



A cross-fostering experiment reveals that prenatal environment affects begging behaviour in a cooperative breeder



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ARTICLE INFO

Article history:

Received 6 November 2014

Initial acceptance 3 December 2014

Final acceptance 20 January 2015

Published online

MS. number: 14-00899R

Keywords:

begging

birds

cross-fostering

family conflict

helping behaviour

maternal effects

parent–offspring conflicts

Prenatal breeding conditions have broad influences on maternal allocation to reproduction which can strongly affect future begging behaviours of offspring. The social environment is part of the prenatal environment; however, its influence on maternal allocation has been poorly investigated and experimental tests linking prenatal conditions to begging behaviour have seldom been conducted. In cooperative breeders the presence of additional carers, the helpers, generally predicts an increase in provisioning during the nestling stage. Since begging is costly, in these species producing offspring that beg less in the presence of helpers may be a way of saving energy not only for the offspring but also for the future survival and reproduction of females. To date, whether mothers may manipulate begging behaviour in relation to helper presence is unstudied. We conducted a cross-fostering experiment in a cooperatively breeding bird, the sociable weaver, *Philetairus socius*, to disentangle the possible effects of prenatal and postnatal environments on begging behaviour. Pre- and postnatal environments correspond here to the number of carers in the nest of origin and the foster nest, respectively. As predicted, begging was influenced by the prenatal environment, with nestlings originally from larger groups begging less. In addition, chicks fed by more foster birds also begged at a lower rate. We conclude that the prenatal environment influences begging behaviour. This result has important implications for understanding cooperative breeding strategies since producing offspring that beg less with more helpers may allow energy savings for females and related offspring and helpers.

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Individuals modulate their investment in reproduction according to current breeding conditions and their expected future reproduction (Benton, Plaistow, Beckerman, Lapsley, & Littlejohns, 2005; Sheldon, 2000). Parents may fine-tune their investment by changing their provisioning behaviour (Santangeli, Hakkarainen, Laaksonen, & Korpimäki, 2012) or the number of offspring produced (Gliwicz & Boavida, 1996). Females may also adjust their investment per egg (Fox, Thakar, & Mousseau, 1997; Taborsky, 2006) and allocate different levels of costly nutrients before hatching (Verboven et al., 2003). In addition, mothers have the possibility of influencing the soliciting behaviour of their offspring through hormonal allocation to eggs (Smiseth, Scott, & Andrews,

2011). These prenatal maternal effects (Mousseau & Fox, 1998) allow females to further adjust offspring phenotypes and fitness.

Differential allocation is likely to induce conflicts of interest between parents and offspring, which may have different short- and long-term interests (Lessells & Parker, 1999; Trivers, 1974). A major conflict occurs because it is in the offspring's interest to receive more investment than it is optimal for parents to supply at each breeding attempt. This manifestation of parent–offspring conflict can be seen through begging–provisioning interactions when parents adjust their provisioning of resources in response to conspicuous signals given by the offspring (Godfray, 1995; Kilner & Johnstone, 1997) and offspring adjust their begging behaviour in response to the amount of resources received from the parents (Kilner & Johnstone, 1997; Smiseth, Wright, & Kölliker, 2008). Begging behaviours are commonly observed in species with parental care and can be visual, chemical, tactile or acoustic (Kilner & Johnstone, 1997; Mas & Kölliker, 2008). Being a signal, begging behaviour is usually costly in order to be reliable (e.g. having

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predation costs but also metabolic or immunological costs). These costs should be compensated for by a higher food intake but may not always be (Moreno-Rueda & Redondo, 2012). However, offspring begging may also be under maternal control and mothers may manipulate the begging according to offspring need and/or their own need (Moreno-Rueda, 2007; Müller, Lessells, Korsten, & von Engelhardt, 2007).

Mothers can influence offspring demand to match expected resource availability according to prenatal conditions (Helfenstein, Berthouly, Tanner, Karadas, & Richner, 2008; Hinde, Buchanan, & Kilner, 2009; Krause, Honarmand, & Naguib, 2011). Such adaptive maternal effects on offspring begging are expected to occur when the environmental conditions that offspring encounter are sufficiently predictable before laying (Burgess & Marshall, 2014). As pre- and postnatal environments are often correlated it is crucial to conduct cross-fostering experiments in order to show a prenatal effect of environmental conditions on offspring begging. However, prenatal effects of resource availability have been demonstrated by only one cross-fostering experiment on great tits, *Parus major*, which showed that nestlings from eggs laid by carotenoid-supplemented females and raised in small broods begged more intensely (Helfenstein et al., 2008).

