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Nestling begging as a communication network

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Introduction

In many bird species, nestling birds beg for care from their parents. A parent arriving at the nest with food is met by begging nestlings, which are waving their wings, calling and stretching to expose brightly coloured gapes, all within the confines of a nest that may contain several other begging nestlings. This mode of parent-offspring communication has become a model for the study of the evolution of biological signalling.

Hungrier nestlings beg more intensely, so the parent can use the display to decide which nestling to feed and to decide how soon it should return to the nest with food (reviewed by Budden & Wright, 2001). The fact that the parent can extract information on nestling hunger from such a confusing burst of signalling raises numerous questions. How does each nestling ensure that its own signal of need is received above the din of its nestmates' displays? How do parents differentiate among these displays to choose which nestling to feed? How much do the displays, as opposed to the physical jostling toward the parent that also goes on in the nest, determine which nestlings are fed?

To answer such questions we need to understand how the begging behaviours of whole broods function together. Concepts derived from the new field of communication networks seem well suited to this task but have not yet been explicitly applied to begging. As currently defined (McGregor & Dabelsteen, 1996; McGregor & Peake, 2000), a communication network forms whenever several individuals communicate within transmission range of each other's signals. Nestlings noisily begging within the confines of a nest clearly fit this definition, since most or all of the nestlings within a brood are within transmission range of each other's signals.

In this chapter, we hope to show that considering begging as a communication network yields new insights, not only into begging behaviour but also into communication networks in general. We begin by briefly summarizing previous research on begging, most of which has treated the display as dyadic communication: that is, as signalling from one individual, the nestling (or the brood considered as sending one joint signal), to one receiver, the parent. We then apply ideas from studies of communication networks to nestling begging, identifying several conceptual issues that we think studies of begging can help to clarify. Finally, we discuss aspects of the design of begging and parental behaviour that may have evolved in response to the network environment and make some suggestions for future work.

Begging as dyadic communication

In this section, we summarize the theoretical and empirical work on begging to date, most of which has treated parent–offspring communication as a dyadic communication system. This summary provides background information for the discussion of communication networks that follows, while also illustrating some of the strengths and weaknesses of the dyadic approach to begging behaviour.

Theoretical work

Begging has attracted considerable attention from evolutionary biologists largely because of its apparently needless conspicuousness. Because parents are only a few centimetres away from their young, it is not clear why offspring signal for food with such an elaborate display. Perhaps the best-known explanation for this apparent extravagance stems from parent–offspring conflict theory (reviewed by Godfray, 1995; Parker *et al.*, 2002). Natural selection favours parents that distribute resources optimally amongst both their current and future offspring. Each of these offspring, however, is selected to solicit resources so as to benefit its own fitness, rather than the inclusive fitness of its siblings. Therefore, offspring might signal for resources that parents would do better giving to siblings or reserving for future broods. To overcome parental reluctance, offspring may have to send exaggerated signals of need (Trivers, 1974; Godfray, 1995).

This basic explanation has been revised or extended in various ways, making the parent–offspring dyad one of the most thoroughly modelled animal communication systems. Some of the most influential models, both for begging and for animal signals in general, have asked how reliable signalling can evolve in the face of conflict between signallers and receivers (reviewed by Godfray & Johnstone, 2000; Johnstone & Godfray, 2002). Specifically, if young are prone to exaggerate, then

why would parents respond at all to begging signals? The answer is that, whereas parents might easily be able to assess some aspects of their nestlings, like their size, parents might not be able to assess directly important aspects of their nestlings' needs, for example their immediate need for food. If begging provides information on these aspects of nestling need, then parents should provision nestlings according to variation in the begging signal. This situation can be evolutionarily stable, however, only if the signal is costly for nestlings to produce. Therefore, in effect, nestlings might have to put on a costly begging display to prove that they really are hungry (Godfray, 1991).

These results have been largely responsible for the general acceptance of the idea that reliable signals must be costly if they are to evolve. Some of the complexities of this story are less widely known, however. Recently, for example, other models have suggested that, in some situations, nestlings might signal their needs accurately without large costs, for example if exaggeration draws so much care away from siblings that the cost to the signaller's inclusive fitness outweighs the direct benefits of the extra signalling (Maynard Smith, 1994; Bergstrom & Lachmann, 1998; Johnstone, 1999; Price *et al.*, 2002).

For the purposes of this chapter, two features of theoretical work on begging particularly stand out. First, these models have focused on fundamental issues in dyadic communication, such as how signalling can evolve despite conflicts of interest between signallers and receivers. Thus they are relevant to our understanding of a wide range of communication systems. Second, the emphasis these models have placed on particular aspects of signalling, such as its honesty and costliness, has led empirical studies to focus on these aspects of begging to the neglect of others (see below). One of these neglected aspects is the communication network in which begging occurs; although recent attempts to model the effects of signalling on nestmates (reviewed by Royle *et al.*, 2002; Johnstone & Godfray, 2002), which we discuss further below, are steps in that direction.

