.01**	**−0.446** **[−0.72,−0.18]** **P=0**	−0.13 [−0.398,0.142] P=0.17	0.006 [−0.34,0.361] P=0.52			
Helper male r=0.25	**−0.462** **[−0.737,−0.184]** **P=0**	**−0.582** **[−0.842,−0.311]** **P=0**	−0.266 [−0.628,0.104] P=0.08	−0.13 [−0.398,0.142] P=0.17	−0.136 [−0.361,0.098] P=0.13		
Helper female r≤0.125	−0.097 [−0.718,0.523] P=0.38	−0.216 [−0.835,0.406] P=0.24	0.099 [−0.505,0.709] P=0.62	0.235 [−0.448,0.917] P=0.75	0.229 [−0.391,0.848] P=0.76	0.365 [−0.322,1.051] P=0.84	
Helper male r≤0.125	−0.233 [−0.813,0.338] P=0.21	−0.352 [−0.938,0.213] P=0.12	−0.037 [−0.659,0.588] P=0.45	0.099 [−0.505,0.709] P=0.62	0.093 [−0.521,0.722] P=0.6	0.229 [−0.391,0.848] P=0.76	−0.136 [−0.361,0.098] P=0.13

For each comparison, we estimated mean difference, 95% credible intervals and P (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of class on top of the matrix by those of classes on the left (e.g. Breeder female − Breeder male). Credible differences are in bold.

Table A3
Comparison of number of begging calls experienced by different bird classes (estimated from model 1)

	Breeder female	Breeder Male	Helper female r=0.5	Helper male r=0.5	Helper female r=0.25	Helper male r=0.25	Helper female r≤0.125
Breeder male	0.058 [−0.061,0.178] P=0.82						
Helper female r=0.5	0.124 [−0.037,0.282] P=0.93	0.066 [−0.087,0.219] P=0.8					
Helper male r=0.5	0 [−0.152,0.15] P=0.5	−0.059 [−0.197,0.086] P=0.22	−0.125 [−0.288,0.041] P=0.07				
Helper female r=0.25	−0.105 [−0.321,0.105] P=0.17	−0.164 [−0.366,0.039] P=0.05	**−0.23** **[−0.43,−0.019]** **P=0.01**	−0.105 [−0.373,0.163] P=0.21			
Helper male r=0.25	**−0.23** **[−0.421,−0.036]** **P=0.01**	**−0.288** **[−0.471,−0.1]** **P=0**	**−0.354** **[−0.602,−0.089]** **P=0**	**−0.23** **[−0.43,−0.019]** **P=0.01**	−0.125 [−0.288,0.041] P=0.07		
Helper female r≤0.125	0.005 [−0.393,0.403] P=0.51	−0.053 [−0.448,0.337] P=0.39	−0.119 [−0.53,0.274] P=0.28	0.005 [−0.417,0.416] P=0.51	0.11 [−0.315,0.539] P=0.7	0.235 [−0.2,0.659] P=0.86	
Helper male r≤0.125	−0.12 [−0.539,0.296] P=0.28	−0.178 [−0.598,0.243] P=0.2	−0.244 [−0.703,0.226] P=0.14	−0.119 [−0.53,0.274] P=0.28	−0.015 [−0.498,0.463] P=0.48	0.11 [−0.315,0.539] P=0.7	−0.125 [−0.288,0.041] P=0.07

For each comparison, we estimated mean difference, 95% credible intervals and P (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of classes on top of the matrix by the estimates of classes on the left (e.g. Breeder female − Breeder male). Credible differences are in bold.