Cooperatively breeding species represent a well-suited system which offers particularly interesting opportunities to study maternal control of begging behaviour and how this is influenced by the social environment. These species form breeding groups that involve not only parents but also nonbreeding helpers. Helpers are supernumerary individuals that assist the breeders by providing care to their offspring, particularly through additional food provisioned to the nest (Brown, 1987; Emlen, 1991). The presence of helpers thereby represents predictable improved rearing conditions.

In the presence of helpers, parents can either maintain their provisioning effort, in which case helper care is additive, or they can reduce their provisioning effort, which is partially or fully compensated for by the care of helpers (see Hatchwell, 1999 for a review). Helpers can also allow the females to modify their maternal allocation in order to maximize lifetime reproductive success. Cooperative breeders are usually long-lived species (Arnold & Owens, 1998; Covas & Griesser, 2007) and females with good future reproductive prospects are expected to decrease their investment in eggs with an increasing number of helpers in order to maximize their lifetime reproductive success (Russell & Lummaa, 2009). Indeed, recent results have shown that females may invest less by producing smaller eggs when they have helpers, since the additional food brought by the helpers may compensate for this difference in egg size (Canestrari, Marcos, & Baglione, 2011; Paquet, Covas, Chastel, Parenteau, & Doutrelant, 2013; Russell, Langmore, Cockburn, Astheimer, & Kilner, 2007; Santos & Macedo, 2011). Additionally, in the presence of helpers, sociable weaver, *Philetairus socius*, females have been found to deposit less steroid hormones in eggs (Paquet et al., 2013), which are potentially immunosuppressive (see Groothuis, Muller, von Engelhardt, Carere, & Eising, 2005 for a review). Simultaneously, the energy savings associated with reduced investment in eggs may be associated with improved female survival (Paquet, 2013; Russell et al., 2007). In these species, producing offspring that produce less frequent costly begging signals in the presence of helpers may also be a way of saving the offspring's energy, since such lower investment can be compensated for by the additional food provided by helpers. So far, however, whether mothers may manipulate begging behaviour in relation to the number of helpers is unstudied.

In a previous study that investigated whether the allocation of hormones to egg yolks varied with the presence of helpers we

showed that sociable weaver females deposit less testosterone and corticosterone in their eggs when they expect to have helpers at the nest (Paquet et al., 2013). There is strong evidence that maternal hormones, such as testosterone and corticosterone, are involved in the regulation of begging behaviour, especially in birds, at least early after hatching (Saino et al., 2002; Schwabl, 1996; Smiseth et al., 2011). Hence, we hypothesized here that prenatal social conditions influence offspring begging behaviour in this species. Producing offspring that beg less could allow the chicks to spend less energy begging as this lower investment may be compensated for by the additional food provided by helpers. Indeed, clutch size and fledgling mass do not vary with the number of helpers in the sociable weaver (Paquet et al., 2013), or may do so only when breeding conditions are poor (Covas, du Plessis, & Doutrelant, 2008), but chicks receive more food when fed by more birds (Covas et al., 2008). A consequence of lower begging is that it may also reduce the breeding female's provisioning effort, and both parents were found to reduce their feeding rate in the presence of helpers (Covas et al., 2008). To test the possibility of maternal manipulation of offspring begging behaviour in relation to their prenatal social environment, we used a complete cross-fostering experiment in the sociable weaver. Cross-fostering is a powerful method to disentangle prenatal from postnatal effects, the latter being directly influenced by the provisioning rate and the number of carers (i.e. parents + helpers). Complete cross-fostering (see for example Hinde, Johnstone, & Kilner, 2010) is in that case ideal to control for social epistasis effects such as sibling competition (Royle, Smiseth, & Kölliker, 2012). Moreover, complete cross-fostering designs generate experimental variation in the social environment for both offspring and parents (Royle et al., 2012).

