



Parent-absent calls are related to nestling reaction time and parental food allocation in the spotless starling

Blanca Jimeno^{a,*} and Diego Gil^b

^a Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Nijenborgh 7, 9747 AG Groningen, The Netherlands

^b Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain

*Corresponding author's e-mail address: bjimeno@evl.rug.nl

Accepted 29 March 2015; published online 23 April 2015

Abstract

Absent repeat calls (ARC) are produced by nestlings of some bird species when parents are not at the nest, and play a role in sibling interactions and parental investment. We explored if individual traits influencing begging also determine ARC in the spotless starling (*Sturnus unicolor*), and whether this behaviour explains nestling feeding success. We video-taped natural broods and examined the effects of experimental feeding in this behaviour. Experimentally fed chicks stopped calling and received fewer feedings. Among un-fed chicks, absence calls were more frequent in smaller nestlings. We found a positive relationship between nestling reaction time to parental arrival and food acquisition: chicks that reacted first received more feedings than slower chicks. ARC performance was also positively related to reaction time: chicks that produced more calls also reacted first to parents. These results suggest that ARC may have important effects on resource allocation and family interaction networks.

Keywords

parent-absent begging, begging, spotless starling, *Sturnus unicolor*, parental care, sibling competition, sibling negotiation.

1. Introduction

In most altricial birds, nestlings vigorously beg for food when parents arrive at the nest, and these begging displays comprise several visual and acoustic elements that parents can use to assess the relative need of their offspring and distribute food accordingly (Hussell, 1988; Leonard & Horn, 2001a; Kilner, 2002; Marques et al., 2009). A parent–offspring conflict arises because nestlings are expected to demand more than is optimal for parents to give

(Trivers, 1974; Godfray, 1995; reviewed in Kilner & Hinde, 2008). Furthermore, begging displays are also used in interactions among siblings while competing for food (Leonard & Horn, 1998; Parker et al., 2002; Johnstone, 2004; Blanc et al., 2010; Marques et al., 2011).

In the case of altricial species, offspring competing for access to limited parental resources are expected to achieve an optimal balance between the costs of competing for food, the benefits of being fed and the indirect costs of taking food from relatives (Godfray, 1995; Mock et al., 2011; Romano et al., 2012). In this scenario, nestlings in better condition are expected to incur in lower costs and gain relatively smaller benefits for a given begging level than nestlings in bad condition. Additionally, needy nestlings will also have less capacity to afford the costs derived from begging and scrambling with other siblings (Grafen, 1990; Royle et al., 2002). Since benefits of being fed are expected to outweigh the cost of begging only when hungry (Godfray, 1991), we may expect the development of individual-dependent begging strategies. Thus, it would pay hungrier and weaker nestlings to incur in higher begging efforts if this behaviour leads to an increase in their opportunities to obtain the next piece of food (Royle et al., 2002).

According to this perspective, there should be selection for an optimal begging level for each individual (Kilner & Johnstone, 1997; Godfray & Johnstone, 2000; Royle et al., 2002), and this level is expected to depend on individual condition but also on the environmental and social context (reviewed in Royle et al., 2002). A prediction derived from this theory is that, independently of body condition, at the moment of the parental visit, some short-term variable behavioural traits (position at the nest, height reached when begging, etc.) should play an important role in both the adjustment of begging solicitations and parental choice (Kilner & Johnstone, 1997; Royle et al., 2002; Dreiss et al., 2013). These traits are expected to vary between individuals (state, size, etc.) but also to be dependent on the competitive environment within the brood (Godfray, 1995; Royle et al., 2002; Johnstone, 2004; Romano et al., 2012; Ruppli et al., 2013). One of those behavioural traits that may determine feeding success is the 'vigilance component of begging' (Roulin, 2001b; Dreiss et al., 2013). This trait has been defined in terms of (i) stimuli discrimination ability and physical activity maintenance, which is expected to improve with development and (ii) reaction time (starting to beg faster than other chicks when a parent arrives). Reaction time has been shown to predict which nestling gets fed (Teather, 1992; Dearborn,

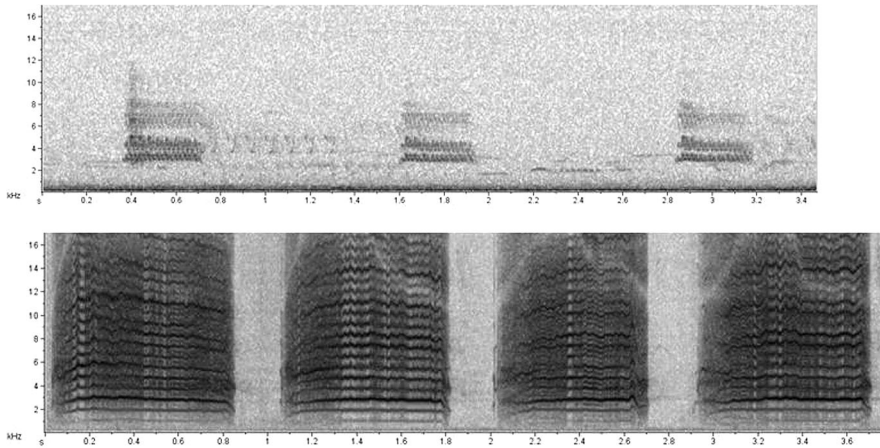


Figure 1. Sound spectrograms of typical examples of spotless starling ARC calls (top) and begging calls (bottom), recorded at 10 days of age. Note the difference in duration and spectral composition. In addition, although intensity readings cannot be taken from spectrograms, begging calls are much louder and conspicuous.