Table A4
Comparison of number of begging calls experienced by different bird classes (estimated from model 2)

	Breeder female	Breeder male	Helper female r=0.5	Helper male r=0.5	Helper female r=0.25	Helper male r=0.25	Helper female r≤0.125
Breeder male	0.067 [−0.051,0.186] P=0.86						
Helper female r=0.5	0.109 [−0.05,0.262] P=0.92	0.042 [−0.106,0.191] P=0.7					
Helper male r=0.5	−0.006 [−0.151,0.137] P=0.47	−0.073 [−0.216,0.069] P=0.16	−0.115 [−0.274,0.037] P=0.08				
Helper female r=0.25	−0.105 [−0.314,0.104] P=0.17	−0.172 [−0.361,0.022] P=0.04	**−0.214** [**−0.406,−0.024**] **P=0.01**	−0.099 [−0.356,0.154] P=0.22			
Helper male r=0.25	**−0.22** [**−0.414,−0.023**] **P=0.01**	**−0.287** [**−0.473,−0.104**] **P=0**	**−0.329** [**−0.577,−0.089**] **P=0**	**−0.214** [**−0.406,−0.024**] **P=0.01**	−0.115 [−0.274,0.037] P=0.08		
Helper female r≤0.125	0.056 [−0.323,0.446] P=0.61	−0.011 [−0.393,0.389] P=0.47	−0.053 [−0.449,0.352] P=0.4	0.063 [−0.337,0.475] P=0.61	0.161 [−0.278,0.59] P=0.77	0.277 [−0.145,0.703] P=0.9	
Helper male r≤0.125	−0.059 [−0.461,0.351] P=0.39	−0.126 [−0.542,0.285] P=0.28	−0.168 [−0.607,0.292] P=0.24	−0.053 [−0.449,0.352] P=0.4	0.046 [−0.441,0.523] P=0.57	0.161 [−0.278,0.59] P=0.77	−0.115 [−0.274,0.037] P=0.08

For each comparison, we estimated mean difference, 95% credible intervals and P (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of classes on top of the matrix by the estimates of classes on the left (e.g. Breeder female − Breeder male). Credible differences are in bold.

Time Spent Brooding

To test whether differences in male and female breeders' intervisit intervals could be due to females responding instead to the need of brooding the nestlings, we fitted a linear mixed model using the 'lme4' R package (Bates et al., 2014). Time inside the nest was fitted as response variable (log) assuming a normal distribution and sex (female/male) was included as a predictor. Only breeders were included in the data set. We also added bird and nest identity as crossed random effects.
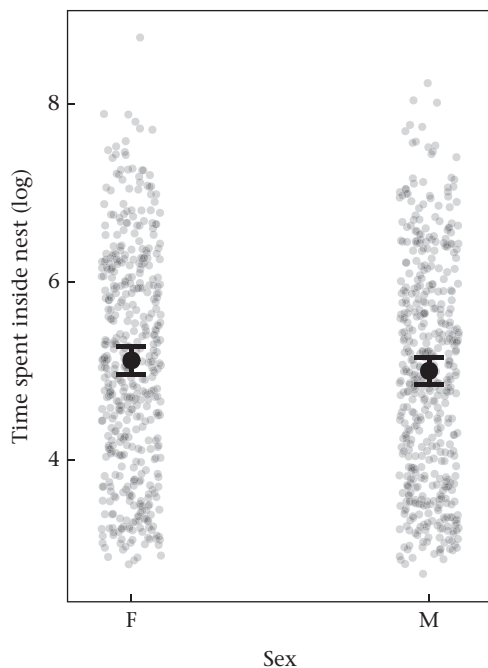

Figure A8. Effect of sex (F: female; M: male) on time spent inside the nest (s; log) at each feeding visit. Points show observed data. Full black circles represent the predicted mean for each sex and bars show 95% confidence intervals (see Table A5).

Table A5
Estimates from a linear mixed model on the differences in time spent inside the nest between breeding females and breeding males ($N=950$)

Fixed effect	Estimate	SE	2.5% CI	97.5% CI	df	t	P
(Intercept)	5.115	0.079	4.961	5.271	94.880	64.892	<0.001
Sex (breeding males)	−0.118	0.106	−0.326	0.091	52.693	−1.120	0.268

Reference level (intercept) for 'sex' is breeding female. CI: confidence interval.