Given that eggs were found to contain less testosterone and corticosterone in the presence of helpers (Paquet et al., 2013), and as both hormones are known to increase begging behaviour (see Smiseth et al., 2011 for a review), we expected an effect of the nest of origin on the begging rate (prenatal effect). More precisely, eggs laid in nests without helpers were expected to produce nestlings with higher begging rates than eggs laid in nests with helpers. As hormonal maternal effects may affect chicks' begging behaviour only during early developmental stages (Saino et al., 2006; Schwabl, 1996), we expected the potential influence of the original group size on chicks' begging to be stronger or only detectable soon after hatching (Saino et al., 2002; Schwabl, 1996). Here we recorded chicks on days 4 and 9 and so we expected a stronger effect on day 4. In addition, begging rate varies with offspring need and, therefore, we expected chicks' begging rate to be lower when they were fed by more birds (postnatal effect).

METHODS

Study Species

The sociable weaver is a colonial passerine endemic to the semiarid acacia savannahs of southern Africa (Maclean, 1973a; Mendelsohn & Anderson, 1997). Sociable weavers are facultative cooperative breeders, breeding in pairs or with up to five helpers (in this study, we had zero to three helpers, mean group size 3.05 birds). The helpers are usually related to one or both breeders. In this species, the overall frequency of food delivery was found to increase with the number of helpers and breeding males feed more than breeding females (Doutrelant & Covas, 2007). At the egg stage, group size is thought to be already fixed because chicks from the previous year help their parents for 1 or 2 years before breeding themselves and another study showed that prebreeding roosting group size and breeding group size are well correlated suggesting the breeding group size is predictable (Paquet, 2013).

Field Methods

Our aim was to swap synchronous whole clutches laid by different females. For this we determined laying dates and clutch sizes for as many nests as possible. In sociable weavers the onset and duration of reproduction are unpredictable, depending on rainfall which is erratic in this semiarid region. To determine the onset of reproduction, 15 study colonies (approximately 400 individually marked chambers, i.e. nest cavities within the communal nest structure where the birds roost and breed) were inspected every 3 days for two breeding seasons (from September 2012 to March 2013 and from September 2013 to February 2014). As soon as an egg was found in a colony, chambers were inspected every day to determine the clutch size and the laying date of a maximum number of pairs. Sociable weavers lay one egg per day and usually three or four eggs per clutch. When two clutches in the same colony were of the same size and laid synchronously or within a 1-day interval, the whole clutches were swapped on the day after the last egg was laid. A total of 80 clutches were swapped. However, because of the high level of snake predation (up to 80%; Covas et al. 2008), only 38 cross-fostered clutches (i.e. 19 swapped pairs) reached fledging age (see Appendix Table A1 for more information on experimental broods).

To identify the prenatal and foster group sizes, we first captured and marked all the individuals roosting in the colony with a unique colour ring combination before the onset of breeding (see Covas, Brown, Anderson, & Brown, 2002 for more details on the captures). Group size was determined as the number of birds seen feeding the nestlings. To identify the individuals feeding at a given cross-fostered chamber and hence the breeding prenatal and foster group sizes, we then conducted at least 6 h of observations on at least 3 different days. Observers were located under a hide placed 3–5 m from the colony. We were able to identify the breeding group size of the 38 cross-fostered chambers that reached fledging corresponding to 14 pairs and 24 groups (of three, four and five birds).

The sociable weaver's nestling period is 21–24 days (Maclean, 1973b). Chicks were weighed on days 4 and 9 after the hatching date of the first chick (hereafter day 4 and day 9). At these times we recorded acoustic begging of the cross-fostered chicks for 6 h with a tie-clip microphone (Olympus ME15, frequency range = 15–12 000 Hz) clipped at the entrance of the chamber and connected to an Olympus WS-750M recorder. Calls were recorded at 44.1 kHz in uncompressed PCM format for further analyses. Owing to technical problems in the field we were only able to record begging of 36 of the 38 broods at day 4 and 33 at day 9.

Begging Analyses

Begging rate has been shown to be linked to the chicks' needs (Price & Ydenberg, 1995) and to the eggs' or chicks' hormones (see Smiseth et al., 2011 for a review). We measured begging rate as the average number of calls/s, using the loudest and most easily distinguishable calls in the spectrogram during intensive begging (Fig. 1) until both begging rates and intensity suddenly diminished, typically corresponding to the departure of a provisioning adult.

