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Begging for answers: How do parents and helpers respond to offspring begging in a cooperatively breeding system?

Rita Fortuna

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Research Center in Biodiversity and Genetic Resources

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Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

Porto, ______/______/_________

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Abstract

In species that provide parental care, parent-offspring conflicts may arise due to the difference between the optimal amount of care that parents should provide from the offspring perspective and from the parents perspective. A good example is parental provisioning in passerines, where there is an ongoing interaction between food demand by begging and the parental response in terms of food provisioning. Conflicts between parents are also expected as each bird should be under selection to minimize its personal effort by trying to shift the greatest possible workload towards its partner. Theory predicts that females may be able to manipulate paternal contribution using maternal effects, specifically by altering androgens levels of the eggs, but few empirical studies have been conducted to test this prediction. In cooperatively breeding systems, where non-breeding 'helpers' also provide care to the brood, this conflict may extend to the rest of the breeding group. For example, conflicts may occur between parents and helpers (and among helpers) about how much care to provide, since each individual should be under selection to minimize its workload and leave as much care as possible to the other group members. In this case, females may be expected to attempt to exploit not only their partners, but also the helpers, and in particular the helpers that are unrelated related to them. In the sociable weavers, *Philetairus socius*, previous work has found that females use the presence of helpers to decrease their own investment in reproduction. Specifically, females with more helpers laid smaller eggs, with lower yolk hormonal levels, and produced offspring that begged at lower rates. The aims of the present study were to follow up on these previous results and further explore the possibility of females influencing conflicts over food provisioning through maternal effects. Specifically to explore 1) if there were differences in the way parents and helpers responded to the begging behaviour of the nestlings and 2) whether nestlings begged in the same fashion towards different classes of birds. The workload of each carer was assessed, their status was attributed (distinguishing breeders by sex and helpers by kin relationships towards offspring and female breeders) and the begging they received was measured (defined by call rate and frequencies). The general results were consistent with the predictions. Birds exposed to higher rates of begging took less time to come back with food and male breeders displayed the highest feeding levels. Begging rate seemed to honestly signal nestlings' hunger as it was positively correlated with their last feeding and the time of the day, but call rate was not significantly different regarding different classes of birds. All the birds responded in the same way to an increase in begging rate. Finally, parents were the ones exposed to the highest frequency calls. This study emphasises the importance of exploring the interactions between offspring demand and provisioning rules among cooperatively breeding systems, with more complex nets of family interactions to better understand the resolution of family conflicts and their underlying mechanisms.

Keywords: Parental care, conflicts, begging, maternal manipulation, cooperative breeding.

Resumo

Conflitos entre pais e crias, nas espécies que exibem cuidados parentais, podem surgir devido à diferença entre a quantidade ótima de cuidado que os pais devem provisionar na perspetiva das crias e na perspetiva dos próprios pais. Um bom exemplo é o cuidado parental existente entre as aves, onde existe uma recorrente interação entre a demanda de alimento, com comportamentos de solicitação pelas crias, e a resposta parental em termos de provisionamento de alimento. Conflitos entre sexos são também previsíveis visto que cada ave deverá ser selecionada para minimizar o seu esforço pessoal e tentar transferir a maior quantidade possível de esforço para o seu parceiro. As fêmeas poderão ter a capacidade de manipular a contribuição paternal utilizando efeitos maternais, especificamente através da alteração do nível de androgénios nos ovos, mas poucos estudos experimentais foram conduzidos no sentido de comprovar esta teoria. Nos sistemas de cria cooperativa, onde "ajudantes" não-reprodutores também cuidam da ninhada, os conflitos poder-se-ão estender para o resto do grupo. Por exemplo, poderão surgir conflitos entre pais e ajudantes (e entre os ajudantes) relativamente à quantidade de cuidado que devem providenciar, visto que cada indivíduo estará selecionado para minimizar a sua carga de trabalho e deixar que os outros indivíduos invistam a uma taxa superior à sua. Neste caso, espera-se que as fêmeas tentem explorar não só os seus parceiros, como também os ajudantes, nomeadamente aqueles que lhes são menos próximos. Nos tecelões sociais, *Philetairus socius*, estudos anteriores verificaram que as fêmeas investem menos na reprodução na presença de mais ajudantes. Especificamente, fêmeas com mais ajudantes puseram ovos mais pequenos, com menor conteúdo hormonal na gema, e produziram crias que solicitavam alimento a taxas mais baixas. O presente trabalho teve como objetivo dar seguimento aos resultados previamente obtidos e explorar a possibilidade de as fêmeas poderem influenciar os conflitos relacionados com o provisionamento de alimento através de efeitos maternais. Em específico, explorar 1) se haveria diferenças na forma como pais e ajudantes respondiam ao comportamento de solicitação das crias e 2) se as crias solicitariam alimento de igual forma estando perante indivíduos de diferente estatuto. Foi calculado o esforço de cada indivíduo, atribuído o seu estatuto (distinguindo os indivíduos reprodutores pelo sexo e os ajudantes pelas relações de parentesco com as crias e com as fêmeas reprodutoras) e o comportamento de solicitação apresentado a cada um foi também medido (definido pela taxa de solicitação e pela frequência acústica das chamadas). De uma maneira geral, os resultados obtidos estão de acordo com o esperado. Indivíduos expostos a maiores taxas de solicitação demoraram menos tempo a regressar ao ninho com alimento e os machos reprodutores foram os que demostraram o maior esforço. A taxa de solicitação pareceu representar honestamente a necessidade de alimento das crias visto que foi obtida uma correlação positiva com a última vez que teriam sido alimentadas e com os períodos do dia em que os indivíduos exibem menor atividade, apesar de não terem sido obtidas diferenças significativas na taxa de solicitação direcionada a indivíduos de diferente estatuto. Todas as classes responderam da mesma maneira a aumentos na taxa de solicitação das crias. Este estudo reforça a importância de explorar as interações entre a demanda das crias e as regras de provisionamento em sistemas de cria cooperativa, com teias de interação familiar mais complexas, para melhor entender a resolução dos conflitos familiares e os mecanismos a si adjacentes.

Palavras-chave: Cuidado parental, conflitos, solicitação, manipulação maternal, cria cooperativa.

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Abbreviations

AIC – Akaike Information Criterion

CHD – Chromo-helicase-DNA-binding

DNA – Deoxyribonucleic Acid

FFT – Fast-Fourier Transform

HD – High Definition

LED – Light Emitting Diode

LMMs – Linear Mixed Models

MAH – Manipulating Androgens Hypothesis

PC – Principal Component

PCA – Principal Components Analysis

PCM – Pulse-Code Modulation

Q25 – Quartile corresponding to 25% of the energy

Q50 – Quartile corresponding to 50% of the energy

Q75 – Quartile corresponding to 75% of the energy

QQ – Quantile-Quantile

Introduction

Parental care occurs across several taxa, assuming numerous forms, and the study of the multiple (and often complex) strategies associated with this behaviour has clarified its importance for the growth and survival of the offspring (Gross & Sargent 1985; Balshine 2012; Smiseth *et al.* 2012; Trumbo 2012). Parental care is most common among mammals and birds and in 90 to 95% of the bird species both parents look after their young chicks (Clutton-Brock 1991; Balshine 2012). Typical joint care actions among birds include nest building, egg incubation, protection against predators and parasites and offspring nourishment (Balshine 2012).

Parental care usually entails costs to the parents' survival and future reproduction (Clutton-Brock 1991; Klug *et al.* 2012). Given this, it will only be beneficial for parents to provide care if the fitness benefits arising from their offspring's increased survival, growth and/or quality are greater than the fitness costs derived from sharing resources and incurring physiological costs while caring for their young (Alonso-Alvarez & Velando 2012; Klug *et al.* 2012). Parents should be selected to optimally distribute their time and energy by their different breeding events (Klug *et al.* 2012). On the other hand, offspring should be selected to prioritize their own survival and hence demand an amount of care greater than the one directed to their siblings from the current or future breeding attempts (Trivers 1974). As a result, a parent-offspring conflict is expected to arise due to the difference between the optimal amount of care that parents should provide from the current offspring perspective and from the parents own perspective (Kilner & Hinde 2012). This 'interbrood conflict' is thought to lead to the evolution of mechanisms through which offspring demand and improve the care they are provided with, possibly persuading parents to supply energy they should instead save for the next breeding attempts (Kilner & Hinde 2012). The behavioural display of this conflict can emerge when both parents and offspring have the possibility to influence parental investment or provisioning (Kilner & Johnstone 1997). A good example is parental provisioning in passerines, where there is an ongoing interaction between begging behaviour and the parental response in terms of food provisioning.

The discussion on whether begging is a truly direct signal of need has been the subject of a long debate (Trivers 1974; Kilner & Johnstone 1997; Johnstone 1999; Godfray & Johnstone 2000; Royle *et al.* 2002; Brilot & Johnstone 2003; Martín-Gálvez *et al.* 2011; Moreno-Rueda & Redondo 2012). Among birds, begging behaviour includes visual cues such as brightly coloured gaping and/or posturing and performing loud and repetitive vocal signals (Kilner & Johnstone 1997). Several authors suggested that offspring begging is used as a manipulative signal originated from the siblings competition in order to obtain more care than what is optimal for parents to provide (initially suggested by Trivers 1974; supported by Stamps *et al.* 1978; Macnair & Parker 1979; Parker & Macnair 1979; Parker 1985; Neuenschwander *et al.* 2003). However, others propose that the cost of this signal prevents it from being manipulative and that it should, at least to some extent, reflect the potential fitness gain for offspring if these were to receive extra resources (Godfray & Johnstone 2000; see Parker *et al.* 2002 and Royle *et al.* 2002 for comparative reviews and discussion). The honesty of this signal is further supported by the idea that the advantages that a nestling would gain by exaggerating its needs should be balanced by the costs of signalling at high levels (i.e. spending energy and attracting predators) and the costs of inclusive fitness (either by reducing the amount of food delivered to their siblings or by exploiting their parents, possibly reducing their future reproduction; Godfray & Johnstone 2000; Moreno-Rueda 2007a). This is thought to make begging an evolutionary stable behaviour and a reliable indicator for parents of their nestling's condition (Godfray 1995; see also Godfray & Johnstone 2000 and Moreno-Rueda 2007a). Furthermore, begging cues have been shown to contain information on offspring need for food (Cotton *et al.* 1996) and this behaviour was empirically studied and commonly seen to be intensified when nestlings were subject to food deprivation experiments (Bengtsson & Rydén 1983; Whittingham & Robertson 1993; Leonard & Horn 2001a; b; Sacchi *et al.* 2002; Reers & Jacot 2011; Klenova 2015). Parents, accordingly, have been shown to adjust their provisioning levels to the increased levels of begging directed towards them (Bengtsson & Rydén 1983; Burford *et al.* 1998; Price 1998; Estramil *et al.* 2013).

In most bird species, both parents provide care to their young (Clutton-Brock 1991). Therefore, biparental care is expected to create another conflict of interest, now between partners, since the amount of care provided by one bird will not only influence the reproductive value of its offspring but probably the amount of care that its partner provides also (Lessells 2012). This means that, although the benefits for the offspring are caused by the combined effort of the pair, the costs for each parent will be due to its own individual effort. Consequently, a sexual conflict may arise because each bird should be under selection to minimize its personal effort by trying to shift the greatest possible workload towards its partner (Houston *et al.* 2005). A few behavioural mechanisms are currently suggested as possible mediators to solve the sexual conflicts arising from parental care, but the negotiation hypothesis is the one that has received most support (Lessells 2012; Lessells & McNamara 2012; see Paquet &

Smiseth 2016 for a review). It suggests that each parent adjusts its levels of care as a direct response to the contribution of its partner by partially compensating for their partner's reduction (McNamara *et al.* 1999; Harrison *et al.* 2009). These mechanisms, however, assume that each partner possesses equivalent strategies to solve the conflicts. Yet, females may be able to influence offspring phenotypes through prenatal maternal effects.