Begging of Older Broods

Methods

Data analysis. Begging and feeding behaviour were recorded at two different ages (day 4 and day 9). Calls of older chicks are considerably louder, longer and have a broad frequency spectrum noisy component (see Fig. A1e); thus, single calls are mostly indistinguishable, which does not allow us to reliably count them either manually or automatically. Therefore, we tried an alternative acoustic measurement on both the day 4 and day 9 data collected in 2017/2018, by quantifying the time spent begging over the 15 s period just after a bird arrived at the nest. We chose a shorter, 15 s duration to reduce the chances of excluding events due to external noise (see below). Time spent begging was estimated by summing the duration of all the over-threshold sounds during this period, using the timer function from the 'seewave' package v. 2.1.4 (Sueur et al., 2008). We used as amplitude threshold 5% of the maximum amplitude recorded for each event, with a time window smooth of 101 points and no overlap. All recordings were initially high-pass filtered at 2000 Hz to attenuate background noise. As for number of begging calls, begging was not quantified if another bird arrived during the event, or for the first begging event recorded for each nest.

Time spent begging was quantified on 398 events ($N = 127$ from 21 nests at day 4 and $N = 288$ from 29 nests at day 9). As intended, this acoustic variable was highly correlated with the number of begging calls that were estimated at day 4 (Pearson correlation: $r = 0.79$, 95% CI = [0.71,0.84], $N = 126$). Therefore, besides testing our predictions on day 9 data using time spent begging, we also

included day 4 data in the models to confirm that we observed similar results using the two begging measures. However, the estimation of time spent begging was performed using amplitude envelopes, and thus all begging events that included any external noise (e.g. other birds' vocalizations, cicadas, etc.) had to be systematically excluded. This severely decreased the sample of analysable events by 85% at day 4 (when comparing the number of events where number of begging calls could be estimated) and by 55% at day 9 (when comparing the total number of events available). This decrease in available sample led to high uncertainty levels for the effect sizes (see below), and we thus consider these results only preliminary. We therefore recommend this alternative measure for future studies only if it is possible to record begging excluding all external noise.

Statistical analysis. We expected different feeding rules as nestlings get older, since at later stages helpers may learn how to respond to begging stimuli (especially the younger individuals) or start increasing their feeding effort because older broods have a higher reproductive value

To study the correlation between intervisit intervals and time spent begging across bird classes at different brood ages, we used similar models to those described in the main text, but now estimating a different nest age intercept and slope for each level of the interaction between social role and sex, and for each relatedness level of the helpers to the brood (see main text). Similarly, to study the differences in time spent begging experienced by different bird classes at different brood ages, we used the begging models described in the main text, but again estimating a nest age effect for each level of the interaction between social role and sex, and for each relatedness level. To assess whether time spent begging was predicted by hunger and birds' feeding activity, we built a second model adding the time interval since last fed (i.e. proxy of hunger) and time passed since sunrise for each feeding event (see main text). The estimates of both models are presented in the results' tables.

Results

Intervisit intervals. We found no evidence that birds responded to the time spent begging by returning faster to the nest at day 4 or at day 9, independently of their role and sex or relatedness (Table A6)

At day 9, the mean slopes of male and female breeders seem to be more similar than at day 4 (Table A6, A7). The lack of evidence for a response of breeding males at day 4 differs from the result obtained in relation to number of begging calls (see main text), even though both begging measures were highly correlated (see above). However, the 95% CrI found here at day 4 is large (Table A6) and contains the effect size obtained when using number of begging calls as response variable (Table 2). This suggests that the available sample of breeding males' feeding response to time spent begging ($N = 15$ breeding males; 38 events) is not large enough to detect this effect. At day 9, where the sample was bigger ($N = 22$ males; 82 events), the breeding males' slope was more similar to that estimated in relation to number of begging calls (Tables 2, A6), even though the effect was not statistically credible. The credible differences in intervisit intervals detected between bird classes at day 9 (Table A8) should be interpreted with caution as the sample for some bird classes was very reduced (see Fig. A9).