Begging spectrograms were analysed and measured using the Syrinx sound analysis program (J. Burt, www.syrinxpc.com). For each recording on the sonogram, we randomly visually isolated 10 feeding events easily identifiable through the calls produced by the parents when entering the chamber immediately followed by the initiation of the chicks' begging calls (Fig. 1). Begging measurements were made blind to the pre- and posthatching group

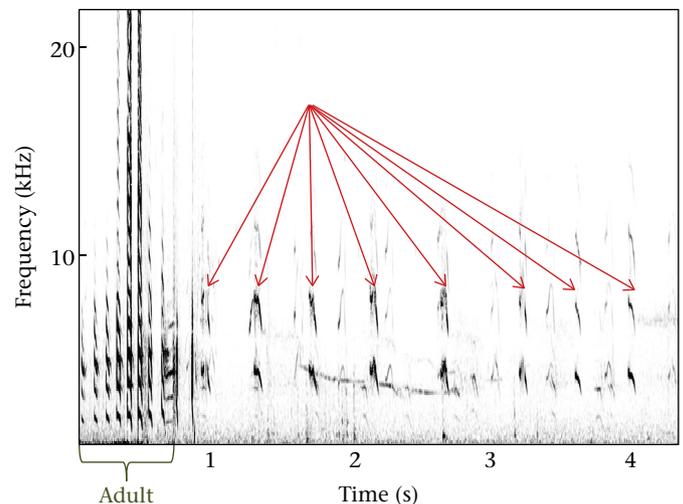


Figure 1. Spectrogram of the beginning of an analysed begging event. The sum of the begging calls of the loudest/most distinguishable chicks (red arrows) was divided by the duration of the intense begging following the entrance of an adult feeder (adult entrance calls on the left-hand side) to obtain the begging rate.

sizes. The mean duration of the selected begging events were 11.62 s at day 4 and 11.60 s at day 9. The duration of the begging events and the time of day when they occurred were not linked to the prenatal or postnatal group sizes (linear mixed models: all P values >0.20).

Statistical Analyses

The main purpose of these analyses was to study the effect of the original and foster breeding group sizes on the begging rate of the chicks at day 4 and day 9 by using linear mixed models with the package nlme in R (R Development Core Team, 2011). As breeding group sizes before and after cross-fostering were not correlated (Spearman rank correlation: $r_s = -0.09$, $P = 0.59$) we were thus able to include both variables in type III statistical models which allowed us to test for a prenatal effect of group size while controlling for the foster group size (and vice versa). The day 4 and day 9 final models were obtained by sequentially eliminating explanatory variables showing P values >0.05 using a backwards stepwise approach. The minimal models provided the P values of significant terms whereas P values for nonsignificant terms were obtained by reintroducing each nonsignificant variable into the minimal model (Crawley, 2002). Model selection by AIC gave the same two minimal models.

To take into account the nonindependence of the 10 begging events recorded per breeding chamber we fitted the random factor 'nest chamber' nested in a 'colony' factor nested in a 'breeding season' factor. The random term 'nest chamber' was highly significant for both begging rates at day 4 and day 9 (likelihood ratio LR = 206.78, $P < 0.0001$ and LR = 192.72, $P < 0.0001$, respectively) indicating a strong begging rate repeatability within chambers.

For the analyses of begging rate on both day 4 and day 9 we fitted the effect of the 'group size of the nest of origin' and the 'foster group size' as two explanatory variables and investigated both linear and quadratic relationships (as the relationship between begging rate and group size may be nonlinear). Although begging rates on day 4 and day 9 were correlated within nests (Pearson correlation: $r = 0.39$, $P = 0.03$), we ran separate analyses

for each, as we predicted that prenatal effects would decrease with time. 'Begging duration' (time during which the begging rate was measured) was added as a covariable to control for any potential correlation with begging rate. The 'date' (Julian day) and the 'time of day' of the begging events were also added as covariables as they may impact feeding and begging behaviour, notably through the effect of temperature (du Plessis, Martin, Hockey, Cunningham, & Ridley, 2012; Ricklefs & Hainsworth, 1968). Finally, the 'mean chick weight' of the clutches and the 'brood size' at day 4 and day 9 were included as fixed terms to control for potential begging rate variations due to variation in chicks' condition (Romano, Caprioli, Boncoraglio, Saino, & Rubolini, 2012) at day 4 and day 9. Brood size was not correlated with the number of helpers before and after cross-fostering (Spearman rank correlation tests: all P values >0.25).

Ethical Note

This work was conducted under an Ethics permit from the University of Cape Town (2009/V12/RCREN and 2014/V1/RC) and a research permit from the Northern Cape Province Department of Environment and Nature Conservation (FAUNA 942/2012).