There is growing evidence on the maternal ability to adjust egg components that are known to influence offspring begging and development (Mousseau & Fox 1998; Groothuis *et al.* 2005; Meylan *et al.* 2012). The causal effects of the female's phenotype on the phenotype of her offspring, over and above the direct effects of the genes that the nestlings inherited from her, are commonly called maternal effects (Mousseau & Fox 1998). These effects can be mediated through several epigenetic mechanisms and often occur in response to the female's prenatal environmental cues (Saino *et al.* 2002; von Engelhardt & Groothuis 2011; Meylan *et al.* 2012). When adaptive, if the environmental conditions that the offspring will encounter are sufficiently predictable by the female, such as the food availability or her male partner's quality (Sheldon 2000; Benton *et al.* 2005), she could adjust her offspring's phenotype to become more adapted to this environment (reviewed by Mousseau & Fox 1998). This adjustment may either be nutritionally mediated - varying the levels of proteins, lipids, carotenoids, etc. - and/or hormonally mediated (Badyaev 2008; von Engelhardt & Groothuis 2011). Nutritional and hormonal levels resulting from the female's investment may influence the amount of care that a carer provides since birds are expected to obtain information on nestlings' needs based on their development and behaviour, which are in turn partially conditioned by those metabolic pathways. Given this potential, females may have evolved this mechanism as an extra tool for solving sexual conflicts and possibly as a manipulation strategy for male contributions towards parental care without the need to directly interact with their partners (Moreno-Rueda 2007b; Müller *et al.* 2007; Paquet & Smiseth 2016). This could be beneficial for females if they are able to either save resources by not responding to begging as males do (Müller *et al.* 2007) or by, for instance, decreasing egg size, redirecting the prenatal cost of egg production (that would only be carried by herself) to the postnatal cost of feeding that she shares with the male (Savage *et al.* 2015; Paquet & Smiseth 2016). Summing up, females should be under selection to adjust their offspring's phenotype in a way that minimises their own investment and that demands as much male care as possible, increasing her fitness and/or possibly her offspring fitness as well (Paquet & Smiseth 2016). The male's amount of care will then derive from the way this conflict is resolved and on whether or not the female can use maternal effects to manipulate his decision on how much care he should provide (Paquet & Smiseth 2016). Nutritional effects may influence, for instance, the offspring's size (which can be used as a cue for nestlings' needs; Smiseth *et al.* 1998), but the hormonal pathway and its consequence on nestling's begging has been the one receiving more attention (MacGregor & Cockburn 2002; Müller *et al.* 2007). Yolk hormones such as androgens or corticosterone were evidenced to influence offspring growth and survival as well as begging behaviour among several bird species (Schwabl & Lipar 2002; Eising & Groothuis 2003; Groothuis *et al.* 2005; Smiseth *et al.* 2011; Perez *et al.* 2016). Moreno-Rueda (2007) reviewed the manipulating androgens hypothesis (MAH) which predicts that if yolk androgens (such as testosterone) increase begging behaviour, and if male parents are more responsive to this increment than females, females may manipulate paternal contribution by increasing the levels of androgens deposited in the eggs (Michl *et al.* 2005; Moreno-Rueda 2007; Müller *et al.* 2007; reviewd in Paquet & Smiseth 2016). A few studies on birds have tried to show some evidence for this hypothesis and the majority of them experimentally increased yolk androgen levels and tested its effect on male parental effort, finding no causal effect (Ruuskanen *et al.* 2009; Müller *et al.* 2010; Barnett *et al.* 2011; Laaksonen *et al.* 2011; Noguera *et al.* 2013). Contrary to the MAH, a study on great tits (*Parus major*) found that males did not reduce their provisioning when eggs were injected with an androgen-blocking substance, while females did (Tschirren & Richner 2008). The fact that these experiments have been directly linked to the androgens specific mechanism for manipulation and that a direct causal effect between yolk androgens levels and male parental effort has not been found, may be due to methodological problems in these empirical studies (reviewed in Paquet & Smiseth 2016). In their recent review, Paquet and Smiseth (2016) suggested that the MAH predictions can be applied to any effects that mothers may be able to adjust, including androgens deposition, but equally other egg components, egg size and/or egg coloration. Thus, the authors proposed the development of new approaches that include experiments independent of the specific mechanisms of manipulation and focus instead on the prenatal environmental conditions that are expected to induce female manipulation (Paquet & Smiseth 2016).

In cases where more than two birds provide care, such as in cooperative breeding systems, the balance between cooperation and conflict becomes even more complex. In these extended family group systems, mechanisms to solve conflicts may represent refined forms of the ones observed among biparental care. In cooperative breeding systems, offspring care (such as food provisioning) is not only conducted by parents but also by other non-breeding individuals, also known as helpers, that may or may not be genetically related to the breeding pair (Cockburn 1998; Cant 2012). Around 9% of all bird species are classified as cooperative breeders (Cockburn 2006). An important aspect of this type of cooperation is that helpers retain their ability to reproduce, which means that cooperating is expected to bring them a larger future fitness (direct or indirect) than the current fitness they would gain from breeding (Cant 2012). As for conflict between the two parents, conflicts between parents and helpers (and among helpers) may happen since each individual should be under selection to minimize its workload and leave as much as possible to the other group members. Moreover, it should be more advantageous to delegate the workload towards unrelated than towards related individuals (Savage et al. 2013). Therefore, it should then be more advantageous for females to obtain more help from individuals that are the least related to them, further leading to the possibility that females may manipulate the care provided not only by the father but also by the helpers she has available, and that this manipulation may be influenced by the number and the relatedness of those helpers (Paquet *et al.* 2015a). But also offspring could be willing to exploit individuals less related to them since, from an inclusive fitness perspective, it would be more costly for them to exploit their parents or siblings than unrelated helpers (Paquet & Smiseth 2016). Previous studies on cooperatively breeding systems, where responses to begging behaviour were empirically assessed, showed that helpers and parents differed in how they responded. In one study on a species where helpers and parents are highly related, both presented similar provisioning levels, while in a species where males and helpers are commonly unrelated to the nestlings and the female, they were the ones responding more to the additional offspring demand (see, respectively, Wright 1998 and MacGregor & Cockburn 2002). In sociable weavers (*Philetairus socius*), a cooperatively breeding monogamous passerine, previous work has found some indirect support for the female manipulation hypothesis (Doutrelant *et al.* 2011; Paquet *et al.* 2013; Paquet & Smiseth 2016). Sociable weaver breeding males are known to feed at higher rates than breeding females or helpers (Doutrelant & Covas 2007) and helpers were found to provision at higher rates when less related to the female (Doutrelant *et al.* 2011). Additionally, both the size of the eggs and the levels of yolk corticosterone and testosterone were smaller when females were, respectively, helped by more individuals or when helpers were present (Paquet *et al.* 2013). Finally, a cross-fostering experiment has shown that eggs from females with more helpers produced offspring that begged at lower rates (Paquet *et al.* 2015a). By lowering the begging rates of her offspring, the female could be adaptively reducing their energy expenditure, as this decrease in food demand can be compensated by the presence of more helpers which provide additional food (Paquet *et al.* 2015a). However, nothing is known about the interactions between offspring begging and the carer's provisioning in this species. In particular, whether and how breeders and helpers respond to begging, whether offspring beg differently towards different carers and whether these interactions depend on the relatedness between parents, helpers and offspring.

This work primarily aims to explore the variation of the provisioning behaviour of parents and helpers, in response to vocal begging, in the cooperatively breeding sociable weavers. The workload of each carer was assessed, their status was attributed (distinguishing breeders by sex and helpers by their kin relatedness towards mothers and offspring) and the begging they received was measured (defined by call rates and frequency). I expected a positive correlation between food supply and begging behaviour and that birds of different status contribute on different levels (breeding males were expected to show the highest provisioning levels Doutrelant & Covas 2007). Under the light of the maternal manipulation hypothesis, we could expect males and unrelated helpers to be the ones increasing the most their workload in response to begging intensification. A second purpose of this study was to assess what influences the begging behaviour of the offspring and, particularly, if nestlings begged differently towards different classes of birds. It was most of all expected that begging should be positively correlated with the hunger levels of the brood and, if female manipulation is acting in this system, to be stronger when directed towards males and helpers unrelated to the female.

Methods

Study species and field methods

The sociable weaver (*Philetairus socius*) is a colonial cooperatively breeding bird endemic to the semi-arid savannahs of Namibia and South Africa's Northern Cape Province (Maclean 1973a). Individuals feed mainly on insects and seeds (Maclean 1973b) and build together massive communal nests with several chambers where they breed and roost throughout the year (Maclean 1973c). Colony sizes are extremely variable, ranging from a few to several hundred individuals (Maclean 1973c). During a breeding season, females may have several breeding attempts and usually lay one egg per day, ending up with clutches of 2 to 4 eggs (exceptionally up to 6; Covas *et al.* 2008). The typical duration of the incubation period is 15 days and nestlings usually hatch asynchronously (1 per day; Maclean, 1973a; Covas *et al*. unpublished data). The subsequent nestling period lasts for 21 to 25 days (Maclean 1973a). Sociable weavers are facultative cooperative breeders, and hence breeding pairs may or may not have individuals helping to raise the brood (30 to 80% of the breeding attempts have 1 to 5 helpers; Covas et al., 2008). The majority of the helpers (93%) are offspring from the previous years of one or both breeders (Covas *et al.* 2006) and females usually just help during their first year. Older and unrelated helpers are mainly males (Doutrelant *et al.* 2004). Helping consists primarily of food provisioning, but helpers also assist with brooding, nest sanitation and building (Ferreira 2015).

This study took place at Benfontein nature reserve near Kimberley (South Africa). The study area is Kalahari sandvelt, consisting of open *Acacia* (*Vachellia*) savannah with grassland and includes approximately 30 sociable weaver colonies (Covas *et al.* 2008). Rainfall is low and inconstant and strongly influences the breeding seasons' duration, clutch size and fledging success (Covas 2002). An additional major factor affecting reproductive output is nest predation by snakes (ca. 70% Covas, 2002).

Individuals in about 15 colonies have been captured using mist nests between late August and early September in most years since 1999 (Covas 2002). Unringed birds are ringed with a unique colour ring combination and a specific numbered aluminium ring, both allowing their posterior visual identification at distance. Blood samples are usually collected during this period for genetic sexing and determination of parentage and kin relationships among individuals. The number of individuals caught in each colony is used as the measure of colony size.

Every year, breeding monitoring is conducted in detail at 13 colonies. Four to six of these colonies are protected from snake predation, by wrapping the tree trunks with heavy duty cling plastic film, to ensure enough data for the experiments underway.

The nest contents in all colonies are inspected every 3 days with an extendable LED lighted mirror from the rooftop of a vehicle parked under the *Acacia* tree that supports the colonial communal nest. All the eggs are marked and weighed and nests are visited again after the 15th day of incubation to determine hatching dates. Hatching order is noted and chicks are marked on their feathers at hatching which enables the relation between laying and hatching orders. When chicks were 9 days old (day 9), the nestlings were weighed and ringed with a unique numbered ring. Blood samples were also taken at this point. Finally, at day 17, the chambers were visited again to weight, measure the tarsus and the wing of the nestlings and provide them with their individual colour combination of rings that allows their identification. Day 17 nests or older were no longer visited since this can induce premature fledging of the young birds. During three different periods of the breeding attempts (around day 4, day 9 and day 17), nests were videotaped during 3 to 6h for feeding rate, group size and group identity assessments.

Weather condition variables (rainfall and temperature) were collected at Kimberley Airport Station, 12 km from the centre of the study site.

This specific study was conducted in 11 different colonies between September and December of the 2014-2015 season. Since the breeding season of 2015-16, during which I conducted field work, was characterized by a particularly low rainfall, unprecedented low levels of feeding visits to the nests and high levels of nestlings' mortality, we decided to include in this thesis only the 2014-2015 data as the two seasons would not have been comparable.

Acoustic recordings

In order to study the effect of the begging behaviour on the food provisioning of the birds, the begging calls from each nest were recorded when the first hatched nestling was four days old (day 4), since there is some evidence that the maternal effects on the nestlings' begging should be more pronounced during the first few days after hatching (Paquet *et al.* 2015a). Early in the morning at day 4, chicks were weighed, recorders were set up to record acoustic begging and a camera was activated to video tape nest visits simultaneously (starting 30 to 60 minutes after sunrise whenever possible; see below and **Figure 6**).

Nestlings' calls were recorded with a tie-clip microphone (Olympus ME15, frequency range = 15 to 12000 Hz) connected to a recorder (Olympus WS-750M) and clipped at the entrance of each chamber. Calls were recorded at 44.1 kHz in uncompressed PCM format for further analyses. In each chamber, there were several nestlings that were thus all recorded together.

Acoustic analysis

Recordings were analysed using Avisoft-SASLab PRO version 5.2.09 sound analysis software (Avisoft Bioacoustics, Berlin, Germany). A final sample of 975 analysed begging events from 22 recorded nests was included in the data and used for statistical analysis. A begging event was the recorded event that began in the first begging call after the feeding adult arrival call and ended 20 seconds after.

The types of acoustic measures extracted are summarised in **Table 1**. Only recordings in which there was a visually assessed signal to noise ratio sufficient to allow reliable measurements on amplitude envelopes and frequency spectra were used.

Table 1. Summary of all the acoustic measures, their unity and the duration used for their measurement. Light grey: measures related to the quantity (intensity) of nestlings' acoustic begging production. Dark grey: measures of frequency parameters of nestlings' acoustic begging production. *Peak frequency = frequency of maximum amplitude, Q = quartile = frequencies corresponding to 25%, 50%, and 75% of energy.*

Measurement	**Unity**	**Sound duration** (seconds)
Begging rate	Number of calls/second	20
Envelope surface area	Unity of surface^2	20
Peak frequency	Hertz (Hz)	10
Q25	Hertz (Hz)	10
Q50	Hertz (Hz)	10
Q75	Hertz (Hz)	10

- The *begging rate* is one of the most used measures in studies of nestlings' acoustic signalling of need and several experiments of food deprivation have shown that begging rate is significantly correlated with nestlings' degree of hunger (Leonard & Horn 2001a, 2006; Marques *et al.* 2009; Reers & Jacot 2011; Klenova 2015). Begging rate was estimated on spectrograms of the recordings (Sampling Frequency=44.1 kHz, FFT length= 512 points, Window= Hamming). The total number of begging calls during 20 seconds was counted. The count began at the first distinguishable begging call after the adult entrance into the nest, right after its last arrival call, and was finished 20 seconds later (**Table 1**; **Figure 1;** see **Figure 2** for examples of individual begging calls).The duration of this measurement was set to 20 seconds and not to 11 seconds (Paquet *et al.* 2015a) as a preliminary inspection of the begging recordings' spectrograms has shown that a considerable number of broods were begging for longer periods than 11 seconds (see examples in **Figure 1**).

