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Animal behaviour

Individual benefits of nestling begging: experimental evidence for an immediate effect, but no evidence for a delayed effect

C. (Kate) M. Lessells[1,*], **Katharina Riebel**[2] **and Tudor Ion Draganoiu**[2,3]

[1]*Netherlands Institute of Ecology (NIOO-KNAW), PO Box 40, 6666 ZG Heteren, The Netherlands*
[2]*Behavioural Biology, Institute of Biology (IBL), Leiden University, PO Box 9505, 2300 RA, Leiden, The Netherlands*
[3]*Laboratoire d'Ethologie et Cognition Comparées, Université Paris Ouest Nanterre la Défense, BSL, 200 Avenue de la République, 92001 Nanterre, France*
**Author for correspondence* (*k.lessells@nioo.knaw.nl*).

The evolutionary stability of honest signalling by offspring is thought to require that begging displays be costly, so the costs and benefits of begging—and whether they are experienced individually or by the whole brood—are crucial to understanding the evolution of begging behaviour. Begging is known to have immediate individual benefits (parents distribute more food to intensely begging individuals) and delayed brood benefits (parents increase provisioning rate to the brood), but the possibility of delayed individual benefits (previous begging affects the current distribution of food) has rarely, if ever, been researched. We did this using playback of great tit *Parus major* chick begging and a control sound from either side of the nest. Male parents fed chicks close to the speaker more when great tit chick begging, but not other stimuli, was played back. In contrast, there was no effect of playback at the previous visit on the chicks that male parents fed. We have thus demonstrated an immediate individual benefit to begging, but found no evidence of a delayed individual benefit in this species.

Keywords: begging; honest signalling; costs; benefits; playback; great tits

1. INTRODUCTION

Honest signalling of offspring need to parents using begging is generally thought to require that begging be costly, with begging levels reflecting the balance between fitness costs and benefits [1]. One of the factors affecting the evolutionarily stable level of begging in broods of more than one offspring is whether these costs and benefits are paid and received by individual offspring, or by the whole brood. For example, energetic costs of begging are likely to be paid individually, whereas the costs of attracting a predator by begging may be paid by all the offspring [2].

Experimental studies in a range of species have shown that begging increases the amount of food received by offspring in two general ways: first, in broods containing more than one offspring, an individual's begging may increase the proportion of food distributed to that offspring—an individual benefit (reviewed by [2]). Second, begging may increase the rate at which the parent brings food to the brood in the future (reviewed by [3]). If that food is then distributed among offspring according to future begging, the benefit of current begging by an offspring is shared between all members of the brood. However, the benefits would be individually gained if begging at one parental feeding visit increases the probability of the individual offspring begging being fed in the future. This could be mediated by individual recognition of offspring, either through individual characteristics or by location within the brood. The existence of such a delayed individual benefit of begging has rarely, if ever, been researched.

We investigated whether delayed individual benefits of begging occur in great tits *Parus major* by playing back chick begging calls and a control sound in a random sequence from either side of the nest. In this species, the duration of begging after food has been distributed to the chicks is typically several times longer than before the food is distributed (personal observations). A delayed individual benefit would explain why the chicks invest so much in begging at a time when begging appears to have only brood benefits. Great tit chick begging calls are not known to be individually identifiable and parents make hundreds of feeding visits to the nest each day during the later part of the brood-rearing period, so that individual identification of chicks before feeding would be relatively costly in terms of time. On the other hand, although chicks do change position in the nest, this occurs over a relatively long time scale, so a parent could increase the chance of delivering food to a previously intensely begging chick by feeding to the area of the brood from which this begging came without this invoking a substantial time cost. Our experimental design allowed us to investigate whether the positions of the playback speaker used at the current and previous visit independently affected the location of the chicks fed, and hence determine whether there are immediate and delayed individual benefits of begging in this species. The possible existence of immediate and/or delayed individual benefits, and brood benefits, of begging are not mutually exclusive. Our experiment investigated whether there was evidence for immediate and delayed individual benefits of begging, but did not investigate whether there were also brood benefits.