Empirical work

The theoretical possibility that begging might be exaggerated led many researchers to test whether begging is indeed a reliable signal of need. Studies in a wide range of species confirm that the intensity of both the visual and vocal aspects of the display increase with food deprivation (Budden & Wright, 2001). In turn, parents use the begging signal in two ways to make provisioning decisions. First, the more intense the begging of the brood as whole, the more often parents return to the nest with food. This level of response has been shown most clearly in experiments in which playback of nestling begging calls stimulates higher provisioning rates (Budden & Wright, 2001). Second, once parents arrive at the nest, nestlings that beg more intensely than their nestmates are more likely to be

fed. Experiments again provide the clearest demonstrations of this effect: parents are more likely to direct feedings to nestlings with brighter gapes (Götmark & Ahlström, 1997; Kilner, 1997; Saino *et al.*, 2000, 2002) or to nestlings placed next to speakers playing higher call rates (Leonard & Horn, 2001a; Kilner, 2002a; but see Glassey & Forbes, 2002a). Therefore, begging appears to communicate to parents the requirements both of the brood as a whole and of individual nestlings.

Begging is more than a simple cry for food, however, for two reasons. First, food deprivation is not the only aspect of nestling need that the begging display advertises. For example, in some species begging may signal long-term nutritional need as opposed to the short-term hunger described above, with nestlings in poorer condition (e.g. having lower mass than nestmates) begging more than their nestmates (Price *et al.*, 2002). Additionally, some aspects of begging, especially begging calls, can change when nestlings lose heat, thus signalling the need for brooding (Evans, 1994; Leonard & Horn, 2001b; Clotfelter *et al.*, 2003; B. Glassey, personal communication). Finally, gape colour in some species may advertise a nestling's immunocompetence (Saino & Møller, 2002). Clearly, the message that begging is sending may be more complex than just short-term hunger.

A second complicating factor is the effect of siblings on nestling begging. Begging intensity, whether measured by the intensity of the postural display or overall call rate, increases with brood size in many species (Budden & Wright, 2001) and may also increase when nestmates beg (e.g. Leonard & Horn, 1998). Also, nestlings compete physically for access to parents (see below) and their display and its effect on parents may vary according to the nature and intensity of this physical competition (e.g. Price *et al.*, 1996; Cotton *et al.*, 1999). Interest in the effects of both signalling interactions and physical competition among nestmates has mainly focused on how they complicate honest signalling of need (e.g. Rodríguez-Gironés *et al.*, 2001; Price *et al.*, 2002). We will be discussing them further below because they are clearly central to any discussion of begging as a communication network.

Summary

This brief review shows that the main emphasis of work on begging has been on how it functions as a signal of need from nestlings to parents. Begging has been treated mainly as a dyadic signalling system: that is involving one signaller (the nestling or the brood considered as sending one joint signal) and one receiver (the parent). Siblings have been included in the picture, but mainly because they might affect the dyadic signalling of need. Only recently have researchers started to consider the effects of competing signalling by nestmates in any detail, an important step toward treating the begging brood as a communication network.

Begging as a communication network

If we are to broaden our view of begging to include the communication network in which it occurs, we must first characterize that communication network. By definition, a brood of begging young is a communication network because nestmates are all within range of each other's signals (McGregor & Dabelsteen, 1996; McGregor & Peake, 2000). Going beyond this definition, however, to characterize the network and explore its implications, raises more conceptual challenges than this simple definition might suggest.

In this section, we discuss three of these issues. First, to apply the definition of communication networks at all, we must distinguish signalling from other acts. This can be especially problematic in the case of begging, in which signalling and direct physical competition are tightly linked. Second, to examine some of the more interesting implications of the network, we must carefully consider the nature of signals and signalling interactions – again, a challenging distinction when applied to begging. Third, there are factors, such as the genetic relatedness of nestlings, which are at least as important for characterizing this communication network as the overlapping transmission ranges of signals that define it. While all three of these areas present challenges for studies of begging networks, they also provide opportunities for testing some key concepts in the study of communication networks.

Physical competition versus signalling

Nestlings form a communication network because they are within signalling range of each other. Unlike members of many other communication networks, however, nestlings are also in direct physical contact with each other. This tight proximity highlights difficulties that can arise when we try to distinguish between signalling and other acts, in this case physical competition. Since a communication network, by definition, consists of signalling (i.e. of behaviours specialized to communicate information (McGregor & Peake, 2000)), this distinction is fundamental for understanding any communication network.