Prior to analysis of the following acoustic measures, recorded files were cleaned from extraneous noise. Each file was first filtered to remove noise below 2 kHz. Moreover, other sounds than begging calls, of a frequency superior to 2 kHz and occurring between begging calls, were manually deleted and replaced by silence of the same duration. When begging calls were covered by other sounds (vocalisations from carers, from birds from other species, from older nestlings in surrounding nests, etc.) they were also replaced by silence.

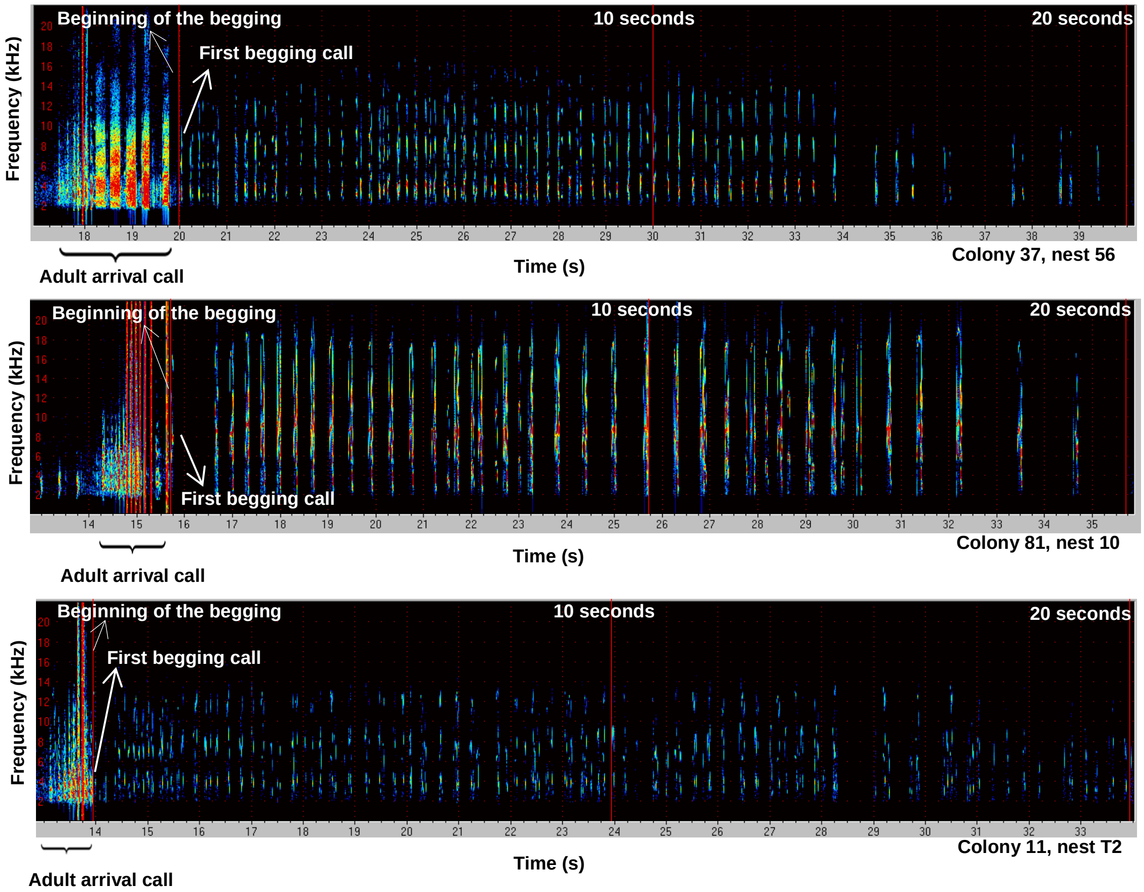


Figure 1. Spectograms (frequency versus time, relative sound intensity represented by a colour scale) of three begging recording events from three different nests and colonies. Red vertical lines mark, sequentially, the beginning of a begging event (in between the adult arrival call – in curly brackets – and the first begging call – in arrows), a 10 seconds middle mark and the end of the 20 seconds.

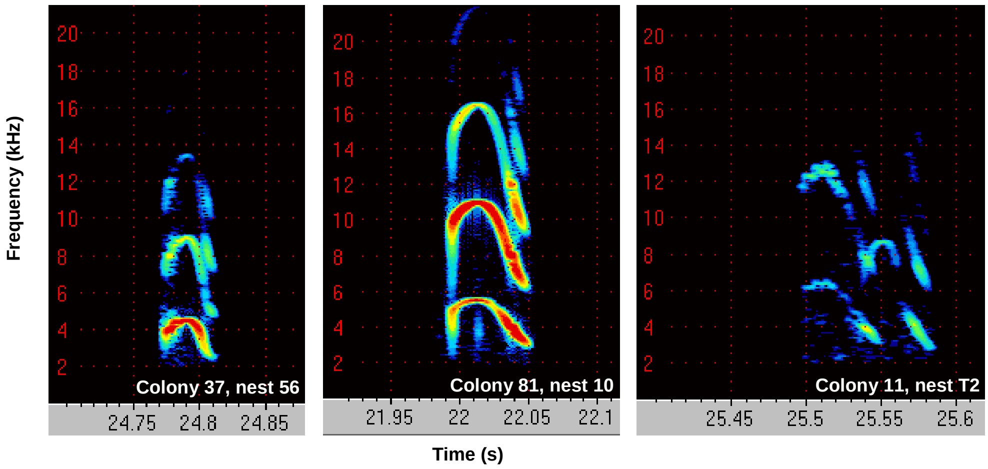


Figure 2. Singular examples of the begging calls are represented in the spectograms (frequency versus time, relative sound intensity represented by a colour scale) of the same three begging recording events (in the third example from colony 11, nest T2, two overlapping begging calls can be observed).

- The *envelope surface area* [1] was estimated using an envelope (positive amplitude versus time) performed on the same first 20 seconds of the begging event (**Figure 3**).

[1] This acoustic measure is not present in current literature but is suggested in this study as an alternative intensity/quantity of the sound measurement.

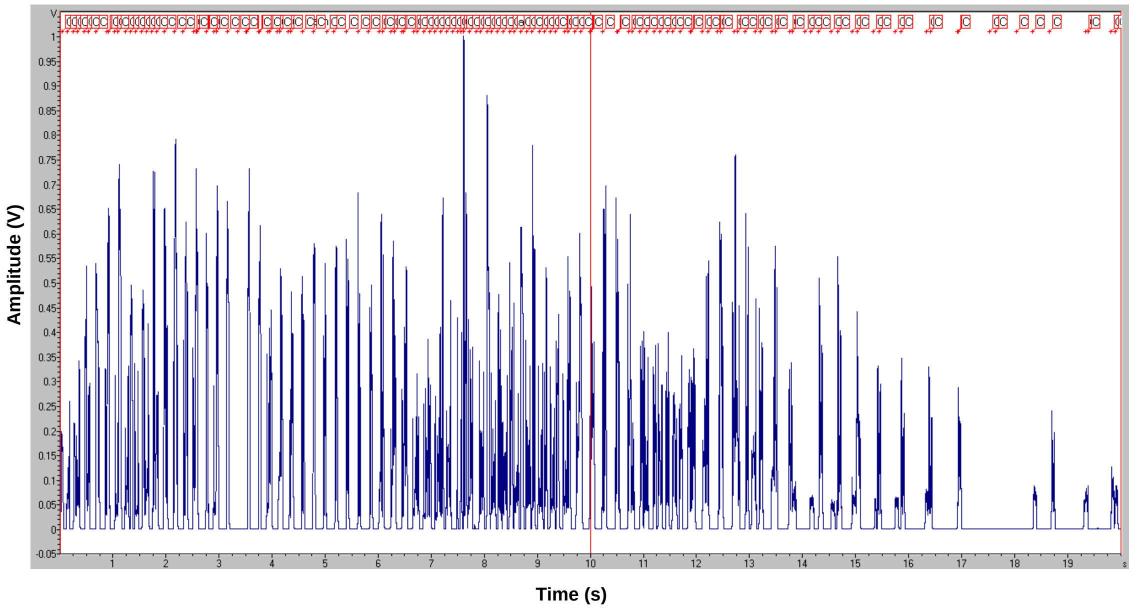
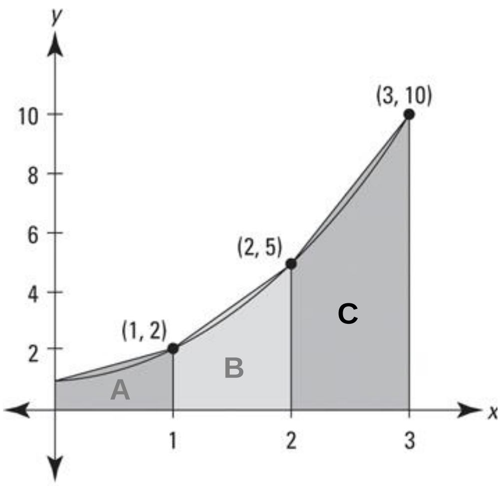


Figure 3. Example of an envelope representation of a 20 seconds begging event (amplitude versus time). Each red box is a manually added label corresponding to each begging call. The surface below the curve was calculated to obtain the measurement of the *envelope surface area*.

The envelope surface area is expected to represent the amount of acoustic activity produced by the nestlings towards each bird. To extract the area under the envelope curve, a formula of the sum of the trapezoids' areas was applied. The **figure 4** shows a demonstrative example and how to calculate the area of the trapezoid **C.**



$$C_{area} = \frac{1}{2} \times (y2 + y1) \times (x2 - x1)$$

$$= \frac{1}{2} \times (10 + 5) \times (3 - 2)$$

$$= 7.5$$

Figure 4. Simplified plot of a curve where 3 trapezoids were drawn (A, B and C). X and Y coordinates are associated to the data points. On the right, it is written the formula used to estimate the trapezoid C area and its calculation as an example. The total area of the graph, estimated by the sum of the 3 trapezoids, would be 12.5. Figure adapted from: http://www.dummies.com/education/math/calculus/how-to-approximate-area-with-the-trapezoid-rule/

- Begging calls' *frequency features* have been previously suggested to be related with nestlings' nutritional needs and body condition (Sacchi *et al.* 2002; Leonard & Horn 2006; Marques *et al.* 2009; Klenova 2015; Ogawa *et al.* 2015). The following frequency parameters were estimated on the frequency spectrum (amplitude versus frequency) performed on the first 10 seconds of the begging events (**Figure 5**)**.** This duration was chosen because it was visually assessed that there were less calls affected by noise if events shorter than 20 seconds were used and noise avoidance is crucial for an accurate estimation of the frequency parameters. The *peak frequency* value (frequency of maximum amplitude) and the value of the quartiles *Q25*, *Q50* and *Q75* (which represent the frequencies on which respectively 25, 50 and 75% of the energy is distributed) were extracted.

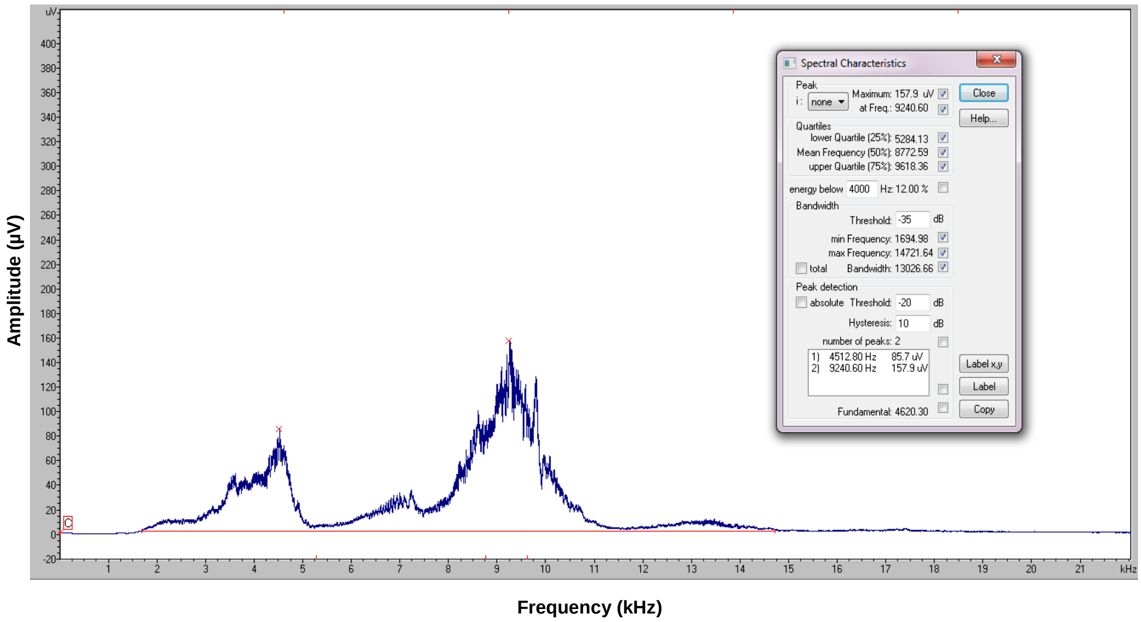


Figure 5. Example of a smoothed (Average over: 101 points) frequency spectrum (amplitude versus frequency) of a 10 seconds begging event (Evaluation window: Hamming). The values of the peak frequency and the quartiles are indicated in the table.