1998; Hofstetter & Ritchison, 1998; Lichtenstein & Sealy, 1998; Roulin, 2001b). This pattern may come about either because parents preferentially feed chicks that are more alert, or else because rapid chicks have advantages in sibling competition.

Nestlings of some altricial species also produce calls in the absence of parents (reviewed in Magrath et al., 2010). Most of these calls are attributed to begging errors and include vocalizations identical to those shown during parental visits, which are generally motivated by false alarms (Budden & Wright, 2001; Leonard & Horn, 2001b; Dor et al., 2007; Rivers, 2009). However, nestlings of some other species perform a different type of calls, shorter and quieter, which are known as absent repeat calls (here referred as ARC, Figure 1) (Roulin et al., 2000, 2009; Quillfeldt, 2002; Sicha et al., 2007; Bulmer et al., 2008). Previous studies have shown that hunger is a key factor influencing ARC levels (Roulin, 2001a; Maurer et al., 2003; Bulmer et al., 2008; Roulin et al., 2009; Dreiss et al., 2010). Additionally, this behaviour may also be used by siblings to obtain or communicate information, and several studies show a link between these calls and the ‘sibling negotiation hypothesis’ (e.g., Roulin et al., 2000; Roulin, 2001a; Johnstone & Roulin, 2003; Dreiss et al., 2010; Ruppli et al., 2013). This hypothesis has been widely studied in the species *Tyto alba*, and data suggest that the main

function of these calls involves negotiating need and access to parental resources. Siblings would use repeat calls to communicate need or motivation to other siblings and minimize competition when parents arrive with food, thus favouring needier brothers or sisters. According to the sibling negotiation hypothesis, a link between ARC level and feeding success for each nestling is expected (Roulin et al., 2000; Johnstone & Roulin, 2003; Roulin, 2004; Dreiss et al., 2010). Additionally, in other species performing ARC, the spotless starling (*Sturnus unicolor*), experimental work has shown that these signals are used in sibling-sibling interactions (Bulmer et al., 2008) and that there is a relationship between the level of ARC produced in a nest and parental investment (Jimeno et al., 2014). All these results suggest that ARC behaviour has important effects on the distribution of resources at the nest, as well as on family interaction networks.

If we want to determine to what extent begging and ARC can be included within the same category of interactions, it is important to know whether those factors that affect nestling solicitation level and feeding success in begging also determine ARC dynamics, as found for example for hunger levels (Bulmer et al., 2008). Some of those other traits are, for instance, flange colour and size, sex, or weight (Kilner, 1995, 1997; Saino et al., 2000b; Gil et al., 2008). The few studies that have so far investigated the relationship between individual traits and ARC levels, have only examined body mass, hunger level and hatching asynchrony (Dreiss et al., 2010; Roulin, 2004). However, nestlings performing higher ARC also tend to perform higher relative begging signals (Roulin, 2001b; Bulmer et al., 2008), and in *Tyto alba*, more vigilant and faster reacting nestlings vocalized more intensely in the absence of parents than their less vigilant brothers (Roulin, 2001b; Dreiss et al., 2013), and also tended to do so in the presence of parents. Thus ARC levels may predict chick behaviour during the following parental visit, and eventually feeding success. This could occur either because those chicks calling at a higher rate are those with a higher motivation and vigilance, or because ARC may influence sibling competition and lead to higher chances of being fed.

This study aims to explore if individual traits that have been shown to influence begging behaviour also determine ARC performance in the spotless starling, and whether this behaviour leads to possible direct benefits in terms of feeding success. To this end, we video-taped natural broods under control conditions and also examined the effects of an experimental feeding in this

behaviour, allowing us to test the degree of honesty and hunger-dependence of ARC.

2. Material and methods

We conducted this study between May and July 2012 in a nest-box population of spotless starlings (*Sturnus unicolor*), located in an open oak woodland in Soto del Real (Madrid, Spain). This is a sedentary and highly philopatric passerine, showing in our population a complex breeding strategy, including polygyny and interspecific nest parasitism. Females invest more than males in rearing the brood, but parental care varies widely among males (Moreno et al., 1999). Feedings can occasionally be divided among nestlings (1–3 nestlings fed per visit, own data) and consist mainly of insects, larvae and earthworms. Modal clutch size is five eggs (López-Rull et al., 2007), and overall visiting rate is 10.4 visits/h (SD = 5.17) when nestlings are 14 days of age (Bulmer et al., 2008). Fledglings leave the nest when they are approx. 23 days of age. Upon parental arrival at the nest, nestlings compete for food by lifting their bodies, opening their beaks in the direction of parents and calling loudly. In parental absence, they only perform minor movements and produce less conspicuous, although continuous repeated calls (ARC).

2.1. Field procedures and video recordings

The study was conducted over two consecutive days in each nest ($N = 15$, average brood size = 3.8 nestlings, range = 2–6), when chicks were between 10 and 12 days of age ($N = 57$, note that some nestling mortality and failure to determine sex in some samples reduced the sample to 47 nestlings). At this age ARC are very clear and conspicuous, and at the same time nestlings are still not big enough to fight for privileged positions (e.g., jumping close to the entrance, whole monopolization of the entrance, etc.) when parents arrive with food (own observations).

