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THE EVOLUTION OF COMPLEX BEGGING DISPLAYS

Rebecca M. Kilner

*Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, U.K.
(rmk1002@zoo.cam.ac.uk)*

ABSTRACT

Passerine nestlings solicit food by performing a vigorous postural display, while revealing a brightly coloured gape and calling repetitively. In this chapter, I suggest that the individual elements of the begging display may collectively function in the resolution of parent-offspring conflict. A general conclusion from two experimental studies is that the multiple elements increase the information content of the display, thereby preventing exploitation of parents by potentially manipulative offspring. I also review experimental evidence that provisioning males and females respond differently to the various elements of the begging display, and suggest four hypotheses to explain this curious observation.

INTRODUCTION

The arrival of an adult with food at the passerine nest typically provokes a frenzy of nestling begging activity. Nestlings reveal brightly coloured gapes (Pycraft 1907), and assume a range of begging postures (e.g. Redondo & Castro 1992). They also call loudly (e.g. Haskell 1999) and jostle for position in the nest (e.g. McRae et al. 1993).

The evolution of such bizarrely excessive nestling begging displays has been attributed to conflicts of interest at the nest over the allocation of investment among dependent offspring (Trivers 1974; Parker & Macnair 1979; Godfray 1995a; Mock & Parker 1997). Such conflicts can arise because selection yields different optimal patterns of investment for

parents and young (Hamilton 1964; Trivers 1974; Mock & Parker 1997). Within each brood, parents and young may be in conflict over the division of investment among offspring, with individual offspring seeking greater levels of investment than parents should be selected to provide (intra-brood conflict: Macnair & Parker 1979). Between broods there can be additional conflict, with offspring effectively demanding resources which parents would do best by allocating to future young (inter-brood conflict: Trivers 1974; Parker & Macnair 1979; Lessells & Parker 1999). Extravagant begging may have evolved originally either to facilitate offspring attempts to extort additional resources from resistant parents (Trivers 1974) or through sibling competition for limited parental resources (Rodríguez-Gironés et al. 1996). Begging is thought to persist today because it plays a key role in resolving parent-offspring conflict (Godfray 1995a), both within and between broods.

The specific function of begging in the resolution of parent-offspring conflict varies between models. In those concerned with food allocation during each nest visit, begging might be a means of scramble competition for food (Parker & Macnair 1979) or it might be a signal, honestly advertising need (Godfray 1995b). Similarly, begging may influence nest visit rate either by signalling offspring condition (Godfray 1991) or by blackmailing parents into providing food, thereby preventing further wasteful solicitation (Zahavi 1977; Parker & Macnair 1979; Eshel & Feldman 1991; Johnstone 1996a). Despite the range of possible functions, individual models typically treat begging intensity as a univariate parameter with a single function. However, even a brief glimpse at a nest crowded with nestlings gaping, posturing and calling indicates that this is likely to be an oversimplification.

This chapter suggests ways in which the complexity of nestling begging displays, namely their multiple components with various functions, could generally serve to resolve parent-offspring conflict. I begin with an overview of the functions of the individual elements that make up the begging display before discussing more recent experiments looking at the collective function of the multiple elements. The chapter concludes by discussing why mothers and fathers react differently to complex begging displays. Aside from their role in resolving family conflicts, the individual elements of the begging display may collectively enhance the efficacy and efficiency of communication at the nest (see A.G. Horn & M.L. Leonard this volume), but this possibility will not be discussed further here.

WHY DO NESTLINGS HAVE COMPLEX BEGGING DISPLAYS?

Each Element Has a Discrete Function

An intuitively appealing idea is that multicomponent begging displays have evolved because each element is discretely involved in a different aspect of nestling solicitation behaviour. For example, nestling mouth colour might function to enhance nestling detectability (Pycraft 1907; Swynnerton 1916; Ingram 1920), while posturing may settle scramble competition for food at each nest visit and calling could determine nest visit rate (see Kacelnik et al. 1995). The conceptualisation of the begging display in this way by empiricists has probably been reinforced by theoreticians using separate models for dealing with detectability (Johnstone 1998), intrabrood conflict (e.g. Parker & Macnair 1979; Godfray 1995b) and interbrood conflict (e.g. Parker & Macnair 1979; Godfray 1991, but see Rodríguez-Gironês et al. 2001). Given its roots in empirical observation, it is not hard to find work which supports this idea.