Video recordings

Video cameras (Sony Handycam HD) were placed on tripods under the colonies pointing to the entry of the target nests in order to identify which and how many birds were feeding and quantitatively evaluate their feeding behaviour (**Figure 6**). Nests were taped during 4 to 6 hours. We obtained a final sample of 22 nests, with both acoustic and video recordings data usable for statistical analyses.

Figure 6. Top left side: bottom view of a colony; Top right side: image obtained from a video recording of a sociable weaver entering the chamber with prey in the bill; On the bottom: a picture of the communal nest in an *Acacia* tree while breeding monitoring procedures are on course.

Video analysis

During the video analysis, the entry and exit time of each bird that came to the nest, as well as their unique colour combination was extracted. This information allowed the *a posteriori* estimation of individual identity and group size and hence enabled the assessment of the time it took for the feeding bird to come back (in seconds). This measure was the one chosen to quantify the food provisioning behaviour of the birds. The time between two feeding events (in seconds; regardless of the birds' identity) was also extracted.

Group size was determined as the number of different birds seen feeding the nestlings at day 4. Both nests with breeding pairs alone and breeding pairs with helpers, at day 4, were included for further analyses. Videos in which bird identification failed for more than 5% of the visits were excluded from the sample (only in one video; due to direct sunlight on the lens). Groups where incomplete colour combinations (due to lost rings) impeded bird status attribution (see genotyping and kinship relationships estimation section; **Table 2**) had to be excluded as well (two videos). Feeding visits were distinguished from visits for other purposes (as building or sanitation) whenever this was possible to visually assess.

Genotyping and kinship relationships estimation

Sociable weavers do not possess morphological visual characteristics that allow the distinction of sexes on the field, so their sex was determined by amplifying CHD (chromo-helicase-DNA-binding) genes located on the W and Z sex chromosomes (Griffiths *et al.* 1998). Blood samples were preserved in 1mL of absolute ethanol. In preparation for polymerase chain reaction amplification, genomic DNA was extracted using an ammonium acetate precipitation method (Richardson *et al.* 2001; van Dijk *et al.* 2014). Sex was determined using the P2 and P8 universal sex-typing primers (Griffiths *et al.* 1998). A total of 3136 individuals has been genotyped to date using 16 autosomal polymorphic microsatellite markers (GCSW15, GCSW47, INDIGO40, Tgu22_001, GCSW35, INDIGO41, Ppi2-Gga, Tgu01_148, WBSW9, GCSW13, INDIGO29, CAM1, CAM15, Ase18, GCSW31, Tgu07_022; Dawson et al., 2010, 2013; van Dijk et al., 2014; Martinez et al., 1999; McRae and Amos, 1999; Mcrae et al., 2005; Richardson et al., 2000; Sefc et al., 2001; mean = 11.2 alleles; see van Dijk *et al.* 2014 for further details on genotyping methods). Genotyping analyses were conducted at the University of Sheffield (UK).

Since the main purpose of this study was to evaluate the food provisioning behaviour of different birds in a group and to assess the begging that is directed towards them, individuals were distributed among specific categories established according to their sex (in the case of breeders; male breeder or female breeder) and categorical kin relation to the offspring (in the case of helpers; full sibling, half sibling or unrelated; **(1)**, **Table 2**). Alternatively, because of the suggestion that prenatal maternal effects could have some implications on begging behaviour, and perhaps on food provisioning, the status of each helper was also estimated according to their kin relationships relatively to the female breeder (helper related to the female or helper unrelated to the female;

(2), **Table 2**). Each bird was attributed to a categorical status based on both quantitative and qualitative parentage and kinship relationships information.

Table 2. Descriptive table of all the possible categories attributed to the birds in a group. Besides breeders (which were distinguished by sex), each helper was categorized twice: **(1)** concerning its relation to the offspring and **(2)** concerning its relation to the female breeder. Full sibling helpers are offspring of the breeding pair and half sibling helpers are offspring of only one of the breeders. Helpers unrelated to the offspring are birds which are not related to the offspring by any sibling relationship and are also not offspring of any of the breeders. On the other side, helpers related to the female breeder can be either offspring of the breeding pair or offspring of the female breeder only. Finally, helpers unrelated to the female breeder can be either offspring of the breeding male only or helpers which are not offspring of the breeding pair.

STATUS OF THE BIRD		
FEMALE BREEDER		
MALE BREEDER		
HELPER		
	(1) In relation to the offspring	**(2)** In relation to the female breeder
	FULL SIBLING	RELATED
	HALF SIBLING	UNRELATED
	UNRELATED	

To distinguish between breeders and helpers, parentage analyses were performed in Colony v. 2.0.5.9 (Jones & Wang 2010) using the 16 microsatellite loci. Each juvenile was assigned to a most likely father and mother using the full-likelihood analysis method. Since adults regularly disperse (van Dijk *et al.* 2015), specific alleles may occur anywhere in the study population. Given this, all genotypes from all the adult birds ever genotyped were considered (1283 candidate mothers and 1341 candidate fathers) as candidate parents of 76 offspring genotypes from 31 nest chambers of interest. Marker typing error was set to 1% and the probability of the genetic parents being present among the genotyped candidate parents was set to 90% to allow for the possibility of an unknown bird being the parent (all other settings were set to default, no known paternal or maternal sibships were assumed or excluded and no paternity or maternity was excluded). Only pairs with an assigned probability of 1 were included in further analysis. From these tests, parent-offspring relationships were obtained for our sample of individuals of interest, which allowed the categorization of most of the breeders and their helpers (N=70 of successfully attributed status). It was also possible to spot half sibling helpers (and if these were related or not to the female breeder) when the birds were assigned as offspring of only one of the birds that was part of the breeding pair observed in the videos. When both the genotype of the helpers and the breeding pair was available, but a parent-offspring relation was not found, helpers were attributed with the unrelated categories (see **Table 2**; two cases).

Among the sample of individuals for which the parentage analysis was not possible to apply (N=12), other criteria had to be used. These individuals were:

i) Previously cross-fostered birds, that were placed as eggs to a new nest under experimental conditions (Paquet *et al.* 2015a) during previous seasons and hatched in the presence of their foster parents. Some of them were found among our data helping breeding pairs (N=8). Statistical tests were conducted to assess whether these helpers were behaving differently from genetically related birds (see supplement material, appendixes 1 and 2). Providing that their behaviour did not statistically differ from non-cross-fostered helpers, their status was inferred from their social relationship with their foster parents. Given this, if the birds were seen helping both their foster parents, they were considered 1) full siblings and 2) helpers related to the female (four individuals). If they were helping one of their foster parents it was considered that they were 1) half siblings and, if it was the female breeder, 2) helpers related to the female (four individuals) or, if it was the male breeder, 2) helpers unrelated to the female (no examples of this case on the sample); and, in both situations (1 and 2), if they were helping a breeding pair in which neither parents were their foster ones, they would be considered unrelated helpers, although there were no individuals under this condition on the cross-fostered birds' sample.

ii) Birds for which the genotypes were not available, for which some inference criteria had to be used. For instance, when only two birds were seen provisioning food during the day 4 video recordings they were assigned as breeders of the nest (only one case). There is no evidence for extra-group paternity in this species (Covas *et al.* 2006; Paquet *et al.* 2015b) and videos recorded previous to hatchling were used as well to confirm that these two birds were seen incubating the eggs. When helpers' genotype was not available, but the breeding pair of the nest was known, observations from previous seasons were used to assess whether these same parents were seen feeding the helpers during their nestlings' stage (two confirmed cases). In situations where the parents attributed to a helper were not the current breeding pair of the group, this helper was attributed to the unrelated categories (see **Table 2**; one case).

Statistical analyses

A Principal Component Analysis (PCA) was applied to the frequency parameters of the begging (peak frequency, Q25, Q50 and Q75) since they were correlated (**Table 3**) and multicollinearity should be avoided in the models. The PCA replaces the original variables by a smaller number of derived uncorrelated variables (Principal Components or PC) that are created by linear combinations of the original ones (Jolliffe 2002). The *prcomp* function from the package *stats* was applied in R (v3.2.5; R Development Core Team, 2016).

Table 3. Spearman's rank correlation coefficients (**ρ**) and corresponding P-values for the begging frequency parameters (N=444).

	Peak frequency	**Q25**	**Q50**	**Q75**
Peak frequency		**ρ=0.81** (P<0.0001)	**ρ=0.42** (P<0.0001)	**ρ=0.17** (P=0.0004)
Q25			**ρ=0.64** (P<0.0001)	**ρ=0.39** (P<0.0001)
Q50				**ρ=0.73** (P<0.0001)
Q75				

The first two principal components (PC1 and PC2) explain approximately 91% of the total variation of the data (N=444; **Table 4**). The first component explains alone 71% of the variation and presents large magnitude loadings which reflect a substantial weight of all the four variables in explaining its variation (**Table 4**). All the original variables in PC1 vary in the same direction in this component (**Table 4**). PC1 has a greater correlation with the Q25 and Q50 variables which present absolute coefficient values above 0.5 (**Table 4**). The PC2 is strongly correlated with the Q75 variable (loading above 0.7; **Table 4**).

Table 4. Importance of components: loadings of the original variables which illustrate the weight of a specific factor in each component. The table contains the eigenvalues, the standard deviations and the cumulative percentage of total variation explained by the first two principal components.

	PC1	**PC2**
LOADINGS		
Peak frequency at maximum amplitude	**0.505**	0.488
Q25	**0.527**	0.334
Q50	**0.544**	-0.177
Q75	0.414	**-0.786**
EIGENVALUES	**2.869**	**0.759**
STANDARD DEVIATION	**1.694**	**0.871**
CUMULATIVE PERCENTAGE OF TOTAL VARIATION	**71.720**	**90.690**

Both PC1 and PC2 seem informative considering their singular coefficients and the proportion of total variance these explain together. However, PC1 explains by itself more than 70% of the total variation. Moreover, it is the only component with a eigenvalue higher than 1 which is also a commonly used criterion (Kaiser criterion; Kaiser 1960) to select the most informative principal components, which places PC2 as a borderline meaningful derived variable. Yet, PC1 and PC2 were both chosen for posterior begging acoustic behaviour analysis.

A Spearman's rank test for correlation coefficients was also conducted for the remaining variables. The envelope surface area and the begging rate intensity measures were correlated ($\rho=0.79$; $P<0.0001$), and it was thus decided to exclude the envelope surface area from the results analysis to avoid redundant variables in the models. Both measures were estimated in order to represent the intensity of the sound, but the begging rate measure was the only one maintained for further analysis since it allowed including a larger data sample, if included individually, and was already shown by many previous studies to be important. Its correlation with the principal components was $\rho=-0.34$ ($P<0.0001$) for the PC1 and $\rho=-0.15$ ($P=0.0014$) for the PC2. Brood size and average chicks' weight presented a relatively high Spearman's rank correlation coefficient ($\rho=-0.56$; $P<0.0001$). Bird age and bird status (with helpers' relatedness towards the female) were also correlated $\rho=0.5$ ($P<0.0001$).

The first aim of these analyses was to assess whether the food provisioning behaviour of parents and helpers varies with the begging rate and the frequencies of the begging calls they are exposed to. A second aim of the statistical tests was to explore the begging behaviour of the nestlings and, particularly, assess whether they beg differently depending on the status of the birds feeding them. Linear Mixed Models (LMMs) were applied using the *nlme* package in the R software. Normality of the residuals and homoscedasticity were visually inspected using QQ plots, fitted versus residuals plots and histograms. The statistical unit used in these analyses was 1 feeding event (i.e.: each arrival to the nest for food provisioning and each begging event). Lastly, individual, nest and colony identity were nested and included as random factors in all models.

For each of the four dependent variables under study (time to come back, begging rate, PC1 and PC2 summarizing frequency parameters), two tests were applied that differed on the helpers' relationships categories included. The bird status explanatory factor included different categories: female breeders, male breeders and helpers categorized twice as explained in **Table 2**. For each dependent variable, the tests were conducted using all the same explanatory variables, but alternatively including a status term considering the breeders and the relationship of the helpers towards the offspring (test 1) or the breeders and the relationship of helpers towards the female breeder (test 2).

The main final models were obtained by sequentially eliminating explanatory variables showing $P>0.05$ using a backwards stepwise approach. This approach was chosen because it allowed a simpler presentation of results. The minimal models provided the P-values of significant terms. To obtain the P-values for nonsignificant terms each nonsignificant variable was reintroduced into the minimal model (Crawley 2002). Model selection was confirmed using Akaike information criteria estimations as well.

