Sexual Differences in Parental Investment in Response to Parent-Absent Calls

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Abstract

Begging in birds is a complex behaviour used by nestlings to solicit feeds from caregivers. Besides calling when parents are present, nestlings of some species also perform less conspicuous repeat calls when parents are absent. The fact that these calls are produced when parents are not at the nest does not mean that parents cannot hear them when they approach the nest or forage in its vicinity. In this study, we experimentally investigated the relationship between parent-absent repeat calls (ARC) and frequency of parental visits, considering parent/offspring communication as a possible implication of these acoustic signals. A playback experiment was conducted to detect changes in parental investment in response to increases in parent-ARC, expecting a differential sexual response. Results showed that females clearly responded to repeat calls, increasing their visit rate significantly with respect to females that received the control treatment. Males, on the contrary, did not change their visit rate in response to the treatment. This result provides evidence for a role of parent/offspring communication in parent-absent repeat calling, an additional function to sibling negotiation processes. The sex-specific response that we found is in agreement with previous studies that have found that females are more responsive than males to variation in solicitation and hunger signals performed by nestlings.

Introduction

Begging in avian nestlings is a complex behaviour that comprises multiple signals (visual, acoustic, etc.) that is mostly used by offspring to solicit feeds when parents arrive at the nest. This kind of behaviour has been widely studied because of its signalling role: adults obtain important information about the immediate needs of each nestling, as well as their general state or condition (Hussell 1988; Price & Ydenberg 1995; Kilner & Johnstone 1997; Leonard & Horn 1998, 2001b; Roulin et al. 2000; Marques et al. 2009). However, theory predicts a parent/offspring conflict over parental investment, as nestlings are expected to demand more than is optimal for parents to give (Trivers 1974; reviewed in Kilner & Hinde 2008). Additionally, several studies suggest that the functional significance of all these begging behaviours is related not only to parental/offspring communication, but also to a sibling interaction mechanism (competition or cooperation) that could be used by offspring to get more parental attention while minimizing the energy invested (Godfray 1991, 1995; Leonard & Horn 1998; Godfray & Johnstone 2000; Parker et al. 2002; Johnstone 2004; Blanc et al. 2010; Marques et al. 2011; Romano et al. 2012).

In addition to begging calls when parents are present, nestlings of some altricial species also call when parents are absent. In this context, it is highly important to make the difference between at least two types of behaviours (reviewed in Magrath et al. 2010). Firstly, most of these calls have been attributed to *parent-absent begging* (or *begging errors*) behaviour, which is associated with false alarms or cognitive fails, and comprise long, loud, broad frequency vocalizations, identical to those showed during parental visits (Budden & Wright 2001; Leonard & Horn 2001a; Dor et al. 2007; Rivers 2009). Secondly, nestlings of some other

species perform shorter, quieter repeat calls, with a much narrower sound frequency and generally less detectable (Roulin et al. 2000; Quillfeldt 2002; Sicha et al. 2007; Bulmer et al. 2008). This second kind of signal, which is clearly different from the first category (Magrath et al. 2010), is the focus of this study, and we will refer to them as *parent-absent repeat calls* (ARC). They have been observed in several bird species such as the barn owl (*Tyto alba*, Tytonidae, Roulin et al. 2000), the spotless starling (*Sturnus unicolor*, Sturnidae, Bulmer et al. 2008) and other species included in the bird families Coracidae (J.M. Avilés, pers. comm.), Icteridae (Price & Ydenberg 1995; Rivers 2009), Picidae (Glutz von Blotzheim 1966–1997) and Acanthizidae (Maurer et al. 2003).