Time spent begging. We found no credible differences in the time spent begging towards different bird classes at day 4 or at day 9 (Tables A9–A11). In contrast with the models including number of begging calls (see main text), we did not detect a difference between begging experienced by helpers $r = 0.25$ and more related individuals at day 4, or at day 9 (Tables A10, A11). As expected, older broods begged for longer than younger broods (Table A9, Fig. A9). Time spent begging, as number of begging calls (see main text, Table 3), increased with time since sunrise (Table A9), while the correlation between time spent begging and our proxy of hunger (interval since last fed) was in the expected direction but not as clear (Table A9).

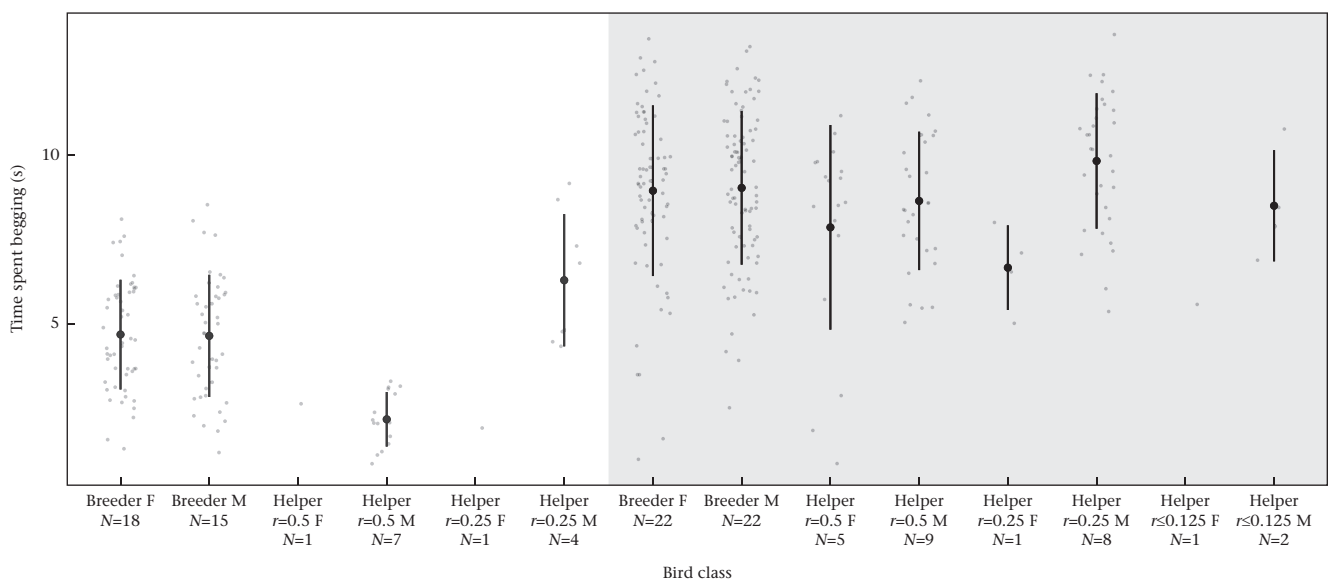**Figure A9.** Observed data and means ± SD of time spent begging (s; out of 15 s) towards birds of each class, at day 4 (white) and at day 9 (grey). Points show observations ($N = 363$), circles show mean time spent begging and bars show SD. F: female; M: male Below each class is the number of birds sampled in each category (N; total = 46 birds at day 4 and 70 birds at day 9). The 'r' values show helper relatedness to the brood.