When final models included categorical factors with more than two levels (i.e. bird status), post-hoc comparisons were applied in order to identify what categories of birds differed from the others. In R, the function *glht* from the *multcomp* package was used, which performs contrast statistic tests that assess the difference between the means of all the possible pair-wise combinations of factor levels (Tukey's test; Tukey 1949).

1) Time to come back

To test whether the acoustic begging influenced differently the food provisioning behaviour of the different categories of birds, LMMs were used with the $\log_{10}$

transformed time to come back as the dependent variable (for normality). The explanatory variables included in the initial models were the feeding bird status (breeders distinguished by sex and helpers categorized regarding their kin relation to the offspring – test 1 – or to the female breeder – test 2 – as defined in **Table 2**), group size (number of breeders and helpers feeding the chicks at day 4), age of the feeding bird (bird minimal age in years), brood size (number of chicks per nest at day 4), average weight of the chicks (g), colony size and the interactions between the status of the bird and each begging measure (bird status*begging rate; bird status*PC1; bird status*PC2). Moreover, the time since sunrise of each feeding event in its linear and quadratic forms (min) were set as explanatory covariables since birds' activity is expected to be higher when temperatures are lower. Two environmental explanatory covariables were added to the model: the maximum day temperature (^{o}C) and the sum of rainfall during the 30 previous days to the observation (mm), which have shown a correlation coefficient below 0.4 (ρ=0.39; P<0.0001).

2) Begging behaviour

Begging rate and frequency parameters (PC1 and PC2)

In order to assess whether birds of different status were overall exposed to different begging levels, we started by testing the effect of status on the begging features with LMMs and the begging rate, PC1 or PC2 scores as dependent variables. In addition, to investigate other possible variables that may affect begging, we conducted further analyses including: the previous time the chicks were fed (in seconds; independently of the feeding bird); the group size (number of adults feeding the chicks at day 4); the brood size (number of chicks per nest at day 4) as larger broods are expected to produce stronger begging (mainly higher begging rates); the average chicks' weight (g); the age of the feeding bird (minimal age in years); the time since sunrise of each feeding event in its linear and quadratic forms (min), because begging is expected to be stronger when feeding birds are less active (i.e.: during the warmer parts of the day); and the status of the birds (breeders distinguished by sex and helpers categorized regarding either their kin relation to the offspring – test 1 – or to the female breeder – test 2 – as defined in **Table 2**). The results obtained were qualitatively similar from the analyses including only bird status or the other explanatory variables. Hence I present here the results of the models that included all the covariables and the simple models are presented in the Appendix 3 of the Supplement materials.

Results

1) Time to come back

The time it took birds to come back with food varied from 7 seconds to almost 3 hours. A visual direct representation of the time to come back in relation to the begging rate, along with the sex of the breeders and helpers' status in relation to the offspring (test 1), is presented graphically in **Figure 7**.

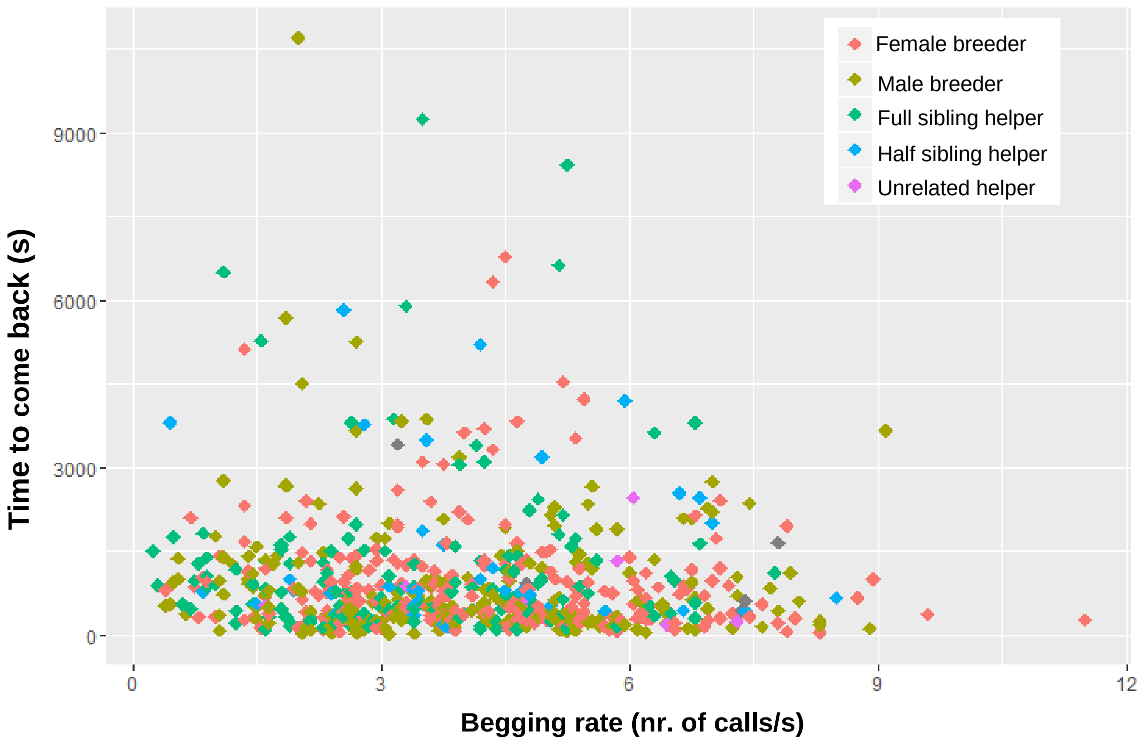


Figure 7. Time to come back (in seconds) as a function of the begging rate (in number of calls per second). The data points have different colours corresponding to the different status of the birds in test 1, as represented in the label.

The log transformed time to come back was significantly affected in a negative linear way by the begging rate (**Tables 5 and 7; Figure 8**), with birds exposed to more begging taking less time to come back to feed. The status of the birds also affected their time to come back with male breeders taking the least time to come back, followed by the female breeders and, finally, the helpers. (**Tables 5 and 7**) The time to come back was not significantly affected by the interactions between begging and status of the birds or by any other variable (all P>0.10 **Tables 5 and 7**).

Table 5. Results from the LMMs for the time to come back as dependent variable when bird status includes breeders and helpers' kin relationships to the offspring (N=903; Test 1). Estimates and SE are given for the significant explanatory terms (in bold). The same minimal model was obtained by AIC model selection.

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**2.950**	**0.056**
Begging rate	**7.018**	**557**	**0.008**	**-0.026**	**0.010**
Status of the bird	**3.298**	**44**	**0.019**		
Male breeder				**-0.074**	**0.039**
Full sibling helper				**0.050**	**0.048**
Half sibling helper				**0.154**	**0.082**
Unrelated helper				**0.126**	**0.164**
Bird age	0.087	556	0.767		
Time since sunrise^2	0.630	556	0.428		
Time since sunrise	1.429	556	0.232		
Brood size	0.171	10	0.687		
Average chicks' weight	0.013	10	0.912		
Colony size	0.038	9	0.849		
PC1	0.101	354	0.751		
PC2	0.001	354	0.979		
Group size	0.029	10	0.868		
Rainfall	0.017	10	0.898		
Maximum day temperature	2.050	10	0.183		
Begging rate*Status of the bird	1.063	553	0.374		
PC1*Status of the bird	0.605	350	0.660		
PC2*Status of the bird	1.946	350	0.102		

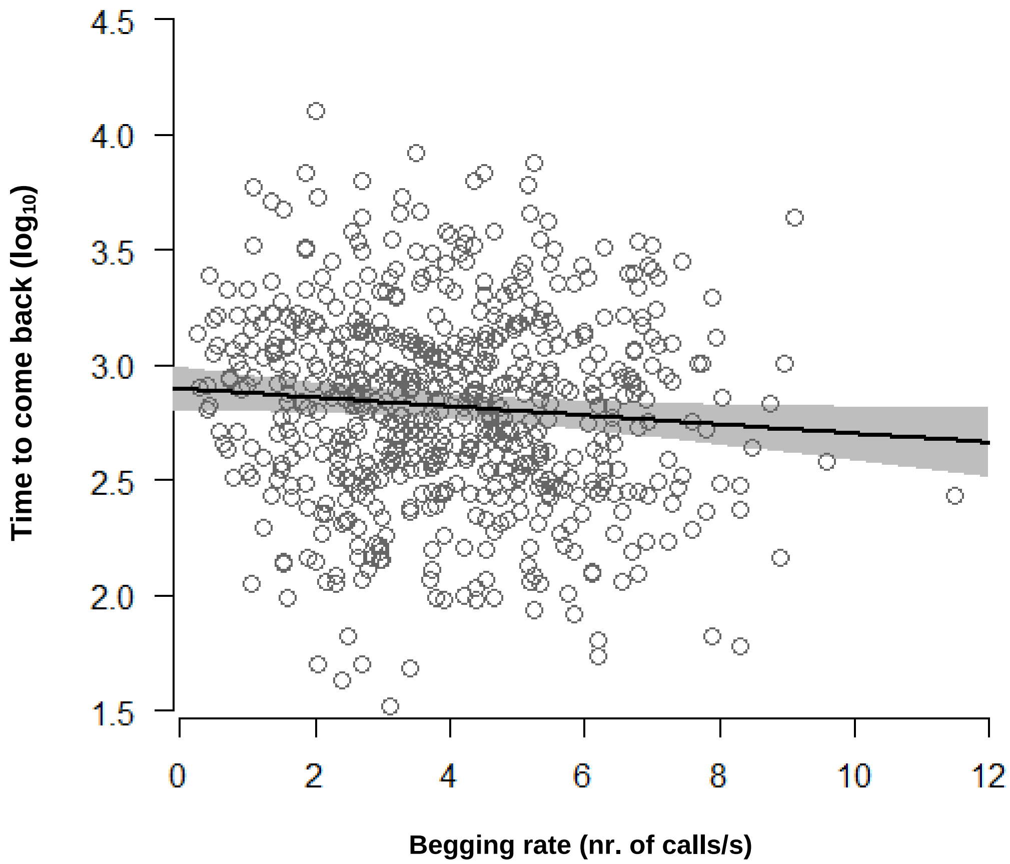


Figure 8. Graphical representation of the linear negative effect of the begging rate on the log_{10} transformed time to come back (N=633). The predicted linear regression (black line) and the confidence band (grey area) were estimated from the best model (**Table 5**).

Concerning test 1, the post-hoc comparison suggested a significantly shorter time to come back of male breeders compared to the helpers related to the offspring (**Table 6**). The results did not differ for helpers with different levels of kin relationships (full siblings, half siblings and unrelated), but there was however only one unrelated helper in this sample. These differences can be observed graphically in **figure 9**, where it is also possible to confirm the high standard errors for the unrelated helpers' category due to the small sample size it presents for this specific test.

Table 6. Results from the post-hoc Tukey's test for the minimal model of time to come back as dependent variable when bird status includes breeders and helpers' kin relationships to the offspring (N=628; Test 1). Estimates, standard errors, standard scores and its probability are presented for all the pair-wise levels combinations. Significant differences between means are presented in bold and nearly significant comparisons are presented in italic bold.

Comparison	Estimate	Std. Error	z value	Pr (>|z|)
FULL SIBLING - FEMALE BREEDER	0.050	0.048	1.044	0.811
HALF SIBLING - FEMALE BREEDER	0.154	0.082	1.875	0.294
MALE BREEDER - FEMALE BREEDER	-0.074	0.039	-1.893	0.284
UNRELATED HELPER - FEMALE BREEDER	0.126	0.165	0.766	0.930
HALF SIBLING - FULL SIBLING	0.104	0.090	1.159	0.745
MALE BREEDER - FULL SIBLING	***-0.124***	***0.049***	***-2.538***	***0.068 .***
UNRELATED HELPER - FULL SIBLING	0.076	0.169	0.450	0.990
MALE BREEDER - HALF SIBLING	**-0.228**	**0.083**	**-2.739**	**0.039***
UNRELATED HELPER - HALF SIBLING	-0.028	0.181	-0.155	1.000
UNRELATED HELPER - MALE BREEDER	0.200	0.164	1.215	0.711