Most of the previous studies that have analysed the origin, causes or benefits linked to ARC behaviour have almost exclusively considered the *sibling negotiation hypothesis* (Roulin et al. 2000, 2009; Roulin 2001; Johnstone & Roulin 2003; Dreiss et al. 2010). This hypothesis focuses on sib–sib interactions and points at communication of need between siblings as main purpose of these calls, which are supposed to evolve thanks to benefits accrued from minimizing competition when parents arrive with food. However, this interpretation neglects possible additional effects of these signals in parent/offspring communication and indeed most studies rule it out as a likely hypothesis (e.g. Roulin et al. 2000; Leonard & Horn 2001a; Quillfeldt 2002; Maurer et al. 2003; Sicha et al. 2007). However, the fact that the calls are produced when the parents are not at the nest does not mean that parents cannot hear them while foraging or when they approach the nest, and thus, it is possible that adults could use these calls to assess the state or need of their nestlings (e.g. Sicha et al. 2007). In this case, we can predict that parents should adjust their investment according to the level of ARC perceived at their nest.

Correlative and experimental evidence shows that the main factor influencing ARC levels is hunger (Roulin 2001; Maurer et al. 2003; Bulmer et al. 2008; Romano et al. 2012). The need to acquire food motivates nestlings to call, most likely because of their impact on parents, although this does not preclude that the same behaviour may be used by siblings to obtain information, or by the sender to manipulate its siblings. According to these interpretations, ARC may have important effects on both the frequency of parental visits and the distribution of resources at the nest.

In spite of acoustic differences between standard begging and ARC, the intensity of the two behaviours could indeed be correlated if they are influenced by the same factors. In that sense, ARC levels could act as a predictor of chicks' behaviour during the following parental visit. Similarly to ARC, begging intensity in the presence of the parents has been shown to be determined by the degree of hunger of the nestlings (Redondo & Castro 1992; Saino et al. 2000; Sacchi et al. 2002). Although many studies have found a strong relationship between nestling begging and parental feeding rate (Ottosson et al. 1997; Burford et al. 1998; Price 1998; reviewed in Hinde & Kilner 2007), it still remains unclear whether this pattern also holds in the case of ARC behaviour (Price & Ydenberg 1995; Roulin et al. 2000; Quillfeldt 2002; Maurer et al. 2003; Sicha et al. 2007). Additionally, many studies report clear sex-specific responses to increases in begging signals (Kölliker et al. 1998; Kilner 2002; Quillfeldt et al. 2004; Hamer et al. 2006; Royle et al. 2012). Typically, mothers, but not fathers, tend to respond to an increase in the begging calls of their offspring by increasing provisioning rate (Kölliker et al. 2000). However, these sex-specific responses have not been considered in previous studies investigating ARC.

This study addresses experimentally the relationship between ARC and the frequency of parental visits, with a view to test the role of parent/offspring communication in the evolution of these acoustic signals. A playback experiment was conducted to detect changes on parental investment in response to increases in ARC, focusing on a possible sex-specific response.

Methods

The study was carried out between March and June 2012 on a population of spotless starlings (*S. unicolor*) breeding in nest boxes in an open oak woodland in Soto del Real (Madrid, Spain). The spotless starling is an altricial, medium-sized passerine. It is a sedentary and highly philopatric species, showing a complex breeding strategy, with high rates of polygyny. Generally, females invest more than males in rearing the brood, but paternal care varies widely, with some pairs exhibiting biparental care and others in which females are left alone to care for nestlings (Moreno et al. 1999). Feedings provided by parents can be divided among nestlings (1–3 nestlings fed per visit, own data) and consists mainly of insects. 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 d of age (Bulmer et al. 2008). Fledglings leave the nest when they are approx. 23 d of age. When parents arrive at the nest, nestlings

compete by opening their beaks vigorously 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).

General Field Procedures

At the beginning of the breeding period, adults were captured and ringed by trapping them inside the nest boxes, and miniature microchips were placed under the skin of their backs (Trovan ID-100A; Trovan Ltd., Douglas, UK). Removable microchip recording devices consisting of an antenna, a reader and a battery are installed at the entrance of nest boxes, allowing identification of the pair owning each nest box and monitoring of both male and female visits. To reduce disturbance, all boxes are equipped with dummy antennas, and the rest of the device is hidden in ad hoc plastic boxes that are permanently attached to the side of the nest box.