Nestling Mouths and Detectability

Evidence that gapes function to enhance nestling detectability dates as far back as 1920 when Ingram first pointed out that the gapes of hole nesting corvids are commonly adorned with broad white fleshy borders which are usually absent from open nesting corvids. A much later study formalised this comparison with a wider range of species, finding a continuous relationship between nest light availability and relative border width (Kilner & Davies 1998). The same study also showed that the brightness contrast between the gape and its surrounding border was at its greatest in dark nests, again presumably to enhance conspicuousness (Kilner & Davies 1998).

When it comes to the colour of the gape itself, however, there is mixed evidence that it functions to enhance nestling detectability. In general, the cruder the measurement of colour and nest light availability, the clearer the patterns that emerge, an observation which may be biologically meaningful given the potential variation in nest lighting conditions within cup-nesting species (Kilner 1999). Classifying species as either yellow or red, Ficken (1965) found that hole-nesting species were more likely to display yellow mouths. The result was replicated in a study using a colour ranking scheme to convert literature descriptions of mouth colour into numbers (Kilner 1999). However, measuring mouth colours directly, using hue, saturation and brightness scores of video

images, no relationship was found between photographic light meter scores of nest light availability and mouth colour (Kilner & Davies 1998). Whether or not nestling mouth colour functions to enhance detectability seems unlikely to be resolved without measuring the reflectance spectra of nestling mouths in conjunction with ambient nest light colour.

Nestling Posture and Food Distribution

Turning to the function of nestling begging posture, virtually every study that has looked for a positive relationship between postural intensity and food allocation has found one (e.g. Redondo & Castro 1992; Kilner 1995; Kacelnik et al. 1995; Leonard & Horn 1998). These results are, of course, simply correlational. It is not clear whether parents are responding to posture *per se*, or some close correlate like nestling height. Observations of sexually dimorphic species like red-winged blackbirds (*Agelaius phoeniceus*, Teather 1992) suggest the latter is more likely, as do studies of brood parasites reared alongside host young (Lichtenstein & Sealy 1998).

It is also unclear in many studies whether posture functions to advertise offspring condition, or to enhance competitive ability or both. Work on Arabian babblers (*Turdoides squamiceps*) suggests it plays an important role in scramble competition (Ostreiher 1997), while in captive canaries (*Serinus canaria*) posture can be a signal (Kilner 1995). In great tits (*Parus major*), parental response to posture may additionally be influenced by nestling position in the nest (Kölliker et al. 1998). Variation in nestling size appears further to complicate the relationship between postural begging intensity, nestling position and the likelihood of being fed in starlings (*Sturnus vulgaris*, Cotton et al. 1999). Postural begging could therefore be just one facet of nestling competitive ability, or it could be a signal which is amplified by a suite of nonsignalling nestling attributes (Lotem et al. 1999), or it could be a combination of the two.

Begging Calls and Provisioning Rate

Experiments in which the calls produced by a brood are artificially supplemented have shown that nestling calling influences nest visit rate (e.g. von Haartman 1953; Muller & Smith 1978; Bengtsson & Ryden 1981; Ottoson et al. 1997). One criticism of this technique is that it is not always clear whether parents are responding to the experimental manipulation alone or the effect it has on the begging of their brood (Muller & Smith 1978; but see Kilner et al. 1999). Although the majority

of experiments augmented brood vocalisations during nest visits alone, provisioning levels could also be elevated when calls were broadcast at other times (Burford et al. 1998; Price 1998; but see Clark & Lee 1998).

Multiple Elements and Multiple Functions

Drawing the evidence together, the empirical work appears at first sight to be overwhelmingly consistent with the hypothesis that each component of the display has a discrete function. A danger, though, is that such a conclusion could be merely an artefact of the simplest experimental and theoretical techniques for understanding begging. More recent experimental data suggest that in reality complex begging displays are likely to have complex functions. The discrete elements of begging displays could have multiple functions. For example, mouth colour may function to enhance detectability, but it can also signal hunger in some finch species (Kilner 1997; Kilner & Davies 1998), and perhaps health in barn swallows (*Hirundo rustica*, Saino et al. 2000). Similarly, the calling of yellow-headed blackbird (*Xanthocephalus xanthocephalus*) young is correlated with both food allocation (Price 1996) and the rate at which parents visit the nest with food (Price 1998). Alternatively, multiple display elements could have the same discrete function. In canaries, food allocation patterns within broods are correlated with postural intensity, but can be altered by broadcasting calls from speakers placed near individual offspring (Kilner 1996).