Table A6
Estimates from model with intervisit intervals as response variable in relation to time spent begging and across different brood ages

Explanatory variable	Level	Mean	95% CrI	$P(>0)$
(Intercept)	(Breeder female day 4)	6.248	[5.595,6.874]	
Age of brood*role*sex				
4 days old	Breeder male	0.522	[−0.339,1.362]	0.88
	Helper female	1.3	[−1.78,4.551]	0.81
	Helper male	1.177	[−2.084,4.46]	0.77
9 days old	Breeder female	0.125	[−0.637,0.878]	0.64
	Breeder male	0.143	[−0.53,0.83]	0.66
	Helper female	−0.516	[−1.25,0.229]	0.08
	Helper male	0.163	[−0.575,0.922]	0.66
Age of brood*relatedness				
4 days old	Helper r=0.25	−1.459	[−4.699,1.584]	0.17
	Helper r<0.125	0.736	[−60.995,62.997]	0.5
9 days old	Helper r=0.25	0.534	[−0.056,1.157]	0.96
	Helper r<0.125	1.054	[−0.097,2.199]	0.97
Age of brood*role*sex*time begging				
4 days old	Breeder female	−0.22	[−0.854,0.433]	0.25
	Breeder male	0.144	[−0.412,0.687]	0.7
	Helper female	0.545	[−1.055,2.261]	0.74
	Helper male	0.362	[−1.425,2.178]	0.65
9 days old	Breeder female	−0.11	[−0.491,0.291]	0.29
	Breeder male	−0.112	[−0.384,0.161]	0.2
	Helper female	0.036	[−0.412,0.482]	0.56
	Helper male	−0.052	[−0.533,0.43]	0.42
Age of brood*relatedness*time begging				
4 days old	Helper r=0.25	−1.061	[−3.005,0.837]	0.14
	Helper r<0.125	0.177	[−61.111,60.203]	0.5
9 days old	Helper r=0.25	−0.281	[−0.9,0.299]	0.18
	Helper r<0.125	0.491	[−1.273,2.356]	0.7
Number of chicks		−0.1	[−0.271,0.059]	0.12
Mean mass of chicks		−0.1	[−0.272,0.072]	0.12
Group size*time begging		−0.094	[−0.257,0.069]	0.13
Group size		0.003	[−0.187,0.197]	0.51
Maximum temperature day		−0.106	[−0.304,0.091]	0.13
Time since sunrise		**−0.191**	**[−0.343,−0.049]**	**0**
Random terms	Standard deviance			
Residuals	0.957		[0.883,1.04]	
Nest ID	0.181		[0.009,0.432]	
Bird ID	0.128		[0.005,0.34]	
Colony ID	0.134		[0.005,0.382]	

Reference for 'Age of brood*role*sex' is Breeder female at day 4 (intercept) and reference for 'Age of brood*relatedness' is Helper r=0.5 (for each sex at day 4). The 'r' values show helper relatedness to the brood. Credible effects are in bold. '$P(>0)$' shows the proportion of the posterior samples that was higher than zero. Marginal R^2 = 0.185 [0.116;0.256] and conditional R^2 of 0.262 [0.159; 0.394].

Table A7
Comparison of intervisit intervals in relation to time spent begging of different bird classes at day 9