Experimental Stimuli

Parent-absent repeat calls recordings (seven different bouts) were obtained from chicks aged 10–11 d by approaching nest boxes (different to experimental ones) using a sound recorder equipped with an omnidirectional microphone (Edirol 9; Roland, USA). One-minute long recordings were then edited using the software Avisoft (Avisoft Bioacoustics, Berlin, Germany), by adjusting them to the species-specific typical average rate of 1 call/s (Quillfeldt 2002; Maurer et al. 2003; Sicha et al. 2007; Bulmer et al. 2008; Grim 2008, own data). Similarly, broadcasting intensity was standardized at 51 dB at 1.5 m from the nest-box entrance, following our own perception of the typical level observed in broods, by using a sonometer (CESVA SC-2c; Barcelona, Spain). Control stimuli were produced by taking environmental background noise recordings (five different samples) obtained in the same way near empty nest boxes.

Experimental Procedure

The sample consisted of 22 nests, with an average brood size of 3.63 nestlings (range 2–5) of 10–11 d of age. In all nests, both male and female had been marked and identified previously, so all parental visits could be detected by means of the transponder readers. The experiment took place in the late morning (after 11:00 am), avoiding the hours with highest feeding rates (early morning, own data), to avoid a

ceiling effect and thus be able to detect possible increases in parental visits. For each nest, the experiment was performed on two consecutive days. The first day was used to estimate baseline feeding rates without any intervention, and experiments were performed on the second day. Microchip readers were placed on the first morning around 11:00 am, and a day later, at the same time, one of two playback treatments was broadcasted uninterruptedly during the duration of the trial in the nest box: (1) Environmental background noise as control treatment (N = 9), (2) Parent-ARC as experimental treatment (N = 13). In this sense, the ARC playback did not differ in intensity or rate with respect to normal ARC calls, the only difference being that it continued uninterruptedly during the whole trial. Microchip readers were left at the nests for the whole duration of the study to minimize disturbance. Recordings were played back with an Archos AV400 audio player (Archos, Igny, France) and amplified by miniature loudspeakers (TRMS02S; Mobile Audio).

Measurement of Responses

On the first morning, the number of visits by each member of the pair was recorded during 2 h, obtaining a baseline visit rate (BasR) for each nest. On the second day, two measures for each nest at the same period of the day were taken and used as repeated measures in the statistical analysis: visit rate during 40 min previous to the playback allocation (PreR), and visit rate during 40 min of playback treatment (PR). In this way, BasR and previous visit rate (PreR) acted as a double control of treatment responses. BasR provided an average investment rate for each nest without intervention, and by means of PreR, we could detect the effect of playback treatment by comparing PR with the immediately previous investment rate during the same period of time. We chose this design because previous data (own data) suggested that levels of parental visits could vary between days, likely because of social instability in the colony (for instance, frequent nest takeovers by males and females), and thus, we wanted to make sure that we controlled for both the average visit rate (indicative of the general level of share of parental care within the pair) and the immediately previous visit rate for each nest.

Statistics

Statistical analysis was performed using R version 2.15.2 (R Core Team 2012). A general lineal mixed model (GLMM) with a repeated factor was used to

detect the effect of playback treatments. The lme function in the R package *nlme* (Pinheiro et al. 2013) was used to perform this analysis. Time was introduced as a repeated factor (Rep) with two levels corresponding to the visit rates obtained before (PreR) and after (PR) the experimental trials. In addition to this repeated factor, sex and treatment (Control or ARC) were introduced as fixed factors, individual as random and BasR as covariate. Nest was introduced as random but was subsequently dropped because it had no significant effect (*L*-ratio test, p = 0.999).