Video recordings were carried out between 8:00 h and 10:00 h, a time interval characterized by high feeding rates (own data). Data from the first day were used to obtain control levels of ARC and feeding patterns, and on the second day, the feeding experiment was performed. In total 100 min of video recordings were obtained each day. Video recordings were made using infrared microcameras (DVR Mini Vehicle 640 × 480 pix. 30 fps) placed inside the nest, and attached to the upper part. False cameras were set two

days before to allow habituation and reduce disturbances. Additionally, pilot recordings were made before the experiment in order to guarantee that the feeding rate obtained during the presence of the camera did not differ from the average levels observed before manipulation.

On the first day, all chicks at the nest were ringed and marked on the head with white correction fluid to allow individual identification in the video analysis. This way of marking has been shown not to affect feeding patterns or parental choice (Bulmer et al., 2008, own data). Several chick measurements were taken: body mass to the nearest mg (Ohaus digital balance; Ohaus, Parsippany, NJ, USA), flange colour and flange width to the nearest mm (Mitutoyo digital calipers; Mitutoyo, Kanagawa, Japan). After 100 min of video recording, cameras were replaced by camera decoys until the next day.

To determine sex, we extracted DNA from blood samples by means of an ammonium-acetate technique. We amplified through PCR a sex-specific CHD gene (Griffiths et al., 1998). Amplified products were visualized in 1.5% agarose gels stained with SYBR safe (Invitrogen, Carlsbad, CA, USA).

On the second day, we ranked the nestlings in each nest by mass and we alternatively allocated each chick to either a feeding treatment (fed with meat baby food until satiation), or a control treatment (chicks were only handled). In each nest we alternated the order in which the experimental/control treatments were allocated. After the feeding, we tape-recorded feeding and begging activities for 100 min, as in the first day.

2.2. Flange colour measurements

Flange colour measures were taken in the rectal commissure using a portable spectrophotometer (Minolta CM-2600D; Konica Minolta, Osaka, Japan). Flange colour spectra obtained for 360–700 nm with the spectrophotometer were reduced using a principal component analysis, extracting orthogonal components to be interpreted as an index of yellowness. The first principal component (PC1) explained 56.29% of colour variation (eigenvalue = 19.22) and showed factor loadings with a negative tendency for all the wavelengths. It was interpreted as an inverse of brightness (total amount of light reflected by a surface). Thus higher values of PC1 associated to darker mouths with less reflectance. The second principal component (PC2) explained 15.58% of colour variation (eigenvalue = 5.76) and showed negative values for intermediate wavelengths (420–480 nm). This pattern corresponds to the effect

of carotenoids accumulation over the reflectance, so PC2 was interpreted as saturation (chroma), being an indicator of carotenoid concentration in mouth flange. These two first components were introduced in the statistical models as descriptors of flange colour.

Recordings taken to illustrate differences between ARC and begging calls (Figure 1) were obtained with a digital sound recorder Edirol R-09 (Roland, Los Angeles, CA, USA), and spectrograms produced with Raven Pro 1.4 software (Cornell Lab of Ornithology, Ithaca, NY, USA) with the following settings: 512-point FFT, Hanning window function and 50% overlap.

2.3. Video analysis

When analysing video recordings, we did not take into account the first 20 and the last 10 min of recordings in order to avoid possible experimenter interference, so a total of 70 min per day (140 per nest) were analysed. The following measures for each nestling were taken: (i) ARC rate (mean time per minute during which the chick performed regular calls), (ii) average reaction rank and (iii) number of feeds received during the observation time. ARC calls are produced at a fairly constant rate (1 per second), so variation between individuals is mainly reflected in differences in the length of calling bouts and not in the number of calls per second. For the reaction rank, we ranked each nestling in terms of the sequence of begging initiation for each parental visit (Hofstetter & Ritchinson, 1998). Nestlings whose reaction was simultaneous were given the same rank. The proportion of feeds received per nestling was calculated as the ratio between the number of feeds received and the number of feeds expected given an equitable division among the number of siblings. In the few cases in which the piece of food was divided to feed two nestlings, both nestlings were considered as fed. The software EthoLog (Ottoni, 2000) was used to register both the number and duration of the parent-absence intervals and the ARC rate per chick.

2.4. Statistics

Statistical analyses were performed using R version 3.1.1 (R Core Team, 2014). The *lme* function in the R package *nlme* (Pinheiro et al., 2013) was used to run all models. Logarithmic transformations were performed to normalize some of the dependent variables. After obtaining the models we checked that residuals showed a normal distribution.

2.4.1. Experimental feeding and ARC behaviour

General lineal mixed models (GLMM) were used to detect the effect of feeding treatment in both ARC performance (first model) and number of feeds received in each nest (second model). Mean ARC (average of total seconds during all the video recording per chick) or relative percentage of feeds (per chick) were analysed as dependent variables. Treatment was introduced as fixed factor and either ARC performed or percentage of feeds received the previous day as a covariate, to control for differences between nests in intrinsic feeding rates. Nest was introduced as a random factor.

2.4.2. Individual traits and ARC behaviour

For this analysis only the video recordings of the first day were used, as we wanted to study the ARC behaviour before any experimental intervention. General lineal mixed models (GLMM) were built for: (i) individual traits determining ARC and (ii) individual traits determining food intake. Additionally, a third model was run to explore those traits that could determine reaction time. Sex was introduced as fixed factor, nest as random and body mass, flange colour components, mouth width and brood size as covariates. ARC and body mass were standardized by individual nest mean because we wanted to explore the effects at the brood level. During GLMM model simplification, non-significant terms were removed according to the maximum-likelihood criteria and followed by lower-order terms in turn from the maximal model until no further terms could be dropped without significantly reducing the fit of the model.