In summary, the hypothesis that each element has a discrete function is intuitively attractive, but probably simplistic. To understand the evolution of multicomponent begging displays, and their possible role in resolving parent-offspring conflict, we should instead consider how the different elements function together.

Multiple Elements Provide More Information

General theoretical analyses provide several alternative explanations for why multicomponent displays may have evolved. One possibility is that the separate elements of the display may interact to enhance parental response to the display. Experimental psychologists have shown with a variety of species that the magnitude of response to multicomponent displays often exceeds the summed response to the individual components alone (reviewed by Rowe 1999). Here, an accessory noninformative display might increase the response to a focal display (Rowe 1999). For example, in the case of complex begging, visual cues might enhance parental responsiveness to vocal cues, providing a

powerful psychological tool for nestlings attempting to extort additional investment from resistant parents. It is possible that the white papillae which adorn the mouths of great-spotted cuckoo (*Clamator glandarius*) nestlings improve their chance of being fed by functioning in this manner (Soler et al. 1995).

Three further hypotheses explain how multicomponent displays could improve parental resistance to potential offspring manipulation by providing more information about nestling condition. For instance, the multiple elements may carry ‘multiple messages’ about nestling quality (Johnstone 1995; Johnstone 1996b). Different parts of the display might be correlated with a different aspect of nestling condition. This hypothesis differs from the idea that each element has a discrete function because there need be no one-to-one relationship between the signal and nestling quality. The individual elements of the begging display could instead be correlated with multiple aspects of nestling quality.

Alternatively, it may be that the multiple elements advertise the same aspect of nestling condition, but are differently correlated with it. Here, multicomponent displays could function to provide more accurate information about nestling quality than individual components can alone. In other words, the separate elements of the display might function as ‘back-up signals’ (Johnstone 1996b).

Finally, it may be that there is redundancy in the display (Partan & Marler 1999). The separate elements might identically advertise the same aspect of nestling quality, so that collectively they provide no more information than each does alone. Redundancy could persist because of perceptual errors by parents, unable to make full use of information advertised in the discrete elements of the display.

Do Individual Begging Elements Interact to Increase Provisioning Rates?

Field experiments on reed warblers (*Acrocephalus scirpaceus*) tested the merit of these various hypotheses. Reed warblers typically rear four young in a cup nest slung between the stems of reeds growing in shallow water. Both parents provide care by brooding and feeding young, and the sexes are monomorphic. From two days after hatching, nestling reed warblers solicit food by displaying bright yellow gapes and calling repetitively. To test whether each element of the display could influence provisioning rate by parents, Kilner et al. (1999) carried out two types of experimental manipulation, using unmarked birds. The first involved changing the brood size, so that broods contained from one to eight nestlings, and hence manipulated both the visual and vocal elements of the display. The second manipulation altered the vocal display alone by broadcasting the calls of different numbers of nestlings at different brood

sizes through a small speaker fixed on the rim of the nest. Combining the two manipulations relaxed the usual tight correlation between the visual and vocal displays, so that variance in provisioning rate could be partitioned to either element.

The experiments revealed that parents responded to both aspects of the display when feeding young at the nest; together visual and vocal begging displays explained more variance in provisioning rate than either could alone. Surprisingly, however, the two elements of the begging display did not interact to influence provisioning rate, as might be expected from the psychological literature (Rowe 1999). The exact reason for this result is unclear at present. One difficulty with interpreting the data is that the parental response to begging measured in the experiments combined the behaviour of both parents. It may be that large scale differences between mothers and fathers in their response to the begging display masked more subtle interactions between the elements on their separate provisioning behaviours.

Do Complex Displays Contain 'Back-Up Signals' or Carry 'Multiple Messages'?

Subsequent laboratory experiments examined the information content of the display. Broods of four nestlings were temporarily borrowed from their natural nest and taken to the laboratory, either three to four days after hatching or six to seven days after hatching. There they were fed until they stopped begging and placed in a heated artificial nest. After ten minutes, and every ten minutes for the next 110 minutes, the brood was induced to beg and the visual and vocal displays were measured. At the end of the experiment, nestlings were fed and returned to their natural nests. Analysis of the experimental begging data supported the suggestion that multicomponent displays carry multiple messages. As anticipated by theory, the visual and vocal elements of the begging display did not broadcast separate information about nestling condition, but were individually correlated both with the extent of food deprivation and the age of the nestlings (Kilner et al. 1999).