During GLMM model simplification, firstly, non-significant interactions were removed according to the maximum-likelihood criteria, rejecting all those models that did not make biological sense 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. During final model selection, Akaike Information Criterion (Akaike 1973) was also considered to identify thoroughly parsimonious models (Burnham & Anderson 2002; Symonds & Moussalli 2011). The three-way interaction Time*Sex*Treatment was *a priori* contemplated, because our hypothesis considered differential responses between sexes to the treatment.

After obtaining the final general model and the main effects, two models (one for each sex) were obtained to analyse in depth different responses detected in males and females for each treatment. All models showed normally distributed residuals.

Results

The final GLMM showed a significant interaction between the repeated factor, sex and treatment (*L*-ratio = 14.2795, p < 0.001), meaning that after controlling for individual feeding rates, males and females showed differential visit rates in response to playback, as well as differential responses depending on the treatment (Table 1).

Once differentiated by sex, partial models showed that females, but not males, showed a clear response to ARC treatment (Tables 2 and 3). For females, a significant Treatment*Time interaction (p = 0.027) was obtained, showing a differential response to each treatment: females exposed to ARC playback significantly increased their visit rates (*t* = 1.70, p = 0.05), whereas females exposed to the control treatment reduced their visit rate, although not significantly so (*t* = −1.46, p = 0.1, Fig. 1). Males, on the contrary, did not change their visit rates in response to the treatment type (Control vs. ARC) or the manipulation itself (PreR vs. PR) in any case (Fig. 2).

Table 1: Results of the general mixed model analysing the effect of the playback experiment on parental visit rate. For abbreviations see Methods

	Value	SE	df	*t*	p
Intercept	1.40	1.38	39	1.02	0.36
BasR	0.65	0.12	38	5.42	<0.001***
Females	2.52	1.81	38	1.40	0.18
ARC	1.41	1.66	38	0.85	0.40
PR	−1.78	1.76	39	−1.01	0.32
Females*ARC	−3.61	2.31	38	−1.56	0.13
Females*PR	−1.61	2.49	39	−0.65	0.52
Females*PR*ARC	6.24	2.29	39	2.73	0.01**
Males*PR*ARC	−0.10	2.32	39	−0.04	0.97

ARC, absent repeat calls; BasR, baseline visit rate; PR, playback treatment. Significant effects signalled as: * (p < 0.05), ** (p < 0.01), *** (p < 0.001).

Table 2: Results of the general mixed model analysing the effect of the playback experiment on parental visit rate for female parents. For abbreviations see Methods

	Value	SE	df	*t*	p
Intercept	5.51	2.05	20	2.68	0.01
BasR	0.46	0.18	19	2.61	0.02*
ARC	−2.34	2.85	19	−1.26	0.22
PR	−3.39	2.00	20	−1.69	0.11
ARC*PR	6.24	2.61	20	2.39	0.03*

ARC, absent repeat calls; BasR, baseline visit rate; PR, playback treatment. Significant effects signalled as: * (p < 0.05), ** (p < 0.01), *** (p < 0.001).

Table 3: Results of the general mixed model analysing the effect of the playback experiment on parental visit rate for male parents. For abbreviations see Methods

	Value	SE	df	*t*	p
Intercept	0.013	1.22	19	0.01	0.99
BasR	0.94	0.15	18	6.29	<0.001***
ARC	1.96	1.32	18	1.49	0.16
PR	−1.78	1.37	19	−1.29	0.21
ARC*PR	−0.10	1.82	19	−0.05	0.96

ARC, absent repeat calls; BasR, baseline visit rate; PR, playback treatment. Significant effects signalled as: * (p < 0.05), ** (p < 0.01), *** (p < 0.001).