3. Results

3.1. Experimental feeding

Experimentally food-satiated chicks drastically reduced their average ARC rate to an almost silent level ($F_{1,14} = 15.30$, $p = 0.002$, Table 1), whereas control chicks produced a much higher rate, similar to that produced on the previous day (Figure 2). In fact, in 12 of the 15 nests analysed (80%) ARC were completely suppressed in fed chicks.

Experimentally-fed nestlings also received less feeds from parents ($F_{1,14} = 48.49$, $p < 0.001$, Table 2). During the first day all chicks received approx. 100% of the feeds that would correspond to them according to an equal share among all chicks. However, in the second day a significant effect

Table 1.

Results of the general mixed model analysing the effect experimental feeding on ARC performance.

	Value	SE	df	<i>F</i>	<i>p</i>
Intercept	9.339	2.014	14	34.476	<0.001
Treatment (fed)	−6.345	1.639	13	15.297	0.002**
Prev. ARC	−0.005	0.114	13	0.002	0.967

For abbreviations see Methods.

** Significant effect ($p < 0.01$).

of the treatment caused a large decrease in the feeds obtained by experimentally fed chicks and led to a proportional increase in control chicks (Figure 3).

3.2. Individual traits

Lighter chicks showed higher ARC rates ($F_{1,30} = 7.17$, $p = 0.012$), body mass being the only trait having a significant effect on ARC performance (Table 3). Additionally, reaction time was the only variable that showed a significant effect at explaining the percentage of feeds obtained per chick ($F_{1,30} = 5.61$, $p = 0.025$). Chicks reacting faster to the arrival of the parents obtained more feeds than their slower brothers or sisters (Table 4). ARC performance did not have any effect on the amount of food obtained.

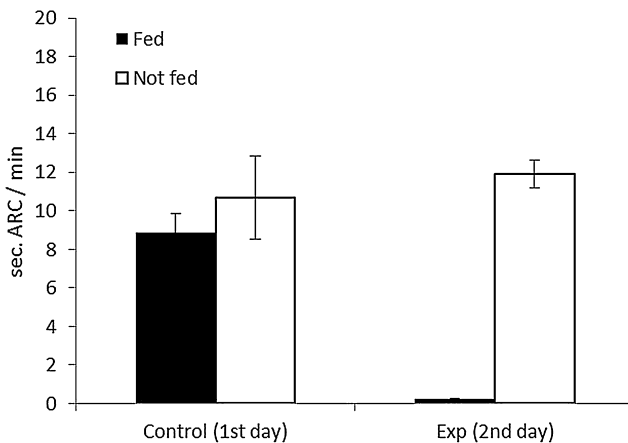


Figure 2. ARC rates of nestlings as a function of treatment (fed vs. not fed) and day (before or after experimental feeding). Bars represent means per chick plus one standard error. White bars: control (not fed chicks, $N = 28$); black bars: fed chicks ($N = 29$). Refer to Results for statistics.

Table 2.

Results of the general mixed model analysing the effect of experimental feeding on food intake.

	Value	SE	df	<i>F</i>	<i>p</i>
Intercept	126.865	39.808	14	89.601	<0.001
Treatment (fed)	-147.582	23.757	13	48.488	<0.001***
Prev. feeds	0.515	0.311	13	2.749	0.121

For abbreviations see Methods.

*** Significant effect ($p < 0.001$).

Finally, a third model was built to explore possible determinants of reaction rank as it was the only trait that we measured that had a significant influence on parental choice (Table 5, Figure 4). The ARC rate was found to have a significant effect on reaction time ($F_{1,29} = 4.38$, $p = 0.045$), and chicks performing higher ARC rates were those that were faster to react to parental visits (lower average reaction rank). Within the other traits only sex was found to have a significant effect ($F_{1,29} = 5.35$, $p = 0.028$), with males showing a faster reactions than females. This fact could be a consequence of males being more competitive or demanding than females.

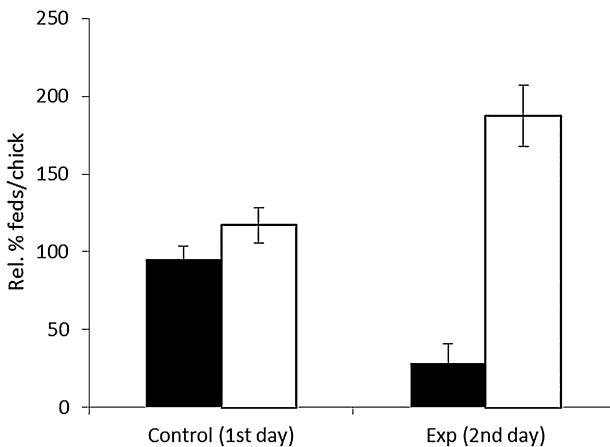


Figure 3. Relative percentage of feeds received per chick as a function of treatment (fed vs. not fed) and day (before or after experimental feeding). Bars represent means plus one standard error. White bars: control (not fed chicks, $N = 28$); black bars: fed chicks ($N = 29$). Refer to Results for statistics.

Table 3.

Results of the general mixed model analysing the effect of individual traits on ARC performance.