The experiments also indicated that the different elements of the display could function as back-up signals. Visual and vocal displays were differently related to nestling age and food deprivation, and together they explained more variance in nestling hunger than either could alone (Kilner et al. 1999). By responding to two signals rather than one, reed warbler parents might therefore gain more accurate information about their young, as well as information about the short and long term needs of their brood. In terms of interbrood conflict, perhaps parents have selected complex displays, so that they can adjust their investment

precisely to the needs of their brood and hence avoid being manipulated by selfish offspring.

Theoretically, two alternative mechanisms explain how multiple signalling equilibria can persist. One requires that the costs of the individual elements of the display be strongly accelerating (Johnstone 1996b), while the alternative view is that one or more of the signalling elements could be cost-free (Bergstrom & Lachmann 1998). A defining characteristic of cost-free signals is that they form pooling equilibria: the signal appears to be a step function of nestling condition. The signals might be cheap, but they send less information (but see Johnstone 1999; Rodríguez-Gironés 1999). In contrast, costly displays yield separating equilibria with signals changing continuously with respect to nestling quality (Bergstrom & Lachmann 1998).

Close inspection of the begging display performed by individual reed warbler broods suggests that the latter mechanism may be the more plausible for explaining how complex begging displays persist (Figure 1). Figure 1a shows the change in the number of gapes displayed by a single brood with respect to increasing food deprivation, a plot which clearly resembles a step function. Although reed warbler parents respond to continuous increases in gape area (Kilner et al. 1999), and gape area is continuously correlated with nestling hunger (Kilner et al. 1999; Kilner & Davies 1999), at each nest visit this signal can only be a step function of brood condition.

Figure 1b shows the equivalent change in call rate which, by contrast, appears to change more continuously. Thus, call rate has the characteristics of a costly signal while gaping bears the hallmark of a cost-free display. Experimental evidence from other species supports the suggestion that call rate is costly. When western bluebird (*Sialia mexicanus*) begging calls were broadcast at a fast rate from fake nests placed on the ground and baited with eggs, more eggs were taken than when calls were broadcast at a slower rate (Haskell 1994). Perhaps, generally, begging calls were selected by parents to supplement the information provided by the cost-free, yet relatively uninformative, gaping display.

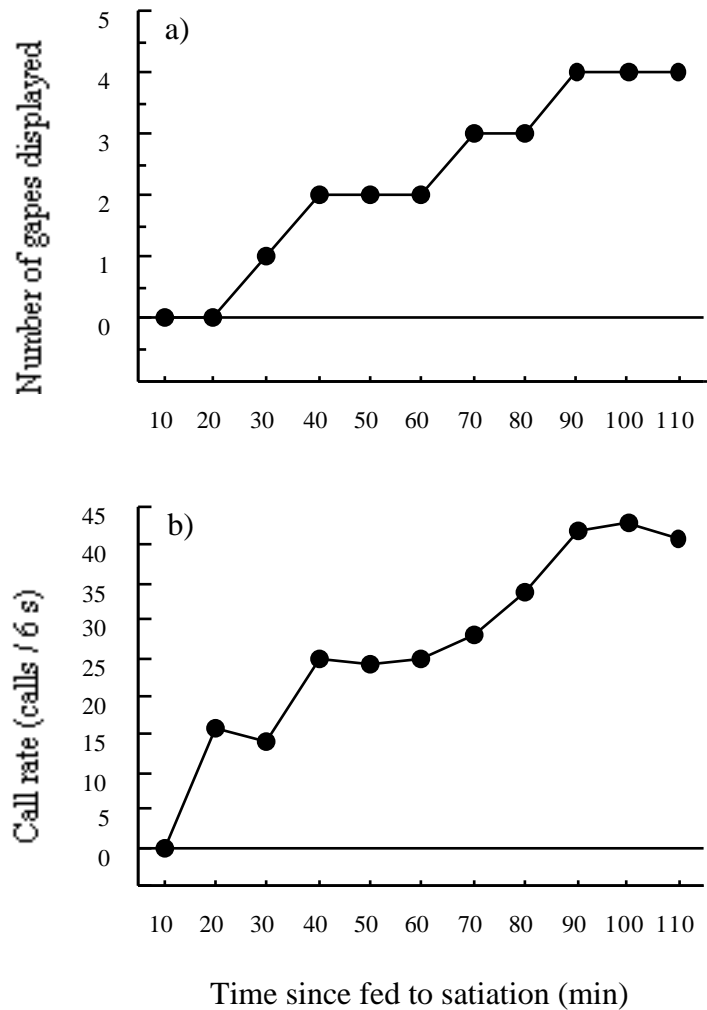


Figure 1. The effect of food deprivation on a) the visual and b) vocal begging displays of a single brood of four reed warblers, six to seven days after hatching.