Discussion

In most communication systems, we can clearly identify the signaller and the receptor, but in some instances, it is not easy to know which receiver drives the evolution of a signal (Endler 1993; Searcy & Nowicki 2005). This is the case for those calls produced by nestlings when parents are not present at the nest, because both fellow nestlings, parents or even predators could be the likely receivers of the signal. Most previous analyses have pointed to a function of these
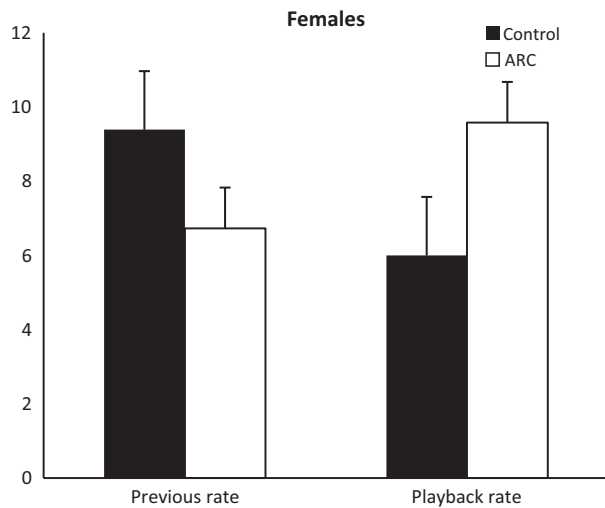
Fig. 1: Visit rates of female parents as a function of experimental treatment and time of manipulation (before and after playback). Bars represent x̄ + 1 SE. Black bars: control (background noise); white bars: parent-absence repeat calls. Refer to Results for statistics.
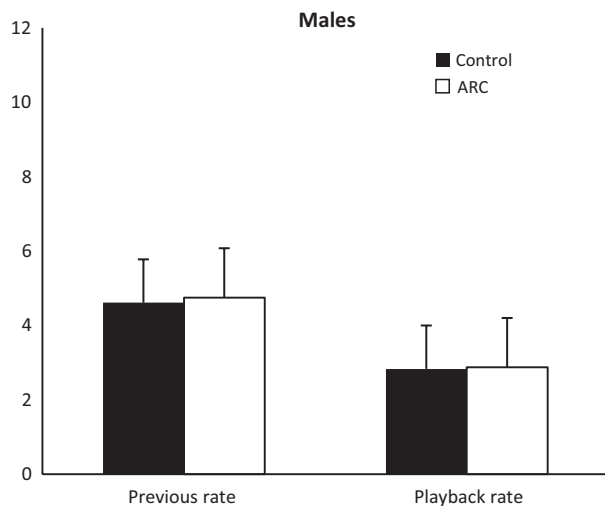

Fig. 2: Visit rates of male parents as a function of experimental treatment and time of manipulation (before and after playback). Bars represent x̄ + 1 SE. Black bars: control (background noise), white bars: parent-absence repeat calls. Refer to Results for statistics.

calls in communication among nestlings, suggesting a sort of cooperative turn-taking when parents arrive with food (Roulin et al. 2000, 2009; Roulin 2001; Johnstone & Roulin 2003; Dreiss et al. 2010). Our study provides evidence of an effect on parents: we found a significant increase in female visit rate in those nests in which ARC were played back. Parents may hear ARC performed by their nestlings when they arrive to the nest to feed, or while foraging in the

neighbourhood, and adjust their investment accordingly.

It could be argued that this sex-dependent effect could arise if females have smaller foraging ranges than males, thus being more exposed to ARC from their nests than males. Although we do not have the data to test this possibility, previous studies have found females to be more responsive than males to nestling need (e.g. Burford et al. 1998; Kölliker et al. 1998; Royle et al. 2012), and thus, it seems more parsimonious to assume that a similar process is operating in this case. Another possibility is that our manipulation may have increased nestling begging during parental visits, and this effect may be the cause of the increase in visits that we detected. We believe that this is unlikely, because previous experiments in the barn owl (e.g. Dreiss et al. 2010) have shown that siblings that do not perform parent-absent calls are less likely to get fed when parents arrive, suggesting some degree of inhibition or turn-taking in favour of needy siblings.