	Breeder female	Breeder male	Helper female r=0.5	Helper male r=0.5	Helper female r=0.25	Helper male r=0.25	Helper female r≤0.125
Breeder male	0.002 [−0.472,0.479] P=0.49						
Helper female r=0.5	−0.146 [−0.729,0.446] P=0.31	−0.148 [−0.664,0.363] P=0.29					
Helper male r=0.5	−0.058 [−0.675,0.543] P=0.43	−0.061 [−0.605,0.484] P=0.41	0.087 [−0.488,0.685] P=0.61				
Helper female r=0.25	0.135 [−0.521,0.798] P=0.65	0.133 [−0.441,0.732] P=0.67	0.281 [−0.299,0.9] P=0.82	0.193 [−0.645,0.996] P=0.67			
Helper male r=0.25	0.222 [−−0.501,0.934] P=0.72	0.22 [−0.429,0.857] P=0.74	0.368 [−0.478,1.246] P=0.79	0.281 [−0.299,0.9] P=0.82	0.087 [−0.488,0.685] P=0.61		
Helper female r≤0.125	−0.636 [−2.621,1.222] P=0.26	−0.639 [−2.599,1.167] P=0.25	−0.491 [−2.356,1.273] P=0.3	−0.578 [−2.619,1.378] P=0.29	−0.772 [−2.745,1.036] P=0.21	−0.859 [−3.01,1.147] P=0.21	
Helper male r≤0.125	−0.549 [−2.424,1.213] P=0.28	−0.551 [−2.388,1.15] P=0.28	−0.403 [−2.325,1.335] P=0.34	−0.491 [−2.356,1.273] P=0.3	−0.684 [−2.622,1.09] P=0.24	−0.772 [−2.745,1.036] P=0.21	0.087 [−0.488,0.685] P=0.61

For each comparison, we estimated mean difference, 95% credible intervals and *P* (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of classes on top of the matrix by the estimates of classes on the left (e.g. Breeder female − Breeder male).

Table A8
Comparison of intervisit intervals of different bird classes at day 9

	Breeder female	Breeder male	Helper female r=0.5	Helper male r=0.5	Helper female r=0.25	Helper male r=0.25	Helper female r≤0.125
Breeder male	−0.018 [−0.508,0.475] P=0.48						
Helper female r=0.5	0.641 [−0.034,1.246] P=0.97	**0.66 [0.143,1.162] P=0.99**					
Helper male r=0.5	−0.038 [−0.642,0.584] P=0.45	−0.019 [−0.505,0.5] P=0.46	**−0.679 [−1.201,−0.126] P=0.01**				
Helper female r=0.25	0.107 [−0.628,0.858] P=0.61	0.125 [−0.483,0.718] P=0.65	−0.534 [1.157,0.056] −P=0.04	0.145 [−0.74,0.984] P=0.64			
Helper male r=0.25	−0.572 [−1.211,0.088] P=0.04	**−0.554 [−1.113,−0.034] P=0**	**−1.213 [−1.952,−0.465] P=0**	−0.534 [−1.157,0.056] P=0.04	**−0.679 [−1.201,−0.126] P=0.01**		
Helper female r≤0.125	−0.413 [−1.592,0.781] P=0.25	−0.395 [−1.513,0.783] P=0.25	−1.054 [−2.199,0.097] P=0.03	−0.375 [−1.619,0.906] P=0.28	−0.52 [−1.675,0.653] P=0.19	0.159 [−1.097,1.421] P=0.6	
Helper male r≤0.125	−1.092 [−2.278,0.063] P=0.03	−1.074 [−2.184,0.083] P=0.03	**−1.733 [−2.982,−0.428] P=0.01**	−1.054 [−2.199,0.097] P=0.03	−1.199 [−2.47,0.168] P=0.04	−0.52 [−1.675,0.653] P=0.19	**−0.679 [−1.201,−0.126] P=0.01**

For each comparison, we estimated mean difference, 95% credible intervals and *P* (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of classes on top of the matrix by the estimates of classes on the left (e.g. Breeder female − Breeder male). Credible differences are in bold.