RESULTS

Begging Rate on Day 4

Begging rate on day 4 was negatively influenced by both the original group size (i.e. the group size at laying, before cross-fostering; Fig. 2a, Table 1) and the foster group size (Fig. 2b, Table 1). The mean weight of the brood positively affected begging rate as well as the time

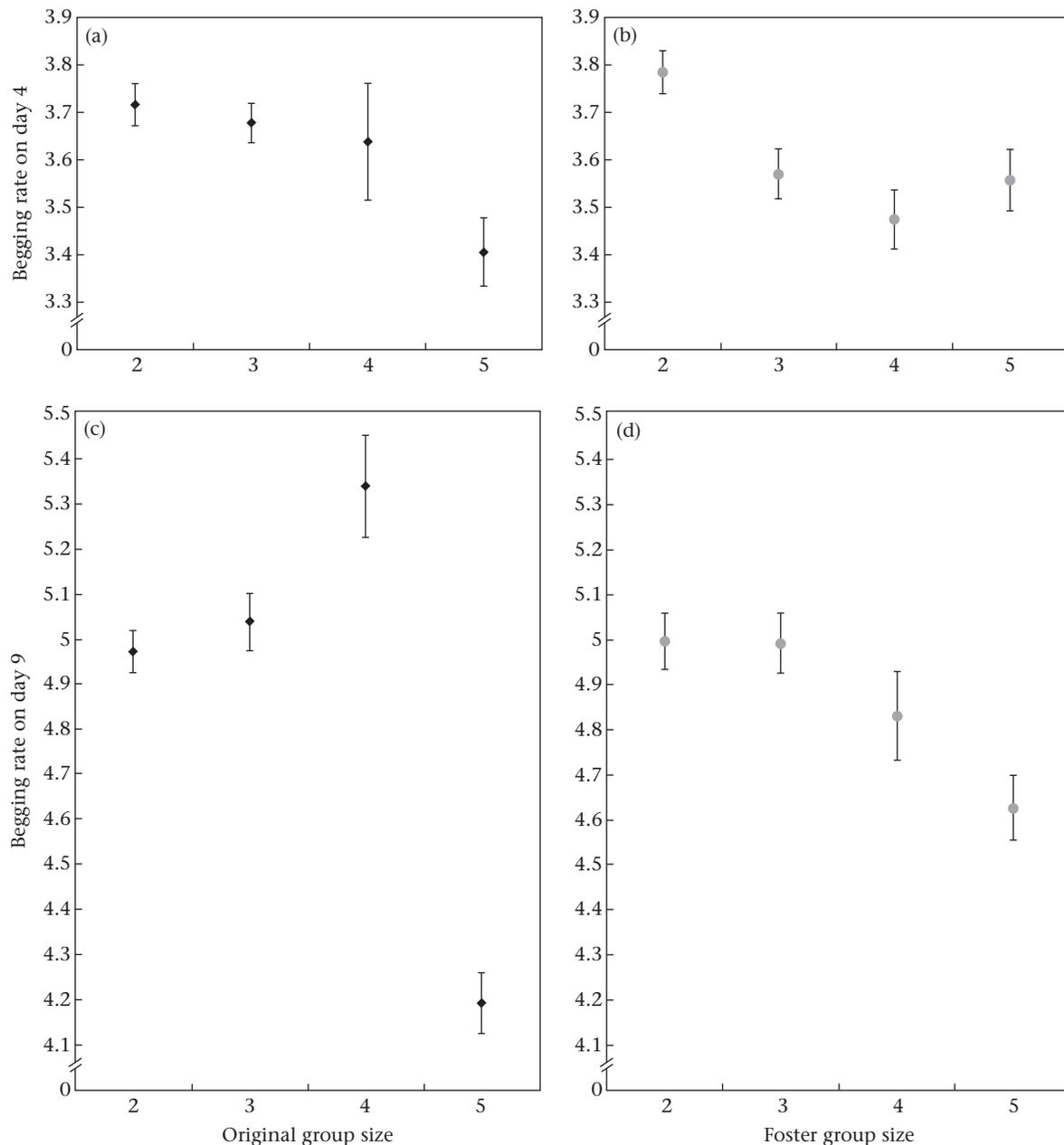


Figure 2. Offspring begging rate (per s) in relation to the breeding group size of the nest of origin before cross-fostering on days (a) 4 and (c) 9 and with the number of adult birds feeding at the foster nest on days (b) 4 and (d) 9. Average begging rates per group size \pm SE are plotted.