2. MATERIAL AND METHODS

The experiment was carried out in 2004–2006 at the Buunderkamp (52°01′ N 5°46′ E), The Netherlands, on great tits *Parus major* provisioning approximately 10-day-old broods of 6–10 chicks. Parents visiting the nest with food were exposed to playback from one of two speakers situated on either side of the nest. The three playback *stimuli* were *great tit* begging calls, *zebra finch* song (as a control sound with approximately the same frequency range) and *no-playback* (see electronic supplementary material for further details). Each stimulus was played from the right or left speaker, giving six possible playback *treatments*. (*No-playback* treatments were designated as being made from the left or right for analytical purposes.) Playback was made from a computer-generated list in which each of the six treatments occurred once in each successive

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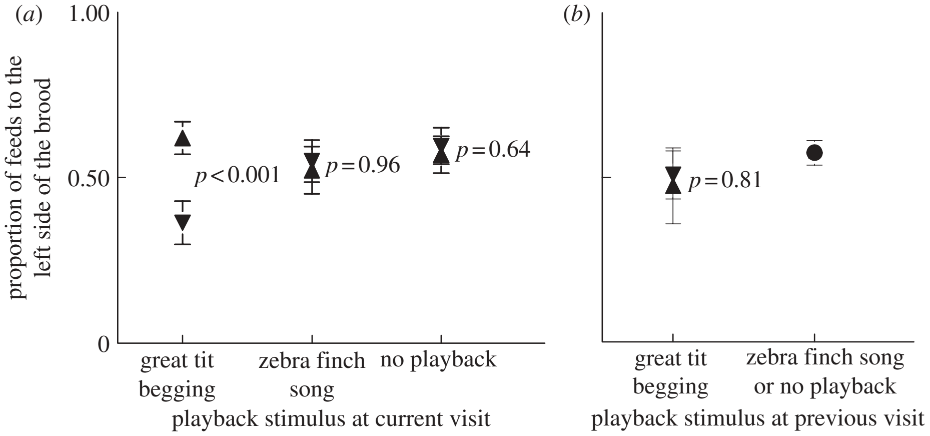

Figure 1. (*a*) Male great tits feed chicks nearer the playback speaker in response to playback of great tit chick begging calls, but not in response to zebra finch song or no playback, but (*b*) do not feed chicks nearer to a speaker broadcasting chick begging calls at their previous nest visit. Points are means + s.e.'s of the proportions for males at different nests ($n = 13$) (i.e. are from the original data, not model estimates). *p*-Values are from generalized linear mixed models with binomial errors for the difference between the proportion of feeds to the left when playback is from the left or right (see text; triangles, playback from left; inverted triangles, playback from right; circles, playback from either).

group of six treatments, in a newly randomized sequence. Each time a parent entered the nest, 15 s of the relevant playback treatment was made. During the experiments, equal numbers of randomly chosen chicks were placed to the right or left of a vertical barrier in the nest cup, dividing the brood into left and right halves. The response to the playback was quantified as the side of the brood which the parent fed. This information, plus the time to the nearest second when the parent entered the nest-box, the sex of the parent and the number of individual chicks begging on either side of the barrier during the visit were obtained by video-recording inside the nest-box during the experiment. Analysis was restricted to the male parents at 13 nests, because females made fewer than anticipated feeding visits (see electronic supplementary material).

We tested whether playback at the current or previous visit affected the side of the brood the males fed using generalized linear mixed models (GLMMs) with the side of the brood fed (left = 1, right = 0) as a binomial response variable, and nest identity as a repeated-measures subject. We tested whether the males' responses to playback could have been indirectly mediated by the chicks' begging behaviour in response to playback using GLMMs with the proportion of chicks begging in each half of the brood during each parental visit as a binomial response variable, the individual visit as a repeated-measures subject, and nest identity fitted as a fixed factor (p always < 0.0001) to control for differences in the amount of begging between nests. We analysed chick begging at visits by either sex of parent. GLMMs were carried out using Proc Genmod of SAS v. 9.1 using type III tests of χ^2 values. These values are given for the tested term entered into the final model (i.e. the model containing only significant terms and terms that are part of significant interactions). All *p*-values are two-tailed.

3. RESULTS

We used data from 566 visits by males at 13 nests to investigate whether playback at the current visit affected which half of the brood was fed (figure 1*a*). Playback stimulus *per se* did not affect the side fed (playback stimulus: $\chi^2 = 6.18$, 3 d.f., $p = 0.10$), but did so in combination with the playback side (playback stimulus × playback side: $\chi^2 = 7.34$, 3 d.f., $p = 0.06$; excluding *zebra finch* stimulus: $n = 388$, $\chi^2 = 7.37$, 2 d.f., $p = 0.02$; interaction illustrated in figure 1*a*, where the vertical separation between points varies with the playback stimulus): when the playback stimulus was *great tit*, the male was significantly more likely to feed to the left side when playback was from the left (model estimate for *great tit* playback to *left* versus *right*: 0.909 ± 0.227, $z = 4.00$, $p < 0.0001$; this estimate is for the vertical separation between the two points for *great tit* playback in figure 1*a*, expressed in units of log-odds), but there was no effect of playback side when the playback stimulus was *zebra finch* (-0.016 ± 0.304, $z = -0.05$, $p = 0.96$) or *no-playback* (-0.138 ± 0.297, $z = -0.47$, $p = 0.64$; figure 1*a*).