Table A9
Estimates from models with time spent begging as response variable

Response	Explanatory variable	Level	Mean	95% CrI		P(>0)
Time spent Begging (model 1)	(Intercept)	(Breeder female day 4)	1.413	[1.019,1.792]		
	Age of brood*role*sex					
	4 days old	Breeder male	0.029	[−0.31,0.365]		0.57
		Helper female	−0.399	[−0.904,0.105]		0.06
		Helper male	−0.213	[−0.634,0.2]		0.16
	9 days old	**Breeder female**	**1.343**	**[1.02,1.66]**		**1**
		Breeder male	**1.341**	**[1.017,1.67]**		**1**
		Helper female	**1.455**	**[1.044,1.844]**		**1**
		Helper male	**1.431**	**[1.038,1.806]**		**1**
	Age of brood*relatedness					
	4 days old	Helper r=0.25	0.12	[−0.368,0.603]		0.68
		Helper r<0.125	0.101	[−60.456,60.261]		0.5
	9 days old	Helper r=0.25	−0.201	[−0.553,0.131]		0.13
		Helper r<0.125	−0.579	[−1.174,0.036]		0.03
	Number of chicks		0.039	[−0.211,0.295]		0.62
	Mean mass of chicks		0.004	[−0.253,0.274]		0.5
	Group size		−0.083	[−0.345,0.195]		0.27
	Maximum temperature day		0.002	[−0.258,0.251]		0.51
	Random terms	Standard deviance				
	Residuals		0.509	[0.472,0.55]		
	Nest ID		0.66	[0.485,0.878]		
	Bird ID		0.112	[0.008,0.231]		
	Colony ID		0.187	[0.008,0.525]		
Time spent begging (model 2)	(Intercept)	(Breeder female day 4)	1.442	[1.048,1.826]		
	Age of brood*role*sex					
	4 days old	Breeder male	0.028	[−0.309,0.354]		0.57
		Helper female	−0.35	[−0.84,0.135]		0.07
		Helper male	−0.272	[−0.686,0.158]		0.1
	9 days old	**Breeder female**	**1.338**	**[1.028,1.65]**		**1**
		Breeder male	**1.373**	**[1.031,1.699]**		**1**
		Helper female	**1.453**	**[1.062,1.846]**		**1**
		Helper male	**1.468**	**[1.075,1.839]**		**1**
	Age of brood*relatedness					
	4 days old	Helper r=0.25	0.049	[−0.475,0.551]		0.58
		Helper r<0.125	0.398	[−62.773,62.825]		0.5
	9 days old	Helper r=0.25	−0.249	[−0.601,0.08]		0.07
		Helper r<0.125	−0.424	[−1.034,0.22]		0.09
	Number of chicks		0.023	[−0.242,0.28]	0.56	
	Mean mass of chicks		0.03	[−0.229,0.3]		0.58
	Group size		−0.125	[−0.393,0.14]		0.17
	Maximum temperature day		0.061	[−0.203,0.331]		0.69
	Interval last fed		0.024	[−0.029,0.077]		0.81
	Time since sunrise		**0.237**	**[0.157,0.315]**		**1**
	Random terms	Standard deviance				
	Residuals		0.482	[0.445,0.523]		
	Nest ID		0.693	[0.516,0.92]		
	Bird ID		0.149	[0.024,0.264]		
	Colony ID		0.177	[0.007,0.518]		

Reference for 'Age of brood*role*sex' is Breeder female at day 4 (intercept) and reference for 'Age of brood*relatedness' is Helper r=0.5 (for each sex at day 4). The 'r' values show helper relatedness to the nestlings. Models are similar but second model includes hunger proxies. Credible effects are in bold. 'P > 0' shows the proportion of the posterior samples that was higher than zero. Model 1: marginal R^2 = 0.403 [0.279;0.516] and conditional R^2 0.795 [0.729; 0.855]. Model 2: marginal R^2 = 0.386 [0.271;0.498] and conditional R^2 0.816 [0.757; 0.874].