	Value	SE	df	<i>F</i>	<i>p</i>
Parameter					
Intercept	−5.741	6.742	30	0.108	0.745
Body mass	−0.631	0.275	30	7.172	0.012*
MouthW	13.358	15.202	30	0.772	0.387
Rejected terms					
Sex (Fem.)	−1.605	3.102	1	0.345	0.562
PC1	−0.018	0.026	1	0.338	0.567
PC2	0.001	0.037	1	0.002	0.961
Brood size	−0.508	1.361	1	0.139	0.715

For abbreviations see Methods.

* Significant effect ($p < 0.05$).

Table 4.

Results of the general mixed model analysing the effect of individual traits on food intake.

	Value	SE	df	<i>F</i>	<i>p</i>
Parameter					
Intercept	13.105	1.699	30	249.691	<0.001
PC1	0.012	0.007	30	2.318	0.138
Reaction	−2.441	1.062	30	5.607	0.025*
Rejected terms					
Body mass	0.008	0.147	1	0.003	0.955
ARC	−0.013	0.072	1	0.044	0.835
MouthW	10.813	10.758	1	0.638	0.432
PC2	−0.016	0.016	1	1.048	0.316
Brood size	0.086	0.626	1	0.270	0.614
Sex (Fem.)	0.545	1.396	1	0.003	0.957

For abbreviations see Methods.

* Significant effect ($p < 0.05$).

Table 5.

Results of the general mixed model analysing the effect of individual traits on reaction time.

	Value	SE	df	<i>F</i>	<i>p</i>
Parameter					
Intercept	-0.069	0.239	29	50.785	<0.001
MouthW	0.676	0.522	29	0.475	0.496
Sex (Fem.)	0.222	0.094	29	5.347	0.028*
ARC	-0.009	0.004	29	4.376	0.045*
Rejected terms					
PC2	-0.001	0.001	1	1.422	0.244
PC1	-0.001	0.001	1	1.685	0.206
Body mass	-0.005	0.011	1	0.185	0.670

For abbreviations see Methods.

* Significant effect ($p < 0.05$).

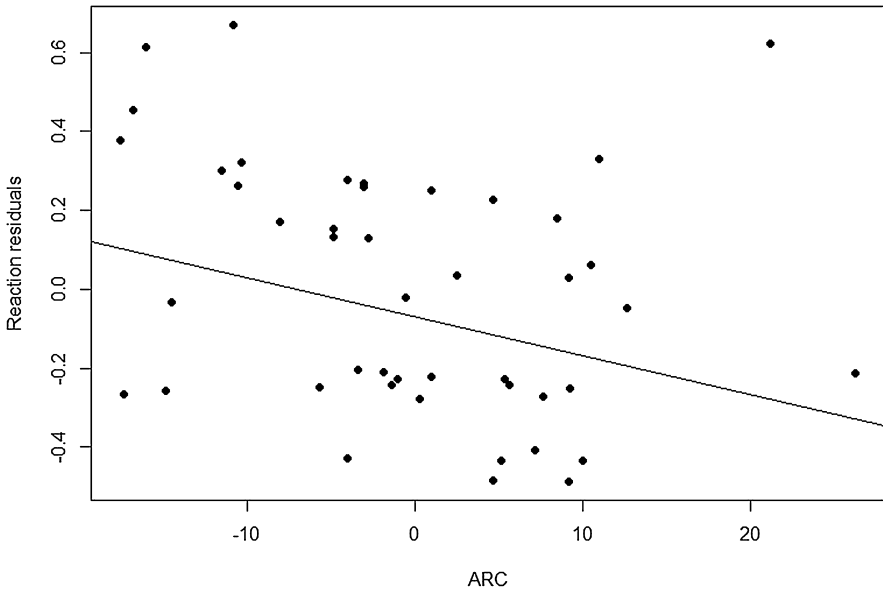


Figure 4. Effect of ARC rate on mean reaction rank residuals (third model, see Methods). Nestlings performing more ARC in each nest reacted to parental arrival faster than their brothers or sisters (third model, refer to Results for statistics).

4. Discussion

The experiment reported here shows that ARC behaviour in the spotless starling is determined by hunger to a large extent, and almost disappears when nestlings are satiated. ARC seems to be also related to begging behaviour and food intake, as satiated and silent nestlings received much less feeds from parents. Moreover, ARC was found to be related to faster reactions to parental arrival, this trait increasing the likelihood of being fed.

4.1. *Experimental feeding*

Our results show that ARC behaviour in the spotless starling is strongly dependent on hunger state. This suggests that an ARC is a honest signal at the individual scale, as shown by our finding that most chicks stopped calling when satiated. This result is supported by previous studies also underlining a link between ARC and need (Bulmer et al., 2008; Roulin et al., 2009), or the strong effect of food supply or deprivation in ARC levels (Roulin, 2001a; Bulmer et al., 2008).

Additionally, the fact that experimentally fed chicks obtained fewer feeds from parents also suggests that these signals have a role in parent–offspring interactions. Although begging behaviour itself was not the focus of this study, it was observed that acoustic and postural begging almost completely stopped for experimental chicks during at least the first 30 min after being fed. This suggests again a close link between both behaviours, as indicated by Dreiss et al. (2010), pointing at parent absent calls as being good predictors of chick begging behaviour and parental choice.