Parasitism by Cuckoos – A Special Case of Redundancy in Complex Displays?

The reed warblers tested in these experiments occasionally succumbed to brood parasitism by the common cuckoo (*Cuculus canorus*, see Brooke et al. 1998 for parasitism rates at the study site during the last 10 years). The cuckoo egg requires less incubation than the reed warbler's own eggs, so often hatches in advance of the host brood. Within a few hours of

hatching, while still tiny, naked and blind, the cuckoo nestling sets about destroying the reed warbler's unhatched eggs and newly hatched young. It manoeuvres them into the small of its back and then climbs backwards up the side of the nest to tip them over the rim. The cuckoo thus dispenses with sibling competition and, reared alone in the nest, becomes the sole beneficiary of parental care. Kilner et al.'s (1999) work, however, suggests such nestling evicting behaviour could also incur a cost. Alone in the nest, the cuckoo presents a deficient visual stimulus of a single gape. To elicit adequate care from its reed warbler hosts, the cuckoo must compensate for this visual discrepancy by calling excessively (Kilner et al. 1999). Nevertheless, despite calling at up to twice the rate of an average host brood, and even though its selfishness is unconstrained by kinship, the cuckoo extracts roughly the same level of care as a brood of host young, for the same level of need (Kilner & Davies 1999). By chance, the complex begging displays of hosts could therefore also function to limit the selfishness of evicting brood parasites and, in some circumstances, might even prevent successful parasitism.

The begging display of common cuckoo nestlings incorporates the display of a vivid orange red gape and production of a highly repetitive begging call. Comparative analyses indicate that other cuckoo species also have redder mouths than their hosts (Kilner 1999). What, then, is the function of such a red gape? Kilner et al.'s (1999) work showed precisely how the gape area displayed and the rate of call production together could account for much of the variance in cuckoo nestling provisioning rate. However, further experiments (Noble et al. 1999) suggest that the colour of the cuckoo's gape is functionally redundant in soliciting care from reed warbler hosts. When the yellow gapes of reed warbler young were painted with orange-red food colouring, there was no change in the rate at which adults provisioned the brood. Since three species of non-brood parasitic cuckoos also display red gapes, one parsimonious interpretation of this experimental data is that cuckoo mouth colour confers no adaptive advantage to brood parasites and their redder gapes are simply the by-product of phylogeny (Kilner 1999).

A more intriguing possibility is that a red mouth may be part of the trickery used by brood parasites to dupe some, but not all, of their hosts. The common cuckoo, for example, parasitises two other hosts in Britain: the dunnock (*Prunella modularis*) which has orange-mouthed nestlings and the meadow pipit (*Anthus pratensis*) whose nestlings display flesh-red mouths (Kilner & Davies 1998). Adult females faithfully parasitise one host species and form distinct 'races' or gens, each recognisable by the egg patterning that usually mimics the eggs of the particular host (Brooke & Davies 1988). In contrast, adult males mate promiscuously across the different female races (Marchetti et al. 1998). Egg mimicry persists, nonetheless, presumably because it is inherited maternally and expressed

only by females. Mimicry of host nestling appearance or behaviour, however, is impossible (Marchetti et al. 1998).

In reed warbler nests, the cuckoo nestling elicits sufficient care from its hosts by exploiting the usual communication system between host young and adults, relying on an exaggerated call to compensate for a deficient visual stimulus of a single gape (Davies et al. 1998; Kilner et al. 1999). Different host species, however, vary in the details of their begging display (Kilner & Davies 1999). To elicit care successfully from its various hosts, perhaps the cuckoo nestling has to perform a variety of begging tricks, some of which may be essential in one host, but quite useless in others. The different provisioning rules of the cuckoo's various hosts may mean that the cuckoo nestling has to resort to vocal trickery with some, but visual trickery with others. A red mouth may be vital for duping meadow pipit hosts, for example, but irrelevant for fooling reed warbler hosts.