Table 1
Factors affecting offspring early begging rate (on day 4)

Explanatory terms	Estimate	SE	df	F	P	AIC
Intercept	3.346	0.509	313	43.241	<0.001	365.40
Original group size	-0.118	0.054	23	4.744	0.040	
Foster group size	-0.120	0.054	23	5.002	0.035	
Begging duration	-0.019	0.0054	313	12.417	0.001	
Mean chick mass per brood	0.133	0.051	23	6.813	0.016	
Time	0.026	0.013	313	4.084	0.044	
Brood size			22	1.281	0.270	369.19
Date			22	0.160	0.693	379.06
Original group size ²			22	0.502	0.486	370.98
Foster group size ²			22	0.206	0.654	371.26

Estimates and SE are given for significant (bold characters) explanatory terms included in the minimal model.

of day whereas there was a significant negative relationship with the begging duration (Table 1). No effects of the brood size, date or quadratic effects of group size were found (Table 1).

Begging Rate on Day 9

There was a quadratic effect of the group size of origin on begging rate on day 9 (Table 2) showing a decrease between groups of four and five birds but not before (Fig. 2c). Begging rate on day 9 also decreased significantly with the number of birds feeding (Fig. 2d, Table 2). In addition, we found a positive effect of brood weight and a negative effect of the duration of the begging event and the date. Begging rate was not affected by the time of day, the number of chicks and the quadratic effect of the foster group size (Table 2).

DISCUSSION

We investigated for the first time in a cooperative breeder whether begging behaviour may be influenced by the prenatal social environment created by the variation in the number of additional carers. As predicted under the hypothesis of prenatal influence, our brood-swapping experiments showed that the nest of origin had a strong influence on the begging rate of the chicks early in life, with the number of helpers from the breeding group of origin being negatively related to chicks' begging rate on day 4. We also found a quadratic effect of the original group size on begging on day 9, which seems to be mainly due to the lower begging of chicks originating from groups of five birds. Finally, as also expected, we found an effect of the rearing environment: chicks begged less when the rearing group size was higher. This shows

Table 2
Factors affecting later begging rate (on day 9)

Explanatory terms	Estimate	SE	df	F	P	AIC
Intercept	296.409	94.349	296	9.870	0.002	454.40
Original group size	1.638	0.484	19	11.439	0.003	
Original group size²	-0.266	0.071	19	14.200	0.001	
Foster group size	-0.257	0.073	19	12.497	0.002	
Begging duration	-0.041	0.005	296	68.347	<0.001	
Mean chick mass per brood	0.086	0.041	19	4.4103	0.049	
Date	-0.007	0.002	19	9.729	0.006	
Time			295	3.503	0.083	459.51
Brood size			18	0.114	0.739	458.75
Foster group size ²			25	0.253	0.621	459.68

Estimates and SE are given for significant (bold characters) explanatory terms included in the minimal model. The superscript '2' indicates a quadratic term.

that both prenatal and postnatal environments are important in determining nestling begging behaviour and indicates that mothers may control to some extent the begging behaviour of their young. Under this hypothesis, females would have the capacity to produce nestlings that beg less when it is less needed, i.e. when the presence of helpers ensures additional food.

We found that the begging rate of the chicks on day 4 decreased with the number of carers in the nest of origin independently of the number of birds that actually fed them. This clearly indicates a prenatal effect on offspring begging early after hatching which can be due to several factors. First, a likely candidate is maternal effects and possibly the lower amount of yolk testosterone and/or corticosterone that has been found in eggs produced by females with helpers in this species (Paquet et al., 2013). Indeed, these maternal egg hormones are typically found to increase begging behaviour at least soon after hatching (Saino et al., 2002; Schwabl, 1996; Smiseth et al., 2011). Concurring with this hypothesis, and the fact that prenatal effects are expected to have a limited posthatching duration (Saino et al., 2002; Schwabl, 1996), the quadratic effect of prenatal group size on day 9 may be explained by the fact that maternal effects of hormones on begging only remain detectable for chicks originating from the largest groups. A second factor that could explain differences in begging behaviour is a sex ratio difference between broods with and without helpers since male nestlings are known to beg more intensely than females (Bonisoli-Alquati, Boncoraglio, Caprioli, & Saino, 2011; von Engelhardt, Carere, Dijkstra, & Groothuis, 2006). However, in sociable weavers, groups with helpers were previously found to produce more males than pairs without helpers (Doutrelant, Covas, Caizergues, & du Plessis, 2004). Hence, we would expect nestlings raised by groups with helpers to beg on average more and not less intensely as reported in this study. Nevertheless, yolk testosterone has been found to be more beneficial for nestling females, which could thus explain higher begging of offspring from pairs without helpers if they indeed have more females (von Engelhardt et al., 2006). Third, our results could arise from a difference in parental quality that is likely to affect offspring phenotype, for instance because bigger or better quality parents have more helpers and produce bigger offspring that beg more. However, again we would expect nestlings raised by groups with helpers to beg on average more and not less intensely as reported in this study. In addition, we controlled for nestling body mass in our analyses of begging rate. Hence the influence of parental quality in the present results is probably limited.