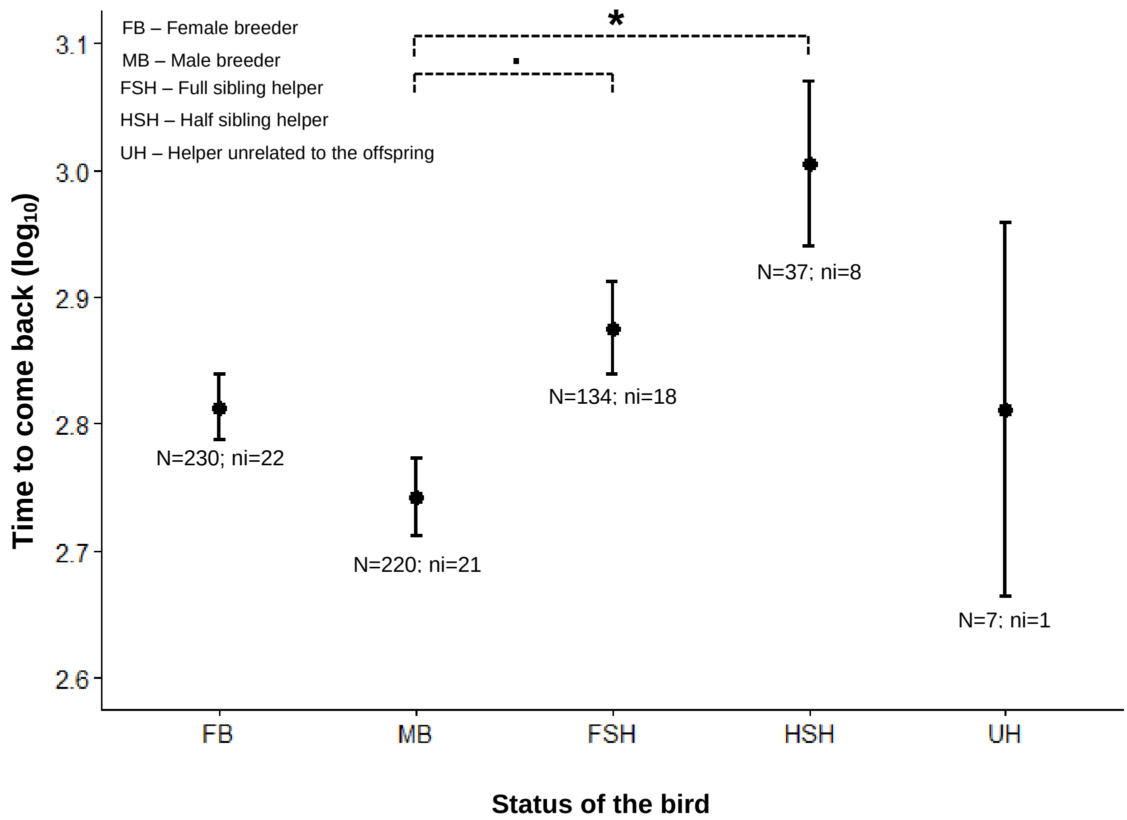


Figure 9. Graphical representation of the transformed time to come back means±SE that characterize each bird status from test 1 (breeders and helpers' status in relation to the offspring). The number of events (N) and the number of individuals (ni) contained in each mean are presented in the graph. Significantly and nearly significantly different categories according to post-hoc tests are signalled as well with the horizontal dashed brackets.

Table 7. Results from the LMMs for the log_{10} transformed time to come back as dependent variable when bird status includes breeders and helpers' kin relationships to the female breeder (N=903; Test 2). Estimates and SE are given for the significant explanatory terms (in bold). The same minimal model was obtained by AIC model selection.

Explanatory variables	**F**	**d.f.**	**P**	**Estimate**	**SE**
Intercept				**2.960**	**0.056**
Begging rate	**7.861**	**561**	**0.005**	**-0.027**	**0.010**
Status of the bird	**4.875**	**46**	**0.005**		
Male breeder				**-0.072**	**0.039**
Related helper				**0.057**	**0.044**
Unrelated helper				**0.217**	**0.102**
Bird age	0.077	560	0.781		
Time since sunrise^2	0.467	560	0.495		
Time since sunrise	1.148	560	0.284		
Brood size	0.023	10	0.882		
Average chicks' weight	0.010	10	0.921		
Colony size	0.046	9	0.836		
PC1	0.364	356	0.547		
PC2	0.003	356	0.959		
Group size	0.043	10	0.839		
Rainfall	0.008	10	0.931		
Maximum day temperature	2.167	10	0.172		
Begging rate*Status of the bird	1.068	558	0.362		
PC1*Status of the bird	0.980	353	0.403		
PC2*Status of the bird	1.600	353	0.189		

Post-hoc tests for test 2 have shown that both helpers related and helpers unrelated to the female breeder took significantly longer to come back than male breeders (**Table 8**; **Figure 10**).

Table 8. Results from the post-hoc Tukey's test for the minimal model of time to come back as dependent variable when bird status includes breeders and helpers' kin relationship to the female breeder (N=633; Test 2). Estimates, standard errors, standard scores and its probability are presented for all the pair-wise levels combinations. Significant differences between means are presented in bold.

Comparison	Estimate	Std. Error	z value	Pr (>|z|)
MALE BREEDER – FEMALE BREDER	-0.072	0.039	-1.869	0.222
RELATED HELPER – FEMALE BREEDER	0.057	0.044	1.290	0.546
UNRELATED HELPER – FEMALE BREEDER	0.217	0.102	2.123	0.132
RELATED HELPER – MALE BREEDER	**0.130**	**0.045**	**2.848**	**0.020***
UNRELATED HELPER – MALE BREEDER	**0.290**	**0.102**	**2.831**	**0.021***
UNRELATED HELPER – RELATED HELPER	0.160	0.107	1.489	0.420

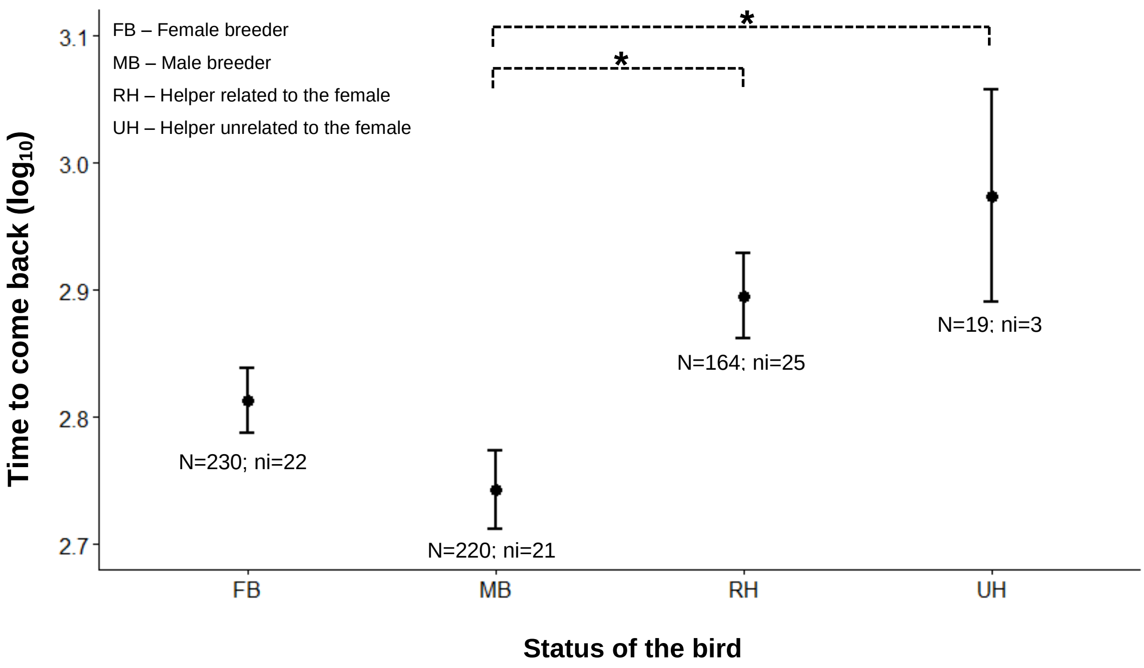


Figure 10. Graphical representation of the transformed time to come back means±SE that characterize each bird status from test 2 (breeders and helpers' status in relation to the female breeder). The number of events (N) and the number of individuals (ni) contained in each mean are presented in the graph. Significantly different categories according to post-hoc tests are signalled as well with the horizontal dashed brackets.

2) Begging behaviour

2.1) Begging rate

The begging rate varied between 0.25 and 11.5 calls per second. It varied in a positive linear way both with the time since sunrise (estimate= 0.002±0.001, F=17.825, P<0.0001; **Tables 9 and 10**) and with the previous time the chicks were fed (estimate= 0.0004±0.0001, F=11.235, P=0.001; **Tables 9 and 10**). No significance of the bird status was observed regarding breeders and helpers' status in relation to the offspring (Test 1; F=0.957, P=0.440; **Table 9**). In test 2 (breeders and helpers' status in relation to the female breeder), bird status has shown a marginal significance (F= 2.571, P=0.064; **Table 10**). The begging rate did not significantly vary with any other variables considered (all P>0.108; **Tables 9 and 10**).

Table 9. Results from the LMMs for the begging rate as dependent variable when bird status includes breeders and helpers' kin relationship to the offspring (N=689; Test 1). Estimates and SE are given for the significant explanatory terms (in bold). The same minimal model was obtained by AIC model selection.

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**3.019**	**0.389**
Time since sunrise	**17.825**	**606**	**<0.0001**	**0.002**	**0.001**
Last feeding	**11.235**	**606**	**0.001**	**0.0004**	**0.0001**
Status of the bird	0.957	47	0.440		
Time since sunrise^2	0.781	605	0.377		
Bird age	0.195	605	0.659		
Brood size	3.108	10	0.108		
Average chicks' weight	0.249	10	0.629		
Group size	0.327	10	0.580		

Table 10. Results from the LMMs for the begging rate as dependent variable when bird status includes breeders and helpers' kin relationship to the female breeder (N=689; Test 2). Estimates and SE are given for the nearly significant explanatory variables (in italic bold). Grey coloured lines represent the significant terms that were obtained which maintain the same values as before (Test 1; **Table 9**). The remaining explanatory variables are not presented since the values can be accessed in **Table 9**. The same minimal model was obtained by AIC model selection.

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				3.019	0.389
Time since sunrise	17.825	606	<0.0001	0.002	0.001
Last feeding	11.235	606	0.001	0.0004	0.0001
Status of the bird	***2.571***	***53***	***0.064***		
Male breeder				***-0.140***	***0.146***
Related helper				***-0.232***	***0.167***
Unrelated helper				***0.735***	***0.376***

2.2) Frequency parameters

2.2.1) PC1 (General frequency scores)

The first frequency component (PC1) varied significantly with the brood size in a negative linear way, meaning that larger broods showed lower frequency calls (Test 1 estimate=-1.681±0.62, F=7.395, P=0.026; **Table 11**; **Figure 11**; Test 2 estimate=-1.648±0.61, F=7.375, P=0.026; **Table 12**). The status of the birds was not significant when helpers' relatedness towards the offspring was considered (Test 1 P=0.131; **Table 11**), but frequencies significantly varied with the status of the bird when considering helpers relatedness towards the female breeder (Test 2; F=3.102; P=0.039; **Table 12**).

Table 11. Results from the LMMs for the PC1 as dependent variable when bird status includes breeders and helpers' kin relationship to the offspring (N=444; Test 1). Estimates and SE are given for the significant explanatory terms (in bold). The same minimal model was obtained by AIC model selection.

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**4.669**	**1.712**
Brood size	**7.395**	**8**	**0.026**	**-1.681**	**0.618**
Status of the bird	1.913	34	0.131		
Time since sunrise^2	0.035	384	0.852		
Last feeding	2.856	383	0.092		
Bird age	2.224	38	0.144		
Time since sunrise	0.008	384	0.928		
Average chicks' weight	1.926	7	0.208		
Group size	0.040	7	0.847		

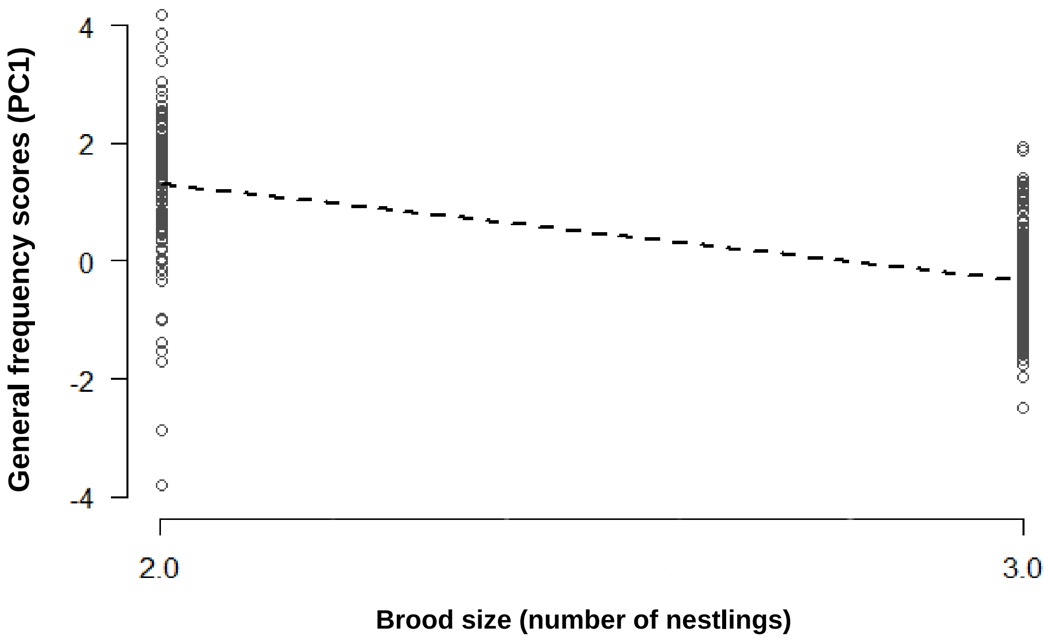


Figure 11. Graphical representation of the relationship between general frequency scores (PC1) and brood size. General frequency decreased when broods were bigger. The dashed line indicates the predicted values from the minimal model (**Table 11**).