Whatever the species of brood parasite, provided that male and female cuckoos are reared by different hosts, there can never be perfect mimicry of host begging displays (Davies 2000) and selection for redundancy in parasitic nestling begging displays may result. It is this possibility of redundancy which might explain generally why red cuckoo nestling mouths persist even though they appear functionally useless for extracting care from some hosts (Kilner 1999).

Multiple Elements are Required to Maintain Reliable Signalling Throughout the Nestling Period

Experiments with captive canaries provide a different explanation for the evolution of multicomponent begging displays. In this species, two signals that play a key role in influencing food allocation among the brood are begging postures and begging calls. Experiments have shown that both elements indicate nestling hunger (Kilner 1995, 1996). Parents actively select nestlings to provision and the amount of food transferred is correlated with the intensity of the nestling's postural display (Kilner 1995). Playback manipulations have further shown that food allocation is influenced by begging calls (Kilner 1996).

A Marginal Growth Cost of Postural Begging

Recent work on canaries has found that postural begging incurs a marginal growth cost (Kilner in press). The marginal cost of begging was measured experimentally at three different stages during the nestling period. Pairs of siblings were removed from the nest, weighed and kept in an incubator.

During the next six hours, nestlings were fed every 20 minutes with the same amount of food, but had to beg for markedly different amounts of time before they were rewarded, which were nevertheless within the range typically observed at the nest. (Nestlings in the low begging treatment solicited for 10 seconds while their siblings in the high begging treatment had to beg for 60 seconds.) After six hours of being fed on one of these regimes, nestlings were weighed and returned to their nest. All the food given to nestlings during the experiments was weighed, as were the faecal sacs produced during the experiment. The net difference in weight between nestlings at the start and end of the test could therefore be attributed only to mass lost through energetic expenditure. In addition, nestlings were filmed to quantify the difference in postural begging intensity experienced by siblings during the experimental manipulation. The marginal cost of begging was measured by comparing the effect of the treatments on siblings.

Three separate lines of evidence revealed a trade-off between energy devoted to growth and energy spent on postural begging. First, excessive begging slowed growth, both during the experiment and in the subsequent 24 hours, and the impact of the manipulation was greatest in nestlings with the highest potential rate of daily mass gain. Second, the greater the difference in postural begging intensity between siblings during the experiment, the greater the difference between them in the mass lost as a result of metabolic expenditure. Third, the treatment had least effect on mass gain, during the subsequent 24 hours, in older nestlings that had completed most growth (Kilner in press).

At first sight, this result appears to stand at odds with the metabolic evidence that the energetic cost of begging is relatively small (M.A. Chappell & G.C. Bachman this volume). However, canary begging displays are typically two or three times longer than those of tree swallows (*Tachycineta bicolor*) or house wrens (*Troglodytes aedon*) and can continue for over 60 seconds. Protracted displays may additionally incur anaerobic costs as a result of sustained muscle contraction. Even so, despite their briefer displays, the energy devoted to house wren begging may still be traded-off against energy for growth. Recalculating data presented in Bachmann & Chappell (1998), the greater the proportion of the daily energy budget that is devoted to growth, the less that is spent on begging (Kilner in press).

The Cost of Postural Begging Declines With Nestling Age

The growth rate of canary nestlings is correlated with a measure of fitness, namely the likelihood of survival to independence. Logistic regression analyses of the growth rates, and subsequent fates, of over 300 nestlings yielded equations relating mass and mass gain at different ages to

the probability of survival to independence. By substituting the experimental data into these logistic regression equations, the decrease in the probability of survival imposed by the high begging treatment can be estimated. Translated into estimates of fitness, the excessive begging treatment proved most costly for younger nestlings, reducing the chance of survival to independence by roughly 5%. For older nestlings, prolonged begging carried virtually no equivalent cost.

The Reliability of Posturing Declines With Nestling Age

The change in the marginal fitness cost of begging with age fortuitously provided the chance to test the theoretical idea that the reliability of nestling begging should be maintained by the cost of the display (Godfray 1991, 1995b). According to this view, a decrease in the cost of signalling should precipitate a decrease in the reliability of signalling. As nestlings get older, theory predicts that their postural displays should become more and more unreliable.