4.2. *Individual traits*

Nestlings with lower body mass performed more ARC. This result is in agreement with hypotheses that view ARC as an indicator of need or a trait dependent on body condition, as shown in other studies (Roulin, 2004; Dreiss et al., 2010). None of the other individual traits influenced this behaviour in our study. Contrary to expectations, brood size did not influence ARC, as showed in previous studies (Roulin et al., 2000; Bulmer et al., 2008; Ruppli et al., 2013). This difference could be attributed to a lower level of variation between nests in chick body condition than in previous studies.

Additionally, reaction time stood out as the only variable out of those that were measured that influenced the percentage of feeds received by the chicks. This finding is in agreement with some previous studies of begging

behaviour (Teather, 1992; Dearborn, 1998; Hofstetter & Ritchison, 1998; Lichtenstein & Sealy, 1998) and ARC behaviour (Roulin, 2001b). However, we found that parents did not feed more those nestlings that performed more ARC before their arrival. They selected nestlings with faster reactions and did not use any of those traits that have been shown to act as indicators of nestling body condition (i.e., body mass, flange width or colour) or body mass. This is in contrast to studies that have found that heavier nestlings with bigger and conspicuously coloured mouths are more successful and are preferentially selected by parents (Kilner, 1995, 1997; Saino et al., 2000b; Gil et al., 2008). Additionally, we found that parents did not feed chicks as a function of their size, which is in agreement with findings reported by Dreiss et al. (2013) for the barn owl, but in contrast to many begging studies with passerines in which body mass influences feeding to a large extent (Kilner, 1995; reviewed in Royle et al., 2002). Since we were not able to measure nestling begging behaviour during parental presence, we cannot discard a possible effect of some other variables in parental reaction. However, our personal observations suggest that all nestlings typically respond with maximum begging postures, in which case reaction time could indeed be the key factor in food allocation.

Interestingly, nestlings performing more ARC reacted faster to parental arrivals. Furthermore, ARC was the only variable of those that we measured that had a significant effect on how fast nestlings started to beg. This relationship was also suggested by Roulin (2001b) for the barn owl. Our results provide for the first time a link between ARC and begging reaction time, using non manipulated broods.

We were surprised at not finding a significant effect of mouth colour in ARC or in food intake, since previous studies have found that these are predictors of feeding success (Kilner, 1997; Saino et al., 2000a). It is possible that this is due to the fact that we could not measure the full UV spectrum with our equipment. Another possibility is that the range of variation in nestling condition was not large in our study, while previous studies may have included in the analyses nestlings which were in high levels of undernourishment.

Spotless starling nestlings with lower body mass performed more ARC. Additionally, nestlings performing more ARC reacted faster to parental arrival, and nestlings showing faster reactions obtained a disproportionate share of feedings from parents. In addition, feedings were relatively well

shared among nestlings, and this finding is also supported by the similar food intakes obtained by the two different treatments during the control day of the feeding experiment. These findings raise the question of why nestlings with higher ARC rates (those of lower body mass), if reacting faster, are not obtaining more food on average. It is possible that other factors such as noise or a high inter-nest or individual variability have precluded us from detecting this link, but the pattern that we found suggests the existence of a compensatory effect brought about by these calls. We propose that smaller chicks, by calling more in absence, increase their probabilities of obtaining food, and bring them to the same level of bigger nestlings. This could come about by two possible, non mutually exclusive ways. Firstly, by a possible direct effect by which ARC would favour an 'alert' state, helping chicks to perform a faster response to parents' arrival and leading to be fed by them. This has been previously proposed by Roulin (2001b) in the case of two-chick broods in the species *Tyto alba*. A second possibility is that parents might select begging or condition traits that have not been included here and that are correlates of both ARC and reaction time. However, since previous studies have found that bigger and stronger nestlings are selected by parents and have higher probabilities of being fed independently of their solicitation level (Hoffstetter & Richinson, 1998; Cotton et al., 1999; Dor et al., 2007), our findings suggests that a kind of equilibrium in food intake between nestlings with different degrees of need might be brought about by ARC levels. Thus ARC could have an important role in the individual and context-dependent strategies performed by nestlings that determine their success at being fed.

The fact that such a conspicuous and potentially costly behaviour as ARC is maintained by evolution rises the question about how far it entails a benefit for those individuals performing it. Although less conspicuous than standard begging, ARC behaviour could also entail important costs. Those costs could be related to nest detection by predators as well as to a prolonged energetic expenditure and sleep deprivation by calling nestlings. Future research should focus both in the compensation hypothesis as well as in the balance of costs and benefits that determine the maintenance of this behaviour.

Our findings are consistent with the idea that ARC could have a compensatory effect in the likelihood of nestlings to obtain resources from parents. Previous studies (Roulin, 2000; Johnstone & Roulin, 2003; Dreiss et al., 2010) have observed a direct ARC–food intake relationship but only in the

feeding immediately following the parental visit. This points to a higher success of chicks performing ARC for a given inter-fed interval, but may not coincide with the average effect during a longer period of time. Moreover, several studies on ARC (Roulin et al., 2009; Dreiss et al., 2010, 2013) did not obtain significant differences in food intake between ‘junior’ (smaller and younger) and ‘senior’ (bigger and older) nestlings either, independently of age (as found in the present study), although there were differences in ARC behaviour. However, they found that nestlings that performed more ARC had higher probabilities of obtaining the next piece of food. To explain this discrepancy of short vs. long-term effects, they suggest that a negotiation between siblings may be taking place before parental arrival. Additionally, we suggest that reaction time could be the link between ARC and parental choice, acting as a possible explanation linking the increased probability of being fed of the ARC calling nestlings with an apparent equal distribution of food among the brood by parents.