Table 12. Results from the LMMs for the PC1 as dependent variable when bird status includes breeders and helpers' kin relationship to the female breeder (N=444; Test 2). Estimates and SE are given for the significant explanatory terms (in bold). The same minimal model was obtained by AIC model selection.

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**4.600**	**1.686**
Brood size	**7.375**	**8**	**0.026**	**-1.648**	**0.607**
Status of the bird	**3.102**	**36**	**0.039**		
Male breeder				**0.100**	**0.102**
Related helper				**-0.256**	**0.115**
Unrelated helper				**-0.098**	**0.264**
Time since sunrise^2	0.029	384	0.864		
Last feeding	2.554	383	0.111		
Bird age	0.137	35	0.714		
Time since sunrise	0.010	384	0.922		
Average chicks' weight	2.025	7	0.198		
Group size	0.001	7	0.977		

A post-hoc analysis revealed that nestlings produced calls at significantly higher frequencies towards the male breeder than towards helpers related to the female (**Table 13; Figure 12**). Frequencies were not significantly affected by the time since sunrise, the previous time the chicks were fed, the age of the bird, the average weight of the nestlings or the group size (all P>0.092; **Tables 11 and 12**).

Table 13. Results from the post-hoc Tukey's test for the minimal model of PC1 as dependent variable when bird status includes breeders and helpers' kin relationship to the female breeder (N=444; Test 2). Estimates, standard errors, standard scores and its probability are presented for all the pair-wise levels combinations. Significant differences between means are presented in bold.

Comparison	Estimate	Std. Error	z value	Pr (>|z|)
MALE BREEDER - FEMALE BREEDER	0.100	0.102	0.979	0.745
RELATED HELPER - FEMALE BREEDER	-0.256	0.115	-2.237	0.102
UNRELATED HELPER - FEMALE BREEDER	-0.098	0.264	-0.370	0.981
RELATED HELPER - MALE BREEDER	**-0.356**	**0.120**	**-2.963**	**0.014***
UNRELATED HELPER - MALE BREEDER	-0.198	0.266	-0.744	0.870
UNRELATED HELPER - RELATED HELPER	0.159	0.280	0.567	0.937

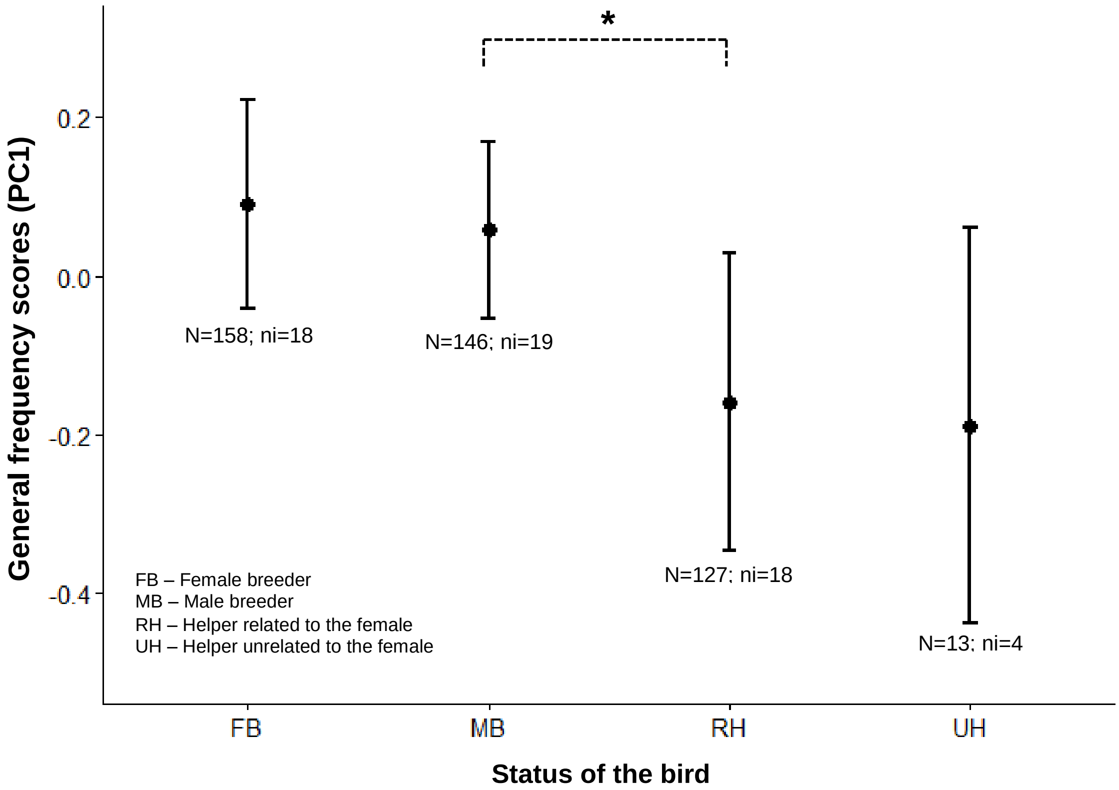


Figure 12. General frequency scores values (PC1 mean±SE) as a function of bird status from test 2 (breeders and helpers' status in relation to the female breeder). The number of events (N) and the number of individuals (ni) contained in each mean are presented in the graph. Significantly different categories according to post-hoc tests are signalled as well with the horizontal dashed bracket.

2.2.2) PC2

No significant terms were obtained when PC2 was used as dependent variable (all P>0.100; **Tables 14 and 15**).

Table 14. Results from the LMMs for the PC2 as dependent variable when bird status includes breeders and helpers' kin relationship to the offspring (N=444; Test 1).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**1.319**	**0.858**
Brood size	2.182	8	0.178		
Status of the bird	2.120	34	0.100		
Time since sunrise^2	0.423	384	0.516		
Last feeding	0.635	383	0.426		
Bird age	1.545	38	0.222		
Time since sunrise	0.483	384	0.488		
Average chicks' weight	1.532	8	0.251		
Group size	0.203	8	0.664		

Table 15. Results from the LMMs for the PC2 as dependent variable when bird status includes breeders and helpers' kin relationship to the female breeder (N=444; Test 2). The intercept values are the same as in **Table 14**. The remaining explanatory variables are not presented since the values can be accessed in **table 14**.

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**1.319**	**0.858**
Status of the bird	0.262	36	0.852		

Discussion

The primary aim of this study was to explore if there were differences in the way parents and helpers responded to the begging behaviour of nestlings in the sociable weaver. The second main objective of this study was to explore the begging behaviour and, specifically, investigate whether nestlings begged in the same fashion towards their parents and the helpers. As expected, we found a negative relationship between the begging rates of the nestlings and the time each individual takes to come back with food. Specifically, male breeders displayed the highest feeding levels, but all types of birds (breeders and helpers) responded in the same way to an increase in begging rate. Begging rates were correlated with the time of the last feeding of the chicks and the time since sunrise, but did not vary with the birds' status. Frequency features of the calls were not related to food provisioning or indicators of hunger, but were significantly higher in smaller broods and when directed towards male breeders than towards helpers related to the female breeder.

First, provisioning adults that were exposed to high rates of begging took less time to come back to the nest. This is a common and thus expected result, as several previous experiments have shown that parents adjusted their provisioning behaviour according to increased begging (Bengtsson & Rydén 1983; Burford *et al.* 1998; Price 1998; Estramil *et al.* 2013). Male breeders were the ones displaying the highest feeding levels (see also Doutrelant & Covas 2007, Doutrelant et al 2011). However, female breeders did not feed at significantly lower rates than their male partners, while all the classes of helpers displayed significantly lower provisioning behaviour than male breeders (i.e. showing the longest periods to come back with food). There was no significant interaction between the begging rate of the nestlings and the status of the feeding birds, suggesting that although some classes of birds seemed to work more than others, the begging rate variation affected the provisioning behaviour of the whole group in the same way. Accordingly to the theoretical model of Savage *et al.* (2013), there should be a positive correlation between the investment of individuals and their relatedness to the offspring (higher investment from breeders and closely related helpers and less by distant relatives). However, the direct benefits of this task might play a stronger role than relatedness in determining provisioning decisions (Heinsohn *et al.* 1988; Emlen 1996; Kokko *et al.* 2002; Richardson *et al.* 2002; but see Griffin & West 2003 and Cornwallis *et al.* 2009). The present result concurs with what was found by Wright (1998) in cooperatively breeding Arabian babblers (*Turdoides squamiceps*).

In this species, where breeding groups are highly related, extra begging caused greater quantities of prey to be delivered by all classes of birds (Wright 1998). Another study on the bell miner (*Manorina melanophrys*), found that male breeders and male unrelated helpers adjusted their food supply in a similar way when both classes were exposed to begging playbacks (McDonald *et al.* 2009), which again is in agreement with our findings. On the other hand, in the superb fairy-wren (*Malurus cyaneus*), where helpers are mainly distantly related or even unrelated to the brood, helpers responded to experimentally increased begging by increasing food provisioning, while the related individuals did not (MacGregor & Cockburn 2002). Our study suggests that unrelated helpers increase their food supply in response to higher begging rates in the same fashion as related birds. However, given the low sample size obtained (only four unrelated helpers) this result demands caution. While all the individuals responded to acoustic cues in the same way in our study, it is possible that individuals differ in the way they respond to other cues such as visual ones (e.g. gape colouration and begging posture). Parents were previously suggested to obtain information on both acoustic and visual components of the begging behaviour and to determine feeding behaviour accordingly (Kilner *et al.* 1999; see also MacGregor & Cockburn 2002). Moreover, visual features were even suggested as possible inducers of variation in the response of breeders, as females and males may respond differently to different cues. For example, females were reported to respond to both begging posture height and intensity in the canary (*Serinus canaria*), while males only responded to height (Kilner 2002a). In another study on great tits, males responded only to gaping and not to vocal cues (Hinde in Kilner 2002b). It would be interesting to increase the sample of unrelated helpers studied, in order to improve our understanding on their food provisioning rules in response to begging, and also to investigate other begging cues towards which birds of different status may respond differently.

The fact that all individuals responded to begging in the same way suggests that females cannot specifically target less related individuals (as males and unrelated helpers) to work more by manipulating the begging rate of the chicks. A previous cross-fostering experiment assessing prenatal effects on the female investment in this species has shown that mothers seem to be able to reduce begging rates of their nestlings when expecting to have more helpers (mostly related, as the major percentage of the helpers are full-siblings and half-siblings of the nestlings; Paquet *et al.* 2015a). This could be justified by the females' possibility to reduce the begging rates of their offspring in order to spare them from the costs of exhibiting high begging levels, as more individuals are available to help and this additional food supply would compensate the decreased begging. In our study, all birds, including related helpers, were seen to adjust their food provisioning effort to the begging rate. Both this result and the one obtained by the cross-fostering experiment suggest that, by inducing their offspring to beg less when more helpers are present, females may reduce the provisioning behaviour of their related helpers.

Secondly, the begging rate of the nestlings seemed related to their hunger levels since it co-varied both with the last time the chicks were fed and with the activity of the birds feeding. These correlations, along with the correlation between begging rate and food provisioning, suggest that begging rate is a honest signal of nestlings' need according to the honest signal predictions proposed by Kilner & Johnstone (1997). The fact that begging rates increased linearly with the time since sunrise (and not with its quadratic form) could be due to the fact that most recordings were done in the morning (only two recordings included events recorded after 2 pm). The class of the birds feeding was not significantly related with offspring begging rates. Under the maternal hypothesis predictions, males and unrelated helpers would be expected to be exposed to higher begging rates, followed by related helpers and finally by females, which was not observed in our study. This means that females do not seem to be able to target specific classes of individuals (by maternal manipulation of the begging), particularly the ones less related to them, to receive higher begging rates. Our sample on unrelated individuals was very low which does not allow to draw any conclusion regarding these birds. Yet, there is a good sample size for male breeders which, in this study, did not seem to be exposed to higher begging rates either. Perhaps, since breeding pairs of sociable weavers commonly mate for life, females might not be so willing to exploit their partners as this could affect their future reproductive success.

Finally, the frequency features of begging were not related with food provisioning. The previous time nestlings were fed, which was introduced in the models as an indirect measure of hunger, did not have any effect on the frequency of the calls either. The brood size, on the other hand, seemed to explain frequencies variation and broods of two nestlings begged at higher frequencies than broods of three nestlings. High frequency calls were previously suggested as signals of nestlings' hunger, but several studies found that this effect may only occur during later nestling stages (Leonard & Horn 2001, 2006; and in the experiment of Klenova 2015 nestlings were 12-15 days old) or after the longest food deprivation periods (Marques *et al.* 2009). Additionally, one plausible explanation for this brood effect is that in the broods of three nestlings there is one 4 days old chick and two younger chicks (as they hatch asynchronously in this species), one of them being only 1 day old, whereas in broods of two chicks both should be between 2 and 4 days old. If we suppose that just hatched chicks beg at lower frequencies than older chicks (Clemmons & Howitz 1990; Redondo & Exposito 1990), the mean frequency of a brood that includes a 1 day old chick would be lower than in broods of two.