The fact that chicks begged at a lower rate when fed by more carers (i.e. foster group size) is consistent with begging rate being a signal of offspring need for food, hence with the expectation that nestlings beg less in foster groups with helpers because they have more food and are more satiated. Indeed, in sociable weavers, as in several other cooperatively breeding species (Hatchwell, 1999), the number of helpers increases the total amount of food provided to the nestlings (controlled for the number of nestlings; Covas et al., 2008). That begging is a signal of need has been shown in many species. For example, an experimental study showed that begging performance of magpie chicks, *Pica pica*, was strongly negatively influenced by their food intake (Redondo & Castro, 1992) and in bell miners, *Manorina melanophrys*, the increase in food delivery induced by begging playbacks caused nestlings to reduce their own begging (McDonald, Kazem, & Wright, 2009).

Taken together, our results suggest that the prenatal social environment has a short-term effect on begging behaviour that is likely to be concealed later in the nestling period by the postnatal environment created by the number of helpers. Indeed, contrary to what was found in superb fairy-wrens, *Malurus cyaneus* (Russell

et al., 2007), we did not find any effect of the experimental addition or suppression of helpers on fledgling mass (i.e. number of helpers after minus before cross fostering; linear mixed model: $P = 0.45$) suggesting that carers adapt their feeding effort to offspring need.

Our study shows an influence of prenatal environment on begging behaviour through a cross-fostering experiment, concurring with a previous study performed on great tits (Helfenstein et al., 2008). In addition, our results both confirm that females may adjust their investment according to prenatal social conditions and open the possibility that reducing offspring begging behaviour is a likely mechanism by which females may save their offspring and themselves energy. In cooperative breeders, load lightening in the presence of helpers has been shown at both egg and nestling stages (Hatchwell, 1999; Russell et al., 2007; Taborsky, Skubic, & Bruintjes, 2007). The possibility that females may reduce offspring begging behaviour according to social prenatal conditions (here the number of helpers) is a particularly exciting new mechanism to study in other cooperative species, as not only offspring and females but also genetically related helpers may benefit from it by reducing their provisioning workload and thereby decreasing the costs of helping.

The results presented here, together with a previous study showing differential hormone deposition with the number of helpers in sociable weavers (Paquet et al., 2013), are in accordance with a possible maternal control of family conflicts (Smiseth et al., 2011). Indeed, even if costly, it could have been in the offspring's interest to beg more when more food can be provided by more carers.

A promising next step to understand family conflicts would be to study carers' response to begging as it may vary depending on the carer's sex (English, Kunc, Madden, & Clutton-Brock, 2008; MacGregor & Cockburn, 2002) or their relatedness to the offspring (Griffin & West, 2003). Individual responses to offspring begging have been poorly studied in cooperatively breeding species but the results obtained so far are in accordance with the hypothesis of female manipulation (Moreno-Rueda, 2007; Müller et al., 2007). In Arabian babblers, *Turdoides squamiceps*, where there is high relatedness within breeding groups, parents and helpers showed the same provisioning rule in response to experimentally manipulated begging (Wright, 1998). On the other hand, in superb fairy-wrens, where breeding males and helpers are most often unrelated to the brood, only these individuals, but not females, responded to increased begging (MacGregor & Cockburn, 2002). Individual response to offspring begging has not yet been studied in the sociable weaver but the observed individual provisioning behaviour of parents and helpers is compatible with the prediction of greater manipulation of nonkin feeders. Indeed, breeding males feed at a higher rate than females and helpers (Doutrelant & Covas, 2007), helpers being found to be first-order kin of the breeding female in 66% of cases (Covas, Dalecky, Caizergues, & Doutrelant, 2006). Additionally, helpers do not reduce their feeding rate with an increasing number of carers but, in accordance with Savage, Russell, and Johnstone's (2013) model, adult helpers' feeding rates are negatively correlated with their relatedness to the breeding female but not with that of the breeding male (Doutrelant, Dalecky, & Covas, 2011).