This study shows, on the one hand, that variables that have been shown to be clear determinants or indicators of begging behaviour in some species, such as mouth colour, flange width or sex, do not appear to influence ARC in spotless starlings. On the other hand, we show that these calls, as honest signals of need, may also be widely influencing other less known behavioural patterns (such as reaction time) that are determinant in nestling success and also a potential focus of study in the context of familiar interactions.

Acknowledgements

Financial support was provided by the research project CGL2011-26318 granted to DG by the Spanish Ministry of Science and Innovation. We thank the town council of Soto del Real and the Environment Division of the Madrid Autonomous Community for allowing us access to the area where this study was performed (Parque Regional del Alto Manzanares). Animal trapping and handling were approved by the Spanish Ringing Scheme (CMA). We wish to thank the help and logistics provided by Lorenzo Pérez Rodríguez, Jaime Muriel, Oscar Magaña, Raquel Monclús and Pablo Salmón.

References

- Blanc, A., Ogier, N., Roux, A., Denizeau, S. & Mathevon, N. (2010). Begging coordination between siblings in black-headed gulls. — *C. R. Biol.* 333: 688-693.

- Budden, A. & Wright, J. (2001). Falling on deaf ears: the adaptive significance of begging in the absence of a parent. — *Behav. Ecol. Sociobiol.* 49: 474-481.
- Bulmer, E., Celis, P. & Gil, D. (2008). Parent-absent begging: evidence for sibling honesty and cooperation in the spotless starling (*Sturnus unicolor*). — *Behav. Ecol.* 19: 279-284.
- Cotton, P., Wright, J. & Kacelnik, A. (1999). Chick begging strategies in relation to brood hierarchies and hatching asynchrony. — *Am. Nat.* 153: 412-420.
- Dearborn, D.C. (1998). Begging behavior and food acquisition by brown-headed cowbird nestlings. — *Behav. Ecol. Sociobiol.* 43: 259-270.
- Dor, R., Kedar, H., Winkler, D.W. & Lotem, A. (2007). Begging in the absence of parents: a “quick on the trigger” strategy to minimize costly misses. — *Behav. Ecol.* 18: 97-102.
- Dreiss, A.N., Calcagno, M., van den Brink, V., Laurent, A., Almasi, B., Jenni, L. & Roulin, A. (2013). The vigilance components of begging and sibling competition. — *J. Avian Biol.* 44: 359-368.
- Dreiss, A., Lahlah, N. & Roulin, A. (2010). How siblings adjust sib-sib communication and begging signals to each other. — *Anim. Behav.* 80: 1049-1055.
- Gil, D., Bulmer, E., Celis, P. & Lopez-Rull, I. (2008). Adaptive developmental plasticity in growing nestlings: sibling competition induces differential gape growth. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 275: 549-554.
- Godfray, H.C.J. (1991). Signalling of need by offspring to their parents. — *Nature* 352: 328-330.
- Godfray, H. (1995). Signaling of need between parents and young—parent—offspring conflict and sibling rivalry. — *Am. Nat.* 146: 1-24.
- Godfray, H.C.J. & Johnstone, R.A. (2000). Begging and bleating: the evolution of parent-offspring signalling. — *Phil. Trans. Roy. Soc. Lond. B: Biol. Sci.* 355: 1581-1591.
- Grafen, A. (1990). Biological signals as handicaps. — *J. Theor. Biol.* 144: 517-546.
- Griffiths, R., Double, M., Orr, K. & Dawson, R. (1998). A DNA test to sex most birds. — *Mol. Ecol.* 7: 1071-1075.
- Hofstetter, S. & Ritchison, G. (1998). The begging behavior of nestling eastern screech-owls. — *Wilson Bull.* 110: 86-92.
- Hussell, D.J.T. (1988). Supply and demand in tree swallow broods — a model of parent-offspring food-provisioning interactions in birds. — *Am. Nat.* 131: 175-202.
- Jimeno, B., Muriel, M., Pérez-Rodríguez, L. & Gil, D. (2014). Sexual differences in parental investment in response to parent-absent calls. — *Ethology* 120: 258-265.
- Johnstone, R.A. (2004). Begging and sibling competition: how should offspring respond to their rivals? — *Am. Nat.* 163: 388-406.
- Johnstone, R.A. & Roulin, A. (2003). Sibling negotiation. — *Behav. Ecol.* 14: 780-786.
- Kilner, R. (1997). Mouth colour is a reliable signal of need in begging canary nestlings. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 264: 963-968.
- Kilner, R. (1995). When do canary parents respond to nestling signals of need. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 260: 343-348.
- Kilner, R. & Johnstone, R.A. (1997). Begging the question: are offspring solicitation behaviours signals of needs. — *Trends Ecol. Evol.* 12: 11-15.