Interestingly, begging frequencies were higher towards breeding males than towards helpers related to the female. This effect seems mainly driven by a difference between parents and helpers, with chicks begging at higher rates towards the parents than towards the helpers (**Figure 12;** confirmed by the fact that a model including only the parents versus helpers levels presented a 5 points lower AIC). This effect of status could be due to differences in the size of the prey brought by parents and helpers. Helpers of this species were previously found to bring smaller preys to the nest when compared to female breeders, although not significantly different from male breeders (Ferreira 2015), so chicks could be directing the highest frequencies towards the birds that bring them the biggest (i.e. higher in quality) preys. But, considering that prey size might not be of great importance when nestlings are so young as they cannot ingest such large preys, alternative ideas should be explored as well. The frequencies of the calls could be related to the nestlings' body mass (which was not confirmed by our data) or condition rather than hunger (Sacchi *et al.* 2002). In this case, it is possible to speculate that, by enhancing parents' perception of their condition, offspring could influence parental decisions to keep investing on them. Another explanation could be that nestlings were producing higher frequency calls towards more familiar birds, which would be the breeders as these are the birds seen to provide more care in this system. For this, offspring would have to differentiate parents from helpers, as they are suggested to have done in our study, which could be done by, for instance, recognition of their arrival calls. This is a curious result and, from my point of view, worth exploring in future acoustic studies on the begging of young nestlings from this species. Regarding PC2, the absence of results is not surprising as this principal component alone explains only (19%) of the variation (when compared to 72% for PC1) and was only associated with one frequency variable (i.e. Q75; **Table 4**).

To summarize, this study suggests that begging rate influences the food provisioning behaviour of all carers in the sociable weavers breeding groups and that all the birds responded in the same fashion to it. Male breeders were the ones showing the highest food supply, significantly more than any class of helpers, which partially corroborates what was previously found for this species. Despite the possibilities offered by a system in which unrelated helpers provide care, our sample size concerning unrelated individuals does not allow for definite answers about the interaction between food provisioning, or begging features, and the relatedness of provisioning adults. One thing that should be taken into account when interpreting our results is that sociable weavers have been found to shift their workload towards helpers throughout the nestling period (Ferreira 2015). This could lead to differences in provisioning levels when different nestling stages are investigated. Studying the provisioning behaviour of parents and helpers in relation to begging throughout the whole nestling period would be an interesting next step to fully understand the provisioning rules in this species. The positive relation between begging rates and both the last feeding of the chicks and the periods of the day with lower feeding activity (midday) further supports the hypothesis of begging rate as an honest signal of hunger in this species. Maternal manipulation and the possibility of targeting individuals less related to the female to provision more food, by increasing begging rates of the chicks, was not corroborated by our results. Despite this, our results show some support for the suggestion that, by reducing offspring begging rates as the number of helpers increases, females could reduce the amount of food provided by related helpers while the overall food provided to the brood increases, as we found that all individuals adjusted their food supply levels to the begging rate (Paquet *et al.* 2015a). Finally, the frequency components of the calls did not affect the food provisioning behaviour and did not show an effect of hunger. Instead, frequencies of the calls were influenced by the brood size (which may be due to the nestlings' different ages, see above) and, interestingly, differed in response to the presence of a parent or a helper, which is a worth exploring suggestion of the ability of young nestlings to recognize their parents. Our work aimed to explore the possible group conflicts solving mechanisms arising from the food supply and demand interactions between nestlings and breeding groups. The results obtained clarified the reliability of begging rate for the food provisioning and suggested the honesty of this stimulus. Furthermore, this study corroborates previously suggested aspects of the provisioning rules on the sociable weavers' breeding groups and highlights the importance to further explore the begging behaviour of nestlings, and its several features, to fully understand what drives the caring behaviour of different classes of birds.

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Supplement material

Appendix 1. Cross-fostered birds' preliminary analyses

The preliminary analysis suggested that cross-fostered helpers show a provisioning behaviour no different from genetically related helpers (Test 1 P=0.530; Test 2 P=0.631; **Tables S1 and S2**) which allowed to include them among the related helpers categories when the time to come back was set as the dependent variable. Cross-fostered helpers seem, in general, to receive the same begging from the nestlings that related helpers do. For the 3 begging dependent variables, it was never found a significant difference between these categories of helpers in both tests concerning their relation to the offspring (test 1) or to the female breeder (test 2; **Tables S3 to S8**). When begging rate is the dependent variable, test 1 shows a significant difference between full siblings and cross-fostered full sibling helpers (F=5.888, P=0.0319; **Table S3**) which is thought to be due to the quite low sample of 2 full siblings cross-fostered birds against 21 genetically related helpers. When PC2 is analysed as dependent variable, test 2 also shows a significant difference between helpers, which is not shown in test 1 (**Tables S7 and S8**).

1) Time to come back

The comparison between cross-fostered related helpers and genetically related helpers did not reveal any significant difference when the $\log_{10}$ transformed time to come back was the dependent variable (F=0.430, P=0.530 in test 1 – helpers' status in relation to the offspring; F=0.246, P=0.631 in test 2 – helpers' status in relation to the female breeder; **Tables S1 and S2**).

Table S1. Results from the LMMs for the log10 transformed time to come back as dependent variable including only cross-fostered related helpers and genetically related helpers in relation to the offspring (N=191; Test 1).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**2.880**	**0.085**
Status of the bird	0.430	8	0.530		

Table S2. Results from the LMMs for the log10 transformed time to come back as dependent variable including only cross-fostered related helpers and genetically related helpers in relation to the female breeder (N=165; Test 2).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**2.894**	**0.113**
Status of the bird	0.246	10	0.631		

2) Begging behaviour

2.1) Begging rate

Cross-fostered related helpers and genetically related helpers revealed a significant difference when the begging rate was the dependent variable in test 1 (helpers' status in relation to the offspring), probably due to be only taking into account 2 individuals for the cross-fostered category (P=0.0319; **Table S3**), but no significance was obtained in test 2 (helpers' status in relation to the female breeder; P=0.1064; **Table S4**).

Table S3. Results from the LMMs for the begging rate as dependent variable including only cross-fostered related helpers and helpers genetically related to the offspring (N=151; Test 1). Estimates and SE are given for the significant explanatory terms (in bold).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**2.334**	**0.681**
Status of the bird	**5.888**	**12**	**0.0319**		
Full sibling helper				**1.569**	**0.647**

Table S4. Results from the LMMs for the begging rate as dependent variable including only cross-fostered related helpers and helpers genetically related to the female breeder (N=186; Test 2).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**3.134**	**0.625**
Status of the bird	2.950	15	0.1064		

2.2) Frequency parameters

2.2.1) PC1 (General frequency scores)

The comparison between cross-fostered related helpers and genetically related helpers did not reveal any significance difference when PC1 was the dependent variable (F=0.0009, P=0.977 in test 1 – helpers' status in relation to the offspring; F=0.0023, P=0.964 in test 2 – helpers' status in relation to the female breeder; **Tables S5 and S6**).

Table S5. Results from the LMMs for the PC1 as dependent variable including only cross-fostered related helpers and helpers genetically related to the offspring (N=105; Test 1).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**0.678**	**0.558**
Status of the bird	0.0009	5	0.977		

Table S6. Results from the LMMs for the PC1 as dependent variable including only cross-fostered related helpers and helpers genetically related to the female breeder (N=127; Test 2).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**0.198**	**0.799**
Status of the bird	0.0023	6	0.964		

2.2.2) PC2

Cross-fostered related helpers and genetically related helpers did not reveal a significant difference when PC1 was the dependent variable in test 1 (helpers' status in relation to the offspring; F= 2.330, P=0.187, **Table S7**) but a significant value was seen in test 2 (helpers' status in relation to the female breeder; F=6.421, P=0.044, **Table S8**).

Table S7. Results from the LMMs for the PC2 as dependent variable including only cross-fostered related helpers and helpers genetically related to the offspring (N=105; Test 1).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**-0.129**	**0.289**
Status of the bird	2.330	5	0.187		

Table S8. Results from the LMMs for the PC2 as dependent variable including only cross-fostered related helpers and helpers genetically related to the female breeder (N=127; Test 2). Estimates and SE are given for the significant explanatory terms (in bold).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**-0.415**	**0.236**
Status of the bird	**6.421**	**6**	**0.044**		
Related helper				**0.588**	**0.232**

To summarize, from the 8 preliminary analyses among the four different dependent variables (the transformed time to come back, the begging rate, the PC1 and the PC2; tests 1 and 2 in each), 2 of them revealed a significant difference between cross-fostered and genetically related helpers. Therefore, these 2 specific models (test 1 with begging rate as dependent variable; test 2 with PC2 as dependent variable) were verified again without the cross-fostered helpers among the sample (see Appendix 2).

Appendix 2. Main analyses without cross-fostered helpers

Begging rate – Test 1 (breeders status and helpers' status in relation to the offspring)

When the cross-fostered helpers were removed from the sample used to test this model, due to the significance obtained in preliminary analyses, the begging rate varied in a positive linear way both with the time since sunrise (estimate= 0.0025±0.0006, F=15.70, P<0.0001; **Table S9**) and with the previous time the chicks were fed (estimate= 0.0004±0.0001, F=10.73, P=0.0011; **Table S9**). The same relevant independent terms were obtained when cross-fostered helpers were included in the sample as related helpers (see Results, section 2.1) Begging rate). The begging rate did not vary with any other variable (all P>0.086; **Table S9**).

Table S9. Results from the LMMs for the begging rate as dependent variable not including cross-fostered helpers in the birds sample (N=651) – Test 1 (helpers' status in relation to the offspring). Estimates and SE are given for the significant explanatory terms (in bold). The same minimal model was obtained by AIC model selection.

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**3.061**	**0.383**
Time since sunrise	**15.698**	**574**	**0.0001**	**0.0025**	**0.0006**
Last feeding	**10.726**	**574**	**0.0011**	**0.0004**	**0.0001**
Status of the bird	0.957	47	0.440		
Time since sunrise^2	1.018	573	0.313		
Bird age	0.398	573	0.529		
Brood size	3.618	10	0.086		
Average chicks' weight	0.482	10	0.503		
Group size	0.240	10	0.635		

PC2 – Test 2 (breeders status and helpers' status in relation to the female breeder)

When the cross-fostered helpers were removed from the sample used to test this model, due to the significance obtained in preliminary analyses, the PC2 lack of significant terms remained unchangeable (all P>0.159; **Table S10;** see Results section 2.2.2) PC2).

Table S10. Results from the LMMs for the PC2 as dependent variable not including cross-fostered helpers in the birds sample (N=414) – Test 2 (helpers' status in relation to the female breeder).

Explanatory variables	**F**	**d.f.**	**P**	**Estimate**	**SE**
Intercept				**1.378**	**0.851**
Brood size	2.419	8	0.159		
Status of the bird	0.308	32	0.820		
Time since sunrise^2	0.497	358	0.481		
Last feeding	0.565	358	0.453		
Bird age	1.866	34	0.181		
Time since sunrise	0.767	358	0.382		
Average chicks' weight	1.613	8	0.240		
Group size	0.255	8	0.627		

The results obtained from both tests were the same as when cross-fostered helpers were included and equivalent final minimal models were obtained as well. Considering that the preliminary analyses have shown a majority of non-significant differences between cross-fostered and genetically related helpers, and that the same minimal models were obtained when cross-fostered helpers were not included in the 2 tests with diverging results, it was considered that the most accurate way to proceed, concerning the aims of this study, was to include the cross-fostered helpers among the related helpers' categories accordingly to what is explained in the "genotyping and kinship relationships estimation" section of the methods (i).

Appendix 3. Begging features and bird status as the only explanatory term

1) Begging rate

Table S11. Results from the LMM for the begging rate as dependent variable and status as the only explanatory variable, including breeders and helpers' kin relationship to the offspring (N=689; Test 1).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**4.105**	**0.324**
Status of the bird	2.043	51	0.102		

Table S12. Results from the LMM for the begging rate as dependent variable and status as the only explanatory variable, including breeders and helpers' kin relationship to the female breeder (N=689; Test 2). Estimates and SE are given for the nearly significant explanatory variable (in italic bold).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**4.135**	**0.317**
Status of the bird	***2.453***	***53***	***0.073***		
Male breeder				***-0.139***	***0.152***
Related helper				***-0.264***	***0.173***
Unrelated helper				***0.769***	***0.388***

2) PC1 (General frequency scores)

Table S13. Results from the LMMs for the PC1 as dependent variable and status as the only explanatory variable, including breeders and helpers' kin relationship to the offspring (N=444; Test 1).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**0.131**	**0.430**
Status of the bird	1.933	34	0.127		

Table S14. Results from the LMMs for the PC1 as dependent variable and status as the only explanatory variable, including breeders and helpers' kin relationship to the female breeder (N=444; Test 2). Estimates and SE are given for the significant explanatory terms (in bold).

Explanatory variables	F	d.f.	P	Estimate	SE
Intercept				**0.132**	**0.428**
Status of the bird	**3.122**	**36**	**0.038**		
Male breeder				**0.105**	**0.102**
Related helper				**-0.253**	**0.115**
Unrelated helper				**-0.105**	**0.264**