To our knowledge, only one playback experiment similar to ours has been carried out so far (Sicha et al. 2007), with a brood parasite species, the common cuckoo (*Cuculus canorus*). This study did not detect increases in parental visit rates when increasing ARC by playback. But important differences between species may explain this discrepancy. On the one hand, in cuckoos, only one parasite nestling performs ARC in the host nest, whereas in starlings, all nestlings potentially produce these calls. But more importantly, hosts are often forced to feed at a maximal rate when feeding large brood parasites (Davies 2000), and thus, an increase in feeding rates may be impossible to achieve (Sicha et al. 2007). Some other studies have looked, although less exhaustively, at the effects of stimulating nestlings ARC in parental investment (Roulin 2001; Haff & Magrath 2011), without finding any clear relation. In our study, males did not show significant differences in their visit rates in any treatment, and those were smaller overall than female rates. The reduction between PreP and PR visiting rates observed in both sexes could be attributed to the natural reduction of adult activity along the morning (own data). Similarly to previous studies, we found that spotless starling males show a lower nestling feeding rate than females (Moreno et al. 1999). Additionally, male investment is expected to depend more strongly on extrinsic factors, not related to the degree or intensity of offspring acoustic solicitations. In the case of the spotless starling, rates of extra-pair paternity attain 19% of broods (Celis 2009), and thus, paternity uncertainty may also contribute to a reduction in paternal

investment. Sexual differences in investment rules have been observed before in other species such as the great tit *Parus major* (Kölliker et al. 1998, 2000; Royle et al. 2012) or the red-winged blackbird *Agelaius phoeniceus* (Burford et al. 1998). These studies have found that females show stronger responses to nestling hunger and body condition than males, keeping a tighter relationship between visiting rate and begging than males do (Burford et al. 1998). In contrast, males seem to select favour some nestlings over others, following certain characteristics that may correlate with nesting survival probability (Kölliker et al. 1998).

Our study provides evidence that parent-ARC performed by nestlings play a role in parent-offspring communication, influencing the degree of maternal investment. To our knowledge, this is the first time that this question has been addressed experimentally in an altricial bird other than a brood parasite. Looking at future research, it seems highly relevant to determine whether ARC and standard begging are part of the same phenomenon or not. Data so far seem to suggest a very close connection indeed. Firstly, both phenomena are hunger dependent (e.g. Redondo & Castro 1992; Price & Ydenberg 1995; Roulin et al. 2000; Saino et al. 2000; Sacchi et al. 2002; Maurer et al. 2003; Dor et al. 2007; Bulmer et al. 2008; Magrath et al. 2010). Secondly, our study shows increases in parental investment, similarly to other studies that have found higher number of nest visit rates with increased playback of nestling calls (Burford et al. 1998; reviewed in Hinde & Kilner 2007) and reduced visit rates when muting nestlings (Glassey & Forbes 2002). These previous results and the results obtained in this study suggest that nestling vocalizations, including those performing in the absence of parents, play a determinant role in short-term adjustments in the rate at which nestlings are fed.

Such a conspicuous behaviour, however, may entail costs due to higher predation risk and energetic expenditure (Johnstone 1999; Rodriguez-Girones et al. 2001; Roulin et al. 2008; Haff & Magrath 2011). If this is so, we would predict that nestlings that perform ARC accrue some type of benefit through better parental care. This suggestion calls for studies that accurately determine the frequency and distribution of ARC behaviour, as well as a quantification of both direct and indirect benefits and costs linked to it. Furthermore, studies should incorporate a perspective of parent/offspring conflict in studying this behaviour (Rodríguez Gironés 1999), with the additional possibility that predators could play an important role if they are able to intercept signals used in this communication system (Thompson et al. 2013).

To conclude, our study shows that ARC behaviour not only entails effects on sibling condition and communication, as found previously (Roulin et al. 2000, 2009; Roulin 2001; Johnstone & Roulin 2003; Dreiss et al. 2010), but also plays a role in sex-specific parental investment responses.

Acknowledgements

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