Table A10
Comparison of time spent begging in visits of different bird classes at day 4 (estimated from model 1)

	Breeder female	Breeder male	Helper female $r=0.5$	Helper male $r=0.5$	Helper female $r=0.25$	Helper male $r=0.25$	Helper female $r\leq0.125$
Breeder male	−0.029 [−0.365,0.31] $P=0.43$						
Helper female $r=0.5$	0.399 [−0.105,0.904] $P=0.94$	0.428 [−0.045,0.887] $P=0.96$					
Helper male $r=0.5$	0.213 [−0.2,0.634] $P=0.84$	0.241 [−0.162,0.629] $P=0.87$	−0.187 [−0.613,0.281] $P=0.2$				
Helper female $r=0.25$	0.28 [−0.263,0.823] $P=0.84$	0.308 [−0.194,0.806] $P=0.89$	−0.12 [−0.603,0.368] $P=0.32$	0.067 [−0.605,0.724] $P=0.58$			
Helper male $r=0.25$	0.093 [−0.378,0.559] $P=0.66$	0.122 [−0.32,0.566] $P=0.71$	−0.306 [−0.975,0.358] $P=0.18$	−0.12 [−0.603,0.368] $P=0.32$	−0.187 [−0.613,0.281] $P=0.2$		
Helper female $r\leq0.125$	0.298 [−59.94,60.95] $P=0.51$	0.327 [−60.06,60.96] $P=0.51$	−0.101 [−60.26,60.46] $P=0.5$	0.086 [−60.03,60.75] $P=0.5$	0.019 [−60.37,60.64] $P=0.5$	0.205 [−60.14,60.68] $P=0.5$	
Helper male $r\leq0.125$	0.112 [−60.17,60.93] $P=0.5$	0.14 [−60.30,60.82] $P=0.5$	−0.288 [−60.56,60.472] $P=0.5$	−0.101 [−60.26,60.46] $P=0.5$	−0.168 [−60.60,60.37] $P=0.5$	0.019 [−60.37,60.65] $P=0.5$	−0.187 [−0.613,0.281] $P=0.2$

For each comparison, we estimated mean difference, 95% credible intervals and P (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of classes on top of the matrix by the estimates of classes on the left (e.g. Breeder female − Breeder male).

Table A11
Comparison of time spent begging in visits of different bird classes at day 9 (estimated from model 1)

	Breeder female	Breeder male	Helper female $r=0.5$	Helper male $r=0.5$	Helper female $r=0.25$	Helper male $r=0.25$	Helper female $r\leq0.125$
Breeder male	0.002 [−0.236,0.249] $P=0.5$						
Helper female $r=0.5$	−0.113 [−0.455,0.218] $P=0.26$	−0.114 [−0.411,0.173] $P=0.22$					
Helper male $r=0.5$	−0.089 [−0.405,0.226] $P=0.29$	−0.09 [−0.365,0.185] $P=0.26$	0.024 [−0.259,0.308] $P=0.57$				
Helper female $r=0.25$	0.088 [−0.204,0.378] $P=0.73$	0.087 [0.209,0.377] $−P=0.73$	0.201 [−0.131,0.553] $P=0.87$	0.177 [−0.244,0.58] $P=0.82$			
Helper male $r=0.25$	0.113 [−0.206,0.431] $P=0.76$	0.111 [−0.224,0.444] $P=0.75$	0.225 [−0.251,0.707] $P=0.83$	0.201 [−0.131,0.553] $P=0.87$	0.024 [−0.259,0.308] $P=0.57$		
Helper female $r\leq0.125$	0.466 [−0.163,1.066] $P=0.93$	0.465 [−0.148,1.031] $P=0.94$	0.579 [−0.036,1.174] $P=0.97$	0.555 [−0.129,1.206] $P=0.95$	0.378 [−0.292,0.988] $P=0.88$	0.354 [−0.381,1.046] $P=0.84$	
Helper male $r\leq0.125$	0.49 [−0.149,1.079] $P=0.93$	0.489 [−0.109,1.054] $P=0.94$	0.603 [−0.08,1.254] $P=0.96$	0.579 [−0.036,1.174] $P=0.97$	0.402 [−0.306,1.07] $P=0.87$	0.378 [−0.292,0.988] $P=0.88$	0.024 [−0.259,0.308] $P=0.57$

For each comparison, we estimated mean difference, 95% credible intervals and P (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of classes on top of the matrix by the estimates of classes on the left (e.g. Breeder female − Breeder male).