We used visits where the previous visit by the male was less than 2 min earlier to investigate the effect of playback at the previous visit. As there was no difference in response to the four *zebra finch* or *no-playback* treatments, we combined them, resulting in three playback *categories* (*great tit left*, *great tit right*, *other*). We carried out analysis on two different subsets of the data: first, we examined the simultaneous effect of treatment category at the current and previous visit ($n = 296$ visits). As before, playback at the current visit affected the side fed (current treatment category: $\chi^2 = 8.48$, 2 d.f., $p = 0.04$), but playback at the previous visit did not do so (figure 1*b*; previous treatment category: $\chi^2 = 0.61$, 2 d.f., $p = 0.74$) and the difference between the two *great tit* categories at the previous visit was small and non-significant (model estimate for *great tit left* versus *great tit right* at previous visit: 0.107 ± 0.449, $z = 0.24$, $p = 0.81$). Second, we examined the effect of treatment category at the previous visit when no playback was made at the current visit (i.e. both experimental *no-playback* and visits missed by the experimenter; $n = 150$ visits). For these visits without playback, previous playback category also had no effect on the side fed (previous playback category: $\chi^2 = 0.26$, 2 d.f., $p = 0.88$) and the difference between the two *great tit* categories at the previous visit was negative and non-significant (model estimate for *great tit left* versus *great tit right* at previous visit: -0.164 ± 0.585, $z = -0.28$, $p = 0.78$).

We used visits by either the male or female ($n = 706$) to investigate whether playback affected chick begging. The playback stimulus affected the proportion of chicks begging (playback stimulus: $\chi^2 = 32.45$, 2 d.f., $p < 0.0001$), with more chicks begging when the playback stimulus was *zebra finch* (model estimate for *zebra finch* versus *no-playback*: 0.413 ± 0.078 (s.e.), $z = 5.30$, $p < 0.0001$), but not *great tit* (*great tit* versus *no-playback*: 0.062 ± 0.079, $z = 0.79$, $p = 0.43$). None of the playback stimuli caused a difference in begging on the sides nearer and further from the speaker (playback stimulus × *nearer* versus *further*: $\chi^2 = 2.69$, 1 d.f., $p = 0.44$; model estimates for the three playback stimuli, difference *nearer* versus *further*: $z < |1.24|$, $p \geq 0.22$). Parental sex also had no effect on begging (parental sex: $\chi^2 = 0.07$, 1 d.f., $p = 0.78$).

Neither playback, nor the side fed at the previous visit by either parent, had an effect on begging at the current visit (see electronic supplementary material).

4. DISCUSSION

Male great tit parents fed chicks nearer to a speaker broadcasting great tit begging calls, demonstrating that there is an immediate individual benefit to begging. This parental response is based on specific characteristics of the begging calls because males did not feed chicks nearer to a control sound (zebra finch song). Moreover, the parental response is a direct response to the playback sound, rather than being mediated by the chicks' response to playback: although playback did affect chicks' begging (a higher proportion of chicks begged when zebra finch song was played back), none of the playback stimuli caused a difference in the proportion of chicks begging in the sides of the brood nearer and further from the playback speaker.

In contrast, we could not find any evidence for a delayed individual benefit to begging: the location of chicks fed by the male was not related to the side of playback of begging calls at the previous visit by the male, whether we analysed which chicks were fed at all visits at which an experimental playback treatment was applied, or only those where no great tit or zebra finch playback was made. There are two reasons why we might not have found delayed individual benefits to begging. First, it is possible that such benefits occur, but are based on individual characteristics rather than the area of the brood from which the most intense begging emanates. This seems unlikely, because suitable individual characteristics that would allow rapid individual identification are unknown for great tit chicks of this age, and the response to playback at the current visit shows that males do respond to begging coming from a general area within the nest rather than from a specific chick. Second, it is possible that a delayed response to begging by parents (in addition to an immediate response) has not evolved because the fitness benefits are not sufficient: one potential benefit of a delayed response is that it favours chicks that beg consistently over successive feeding visits by the parents and discriminates against chicks that attempt to 'cheat' by occasional intense begging. However, this benefit will be reduced or nullified if chicks are usually consistent in their begging in successive visits, if the specific chick fed within an area of the brood chosen on the basis of begging intensity depends on scramble competition between the chicks (e.g. the chick that reaches highest), or if a possible increase in information about a chick's hunger state through its previous begging is counteracted by an increased probability of that hunger state having been changed by the chick having been fed at the previous visit or by the other parent.

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