The reliability of begging was measured by regressing nestling hunger on postural intensity to calculate the standardized regression coefficient R . This statistic quantifies the strength of the relationship between hunger and begging: the weaker the relationship, the less reliable the information that begging conveys about nestling hunger. By measuring R at five different stages of the nestling period Kilner (unpublished data) found that the reliability of the postural display declined with increasing nestling age. Just as predicted by theory, the decline in the cost of posturing was linked with a decline in the reliability of posturing.

If the postural display becomes increasingly unreliable as nestlings get older, parents would benefit by ignoring it in favour of a more informative signal. Detailed observations revealed that the influence of posturing on food allocation by mothers changed during the course of the nestling period. Maternal attentiveness to postural begging was measured by regressing the number of feeds transferred to nestlings on the strength of their display to calculate R : the less attentive mothers were to the display, the lower the measure of R . These analyses revealed that as nestlings grew older, mothers became less and less responsive to the postural display (R. M. Kilner unpublished data).

Begging Calls Provide an Alternative Source of Reliable Information?

Although the postural display became less reliable as nestlings grew older, mothers were not fooled by their increasingly deceptive offspring. One possibility is that they turned to a different element of the display for

reliable information about the condition of their young. A likely candidate is the vocal display. As begging posture decreased in reliability with nestling age, begging calls became increasingly reliable (R.M. Kilner unpublished data).

Exactly why calling should become more reliable with nestling age remains unclear at this point. One possibility is that young nestlings are physically constrained in their ability to call loudly or rapidly, much as the frequency of toad (*Bufo bufo*) croaking is constrained by body size (Davies & Halliday 1978). Perhaps the nature of these physical constraints changes as nestlings get older. Alternatively, it may be that the cost of calling increases with age. Playback experiments using western bluebird calls have demonstrated a marginal predation cost of call rate (see above; Haskell 1994), and the more rapid calling rate of older canary nestlings (R.M. Kilner unpublished data) may therefore incur a greater risk of predation. Perhaps, then, the array of signals acquired during the nestling period successively imposes sufficient costs to maintain reliable signalling throughout this time. Whatever the mechanism enforcing reliability in begging calls, perhaps mothers have selected vocal begging to reduce their vulnerability to exploitation through visual begging by increasingly deceptive young.

WHY DO ADULT MALES AND FEMALES REACT DIFFERENTLY TO COMPLEX BEGGING DISPLAYS?

A curious feature of the canary work described above is that the paternal response to begging was quite different from that displayed by mothers (R.M. Kilner unpublished data; see also Lessells 2001). Detailed work on two other species has also revealed sex differences in the response to individual elements of the begging display.

Using brood size manipulations combined with playback of different numbers of nestlings calling, Hinde (unpublished data) experimentally manipulated the visual and vocal displays produced by broods of great tits and measured the response of both parents. She found that females integrated both elements of the display to determine their brood provisioning rates. In contrast, males responded only to the visual display in terms of the number of gapes displayed. These results replicate Kölliker et al.'s (2000) findings that, whereas female great tits elevate their feeding rates in response to begging calls broadcast at the nest, males do not.

Experiments with the co-operatively breeding superb fairy wren (*Malurus cyaneus*) have found the opposite result. In this species, single females can be assisted in nestling provisioning by one to four males. Observations show that females increase their provisioning rate in

relation to brood age, while males provision at a constant rate throughout the nestling period (Dunn & Cockburn 1996). The vocal display of the brood increases in intensity as nestlings grow. Macgregor (2000) broadcast the calls of older wren broods while males or females fed nestlings in the nest, thus more than doubling the vocal display of the brood. Males responded by increasing their rate of provisioning. Females, however, showed no change at all in the rate at which they delivered food to their young, either when playback was directed exclusively at them, or when all provisioning adults were exposed to additional calls. The results of the playback experiment at first appear to conflict with the observational data. Macgregor, however, suggests that females were simply not fooled by the noisy broods created in the playback treatment. Males, by contrast, alarmed at the female's neglect of the apparently starving brood, boosted their provisioning rate. Perhaps in this species there is a strong interaction between the visual and vocal begging displays on female provisioning rate, so that females cannot be made to work harder by manipulating the begging calls alone. If males respond to vocal begging alone, they would be more easily fooled by the playback experiment.

Exactly why males and females should respond differently to complex begging displays is not easily explained by current theory. I conclude by suggesting four tentative hypotheses, which are not mutually exclusive.