- Kilner, R. (2002). The evolution of complex begging displays. — In: The evolution of nestling begging: competition, cooperation and communication (Wright, J. & Leonard, M.L., eds). Kluwer, Dordrecht, p. 87-106.
- Kilner, R.M. & Hinde, C.A. (2008). Information warfare and parent-offspring conflict. — *Adv. Stud. Behav.* 38: 283-336.
- Leonard, M.L. & Horn, A.G. (1998). Need and nestmates affect begging in tree swallows. — *Behav. Ecol. Sociobiol.* 42: 431-436.
- Leonard, M.L. & Horn, A.G. (2001a). Acoustic signalling of hunger and thermal state by nestling tree swallows. — *Anim. Behav.* 61: 87-93.
- Leonard, M.L. & Horn, A.G. (2001b). Begging in the absence of parents by nestling tree swallows. — *Behav. Ecol.* 12: 501-505.
- Lichtenstein, G. & Sealy, S. (1998). Nestling competition, rather than supernormal stimulus, explains the success of parasitic brown-headed cowbird chicks in yellow warbler nests. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 265: 249-254.
- López-Rull, I. & Gil, D. (2009). Elevated testosterone levels affect female breeding success and yolk androgen deposition in a passerine bird. — *Behav. Proc.* 82: 312-318.
- Magrath, R.D., Haff, T.M., Horn, A.G. & Leonard, M.L. (2010). Calling in the face of danger: predation risk and acoustic communication by parent birds and their offspring. — *Adv. Stud. Behav.* 41: 187-253.
- Marques, P.A.M., Leonard, M.L., Horn, A.G. & Contasti, A. (2011). How nestling tree swallows (*Tachycineta bicolor*) integrate their responses to hunger and signalling by nestmates. — *Ethology* 117: 163-170.
- Marques, P.A.M., Vicente, L. & Marquez, R. (2009). Nestling begging call structure and bout variation honestly signal need but not condition in Spanish sparrows. — *Zool. Stud.* 48: 587-595.
- Maurer, G., Magrath, R., Leonard, M., Horn, A. & Donnelly, C. (2003). Begging to differ: scrubwren nestlings beg to alarm calls and vocalize when parents are absent. — *Anim. Behav.* 65: 1045-1055.
- Mock, D.W., Dugas, M.B. & Strickler, S.A. (2011). Honest begging: expanding from signal of need. — *Behav. Ecol.* 22: 909-917.
- Moreno, J., Veiga, J.P., Cordero, P.J. & Mínguez, E. (1999). Effects of paternal care on reproductive success in the polygynous spotless starling *Sturnus unicolor*. — *Behav. Ecol. Sociobiol.* 47: 47-53.
- Ottoni, E.B. (2000). EthoLog 2.2 — a tool for the transcription and timing of behavior observation sessions. — *Behav. Res. Methods Instr. Comp.* 32: 446-449.
- Parker, G., Royle, N. & Hartley, I. (2002). Begging scrambles with unequal chicks: interactions between need and competitive ability. — *Ecol. Lett.* 5: 206-215.
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2013). nlme: linear and nonlinear mixed effects models. R package version 3.1-113. — R Development Core Team, Vienna.
- R Core Team (2014). R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna. Available online at <http://www.R-project.org/>.
- Rivers, J.W. (2009). Parent-absent begging in the brown-headed cowbird (*Molothrus ater*): the role of short-term need and nestmate size. — *Behav. Ecol. Sociobiol.* 63: 707-717.

- Romano, A., Caprioli, M., Boncoraglio, G., Saino, N. & Rubolini, D. (2012). With a little help from my kin: barn swallow nestlings modulate solicitation of parental care according to nestmates' need. — J. Evol. Biol. 25: 1703-1710.
- Roulin, A. (2001a). Food supply differentially affects sibling negotiation and competition in the barn owl (*Tyto alba*). — Behav. Ecol. Sociobiol. 49: 514-519.
- Roulin, A. (2001b). On the cost of begging vocalization: implications of vigilance. — Behav. Ecol. 12: 506-515.
- Roulin, A. (2004). Effects of hatching asynchrony on sibling negotiation, begging, jostling for position and within-brood food allocation in the barn owl, *Tyto alba*. — Evol. Ecol. Res. 6: 1083-1098.
- Roulin, A., Kolliker, M. & Richner, H. (2000). Barn owl (*Tyto alba*) siblings vocally negotiate resources. — Proc. Roy. Soc. Lond. B: Biol. Sci. 267: 459-463.
- Roulin, A., Dreiss, A., Fioravanti, C. & Bize, P. (2009). Vocal sib-sib interactions: how siblings adjust signalling level to each other. — Anim. Behav. 77: 717-725.
- Royle, N., Hartley, I. & Parker, G. (2002). Begging for control: when are offspring solicitation behaviours honest? — Trends Ecol. Evol. 17: 434-440.
- Ruppli, C.A., Dreiss, A.N. & Roulin, A. (2013). Nestling barn owls assess short-term variation in the amount of vocally competing siblings. — Anim. Cogn. 16: 993-1000.
- Saino, N., Ninni, P., Calza, S., Martinelli, R., de Bernardi, F. & Møller, A.P. (2000a). Better red than dead: carotenoids-based mouth coloration reveals infection in barn swallow nestlings. — Proc. Roy. Soc. Lond. B: Biol. Sci. 267: 57-61.
- Saino, N., Ninni, P., Incagli, M., Calza, S., Sacchi, R. & Moller, A.P. (2000b). Begging and parental care in relation to offspring need and condition in the barn swallow (*Hirundo rustica*). — Am. Nat. 156: 637-649.
- Teather, K. (1992). An experimental-study of competition for food between male and female nestlings of the red-winged blackbird. — Behav. Ecol. Sociobiol. 31: 81-87.
- Trivers, R.L. (1974). Parent-offspring conflict. — Am. Zool. 14: 249-264.