To conclude, our results show that the prenatal social environment influences the begging behaviour of nestlings. Hence maternal effects are likely to play an important role in the resolution of family conflicts and cooperatively breeding species represent promising candidate systems to further study the interplay between maternal interests, offspring demand and family composition. In particular, the variation in the number of carers and their relatedness to the mother provides exciting possibilities to obtain new insights into the role of maternal effects in the dynamics of offspring care and the resolution of family conflicts.

Acknowledgments

We thank all the field assistants and students that helped us monitor the weavers, especially Lisa Malm, Lara Broom, Maxime Loubon, Franck Theron, Margaux Rat and Aurélien Prudor. We are very thankful to Gonçalo Cardoso for helpful comments on the manuscript and to Sandrine Meylan, Andrew Young, Ben Hatchwell and Rene van Dijk for discussions of the results. We also thank Kees van Oers, Gregorio Moreno-Rueda and the anonymous referees for their comments that considerably helped improve the manuscript. De Beers Consolidated Mining Corp. gave us access to Benfontein Nature Reserve, where the work was conducted. Funding was provided by the Department of Science and Technology/National Research Foundation Centre of Excellence at the Percy FitzPatrick Institute, University of Cape Town, South Africa, the Portuguese Science and Technology Foundation (FCT; grant PTDC/BIA-BEC/103818/2008 to R.C.), the region Languedoc Roussillon (program 'chercheurs d'avenir' to C.D.) and the EU 7th framework program Marie Curie-IRSES. R.C. was funded by a 'Ciència 2008' fellowship (FCT), M.P. by the University of Montpellier II and by the Percy FitzPatrick Institute.

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Appendix

Table A1
Additional information on manipulated broods' characteristics

Chamber identity	Original group size	Foster group size	Clutch size	Brood size day 4	Brood size day 9	Season	Dyad identity	Colony identity
1	2	4	3	3	3	2012–2013	1	8
2	4	2	3	3	3	2012–2013	1	8
3	3	2	3	2	2	2012–2013	2	8
4	2	3	3	3	3	2012–2013	2	8
5	2	2	3	3	3	2012–2013	3	8
6	2	2	3	2	2	2012–2013	3	8
7	3	3	4	4	4	2012–2013	4	8
8	3	3	4	4	4	2012–2013	4	8
9	4	5	3	3	3	2012–2013	5	8
10	5	4	3	2	2	2012–2013	5	8
11	2	2	3	3	3	2012–2013	6	11
12	2	2	3	3	3	2012–2013	6	11
13	2	3	4	4	4	2012–2013	7	31
14	3	2	4	3	3	2012–2013	7	31
15	3	2	4	3	3	2012–2013	8	37
16	2	3	4	4	4	2012–2013	8	37
17	2	3	4	4	4	2012–2013	9	37
18	3	2	4	3	3	2012–2013	9	37
19	2	5	4	4	4	2013–2014	19	8
20	5	2	4	3	3	2013–2014	19	8
21	3	3	4	4	3	2013–2014	20	8
22	3	3	4	3	2	2013–2014	20	8
23	3	5	4	4	4	2013–2014	10	11
24	5	3	4	4	4	2013–2014	10	11
25	3	2	3	3	3	2013–2014	16	11
26	5	2	4	4	3	2013–2014	17	27
27	2	5	4	4	4	2013–2014	17	27
28	3	4	3	2	2	2013–2014	11	31
29	4	3	3	3	3	2013–2014	11	31
30	2	2	3	3	3	2013–2014	12	37
31	5	2	3	3	3	2013–2014	13	37
32	2	5	3	2	2	2013–2014	13	37
33	4	3	2	2	2	2013–2014	14	37
34	3	4	2	2	2	2013–2014	14	37
35	3	2	3	2	2	2013–2014	15	37
36	2	3	3	3	3	2013–2014	15	37
37	5	3	4	3	3	2013–2014	18	37
38	3	5	4	3	3	2013–2014	18	37