Maternal Investment is More Costly

One possibility is that the sex differences stem from differences in male and female life history strategies. Some evidence suggests that the costs of care may be greater for females than for males (e.g. Nur 1988) which may select for greater precision in the way that females allocate care between broods. Under selection to allocate investment precisely females may, in turn, utilise complex begging displays as a means of deriving more accurate information about the state of their brood. By contrast, rather than trading off current and future reproductive success, males may be selected to balance rearing young with the opportunity for mating (e.g. Magrath & Elgar 1997). Or they may adjust their level of care to minimise the penalties of investment for females, thereby retaining a fecund mate for future reproduction (Lessells & Parker 1999). Either way, males need only respond to relatively crude indicators of offspring quality, such as gaping.

A Co-operation Rule to Prevent Exploitation by Offspring

Experiments with house sparrows (*Passer domesticus*) show that nestlings can adjust their postural begging intensity in relation to their previous success at obtaining food. In hand-rearing trials, nestlings that were previously trained on a regime of begging weakly for food, showed low levels of begging when tested under standardized conditions of hunger. In contrast, nestlings that had previously been trained to beg more intensely performed stronger begging during testing (Kedar et al. 2000). As Kedar et al. (2000) point out, the possibility of nestlings learning appropriate begging intensities substantially reduces the value of begging as a signal. However, whether nestlings can make equivalent adjustments to their postural begging display in the nest, in response to parental training, is unclear at this stage.

Cross-fostering experiments with great tit nestlings showed no effect of rearing environment on vocal begging intensity, suggesting that calling behaviour is unlikely to be learnt in the nest (Kölliker et al. 2000). Recall that in this species, mothers are responsive to begging calls, whereas fathers largely ignore them (Kölliker et al. 2000). It may be that mothers and fathers use different provisioning rules as a co-operative strategy to prevent nestlings from 'learning' how to beg. If parents respond differently to begging, and cannot be recognised by nestlings, then a given begging intensity will have an unpredictable reward schedule. The provisioning rule used by each sex may have no independent function, but together the different rules may foil nestling attempts at 'learning' how to beg, thus maintaining the information content of the display.

Cryptic Sexual Conflict

Alternatively, it is possible that a cryptic form of sexual conflict underlies the differences in provisioning rules exhibited by the sexes. When females engage in extra-pair copulations, different paternal genomes end up competing for maternal care within each brood. Just as male mice (*Mus musculus*) attempt to manipulate females *via* the hormonal secretions of their unborn offspring (Haig & Graham 1991), so male birds might manipulate their partners *via* the signalling of their nestlings.

Superb fairy wrens exhibit the highest known rates of extra-group paternity, with around half of broods fathered entirely by extra group males, and the remaining broods showing mixed paternity (Mulder et al. 1994). Within each brood, therefore, multiple paternal genomes typically vie for maternal attention. Perhaps female wrens do not respond to vocal begging alone because offspring calls are a paternally

inherited device designed to manipulate mothers into providing more care than is optimal for her. Female wrens might resist paternal manipulation by responding only to an appropriate combination of visual and vocal displays.

A Mechanism for Incomplete Compensation

Finally, sex differences in provisioning rules might persist following their initial evolution, by resolving sexual conflict over nestling provisioning in the manner predicted by Houston & Davies (1985; Wright & Cuthill 1989; Wright & Dingemanse 1999; but see Sanz et al. 2000). The various elements of the begging display can change differently with respect to nestling hunger (Kilner et al. 1999). If mothers and fathers respond to different components of the display they may receive different information about the state of the brood (see also Kölliker et al. 1998). A change in provisioning rate by one parent, and the consequent change in brood begging behaviour, might therefore provoke only a partially compensating change in provisioning by the other parent, as envisaged by the Houston & Davies (1985) model.

FUTURE DIRECTIONS

The emphasis of this review has been on the information content of the begging display, simply because that has been the focus of the few theoretical and experimental studies to investigate the function of complex solicitation displays. Multicomponent begging displays need not have evolved only for their signalling properties. At this stage, it is just as likely that they could enable scramble competition, or blackmail parents into providing food. For example, if the elements of the display are more costly together than they are individually, complex displays may increase the potential for nestlings to blackmail parents for resources. One challenge for future work is to develop a more realistic theoretical framework yielding experimentally testable predictions which can distinguish between these different possibilities. Only then can we unravel the complexities of nestling begging displays.

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