Nestlings jostle with one another for access to parental feeding locations within the nest and their success at reaching the parent strongly affects which nestlings are fed (Budden & Wright, 2001). Nestlings can physically compete in several ways, for example by usurping positions close to where parents arrive at the nest, by blocking parents' access to other nestlings or, particularly in non-passerine species, by directly pushing or pecking one another (Mock & Parker, 1997; Budden & Wright, 2001; Drummond, 2002).

Much of this physical competition is hard to distinguish from signalling. Jostling for position and direct aggression seem to be non-signalling acts by which

nestlings get better access to parents. Parents may nonetheless get information about nestling need and quality from these physical interactions, which they then use to choose which nestling to feed (Rodríguez-Gironés, 1996; Lotem *et al.*, 1999). This informativeness alone does not make them signals. If, however, the interactions are designed to affect that choice, rather than merely to thrust a nestling forward to rob the parent of its choice, then they are signals, by the above definition, despite their outward appearance. Conversely, some features of begging that appear to have been designed partly to convey information and thus are signals by definition (McGregor & Peake, 2000), such as posturing (Kilner, 2002b), seem just as clearly designed for effective jostling toward the parent. Even the design features of begging displays that are adaptations for overcoming interference from nestmates (reviewed below) may be seen either as ways to signal information on need more effectively to parents (Horn & Leonard, 2002) or as scrambles for parental attention (Rodríguez-Gironés *et al.*, 2001; Royle *et al.*, 2002). In the latter case, their ultimate function would differ little from that of physical competition, since by dominating the parents' visual and acoustic fields they too would not inform parents so much as reduce the parents' opportunity to choose which nestling to feed.

Therefore, a nest full of begging nestlings is part communication network, part scrum toward the parent. Which view of begging is more accurate depends largely on how parents interpret begging signals and physical competition, a topic we discuss further below. Given that display behaviours ultimately evolve from non-signalling acts, however, we can at least conclude that begging offers an interesting system for studying how social behaviours besides signalling affect communication networks.

Signalling interactions versus just signalling

One of the aspects of communication that has become more prominent as a result of the communication network approach is the information content of signalling interactions: the give and take of signals among members of the network (McGregor & Peake, 2000). It is from the interactions between signallers, rather than the signals themselves, that some particularly interesting consequences of communication networks arise, such as signalling to avoid interference (Ch. 13) and eavesdropping (Peake *et al.*, 2002; Ch. 2).

Distinguishing signals (directed at the parent) from signal interactions (directed at nestmates) in the case of nestling begging is difficult, however. On the one hand, several lines of evidence show that nestmates' signals influence how a nestling signals. In many studies, nestlings beg more intensely when in bigger broods or when with nestmates than when alone (Budden & Wright, 2001; but see Cotton *et al.*, 1996). More direct evidence comes from studies in which nestlings

increase their postural display when their nestmates do (e.g. Leonard & Horn, 1998) or call more when they hear nestmates calling (e.g. Leonard & Horn, 2001c).

On the other hand, it is not clear that these changes in signalling constitute signalling interactions in the sense implied by current discussions of communication networks, especially work on social eavesdropping (McGregor & Peake, 2000; Ch. 2). According to this work, a signalling interaction consists of a sender directing a signal at a receiver, which then responds. To the degree that begging is directed at the parent, then competitive interactions among nestlings to catch the parents' attention are not signalling interactions in this sense (Royle *et al.*, 2002). By extension, parents that choose to feed nestlings that beg more than their nestmates (Budden & Wright, 2001), like the predators that are attracted to nests whose calling is increased by competition (Haskell, 2002), are interceptive rather than social eavesdroppers, because social eavesdroppers must base their response on signalling interactions not just on signals (Ch. 2).

This conclusion may partly reflect our still sketchy understanding of nestling interactions. For example, Roulin (2002) has recently suggested that at least some signalling by nestlings may be directed at nestmates. Nestling barn owls *Tyto alba*, for example, appear to have calling contests between parental visits, in which nestlings negotiate which of them will receive a feeding when the parent next returns (Roulin, 2002). If nestlings do direct signals to each other in this way, then parents that extract information from these interactions would fit the definition of social eavesdroppers (Ch. 2).

In the particular case of barn owls, nestling negotiations occur when the parent is absent and so cannot be overheard by parents. In principle, however, there is no reason why similar interactions between nestlings could not also occur in the parent's presence, especially in species in which parents spend enough time transferring food to their young that the young have time to interact (e.g. parrots (Psittaciformes); Krebs, 2002). Certainly, if nestlings do direct their signals to each other, the importance of considering nestling begging as a communication network is considerably strengthened.

Functional relationships among nestlings and network structure

Communication networks were first defined in the context of communication among territorial songbirds, which are widely separated on different territories but are interconnected by the overlapping transmission ranges of their songs (McGregor & Dabelsteen, 1996). Song is, thus, the main way in which these birds interact; consequently, characterizing interacting songbirds as a communication network captures much of how they affect each other's signalling behaviour.

Nestlings packed together within a nest, however, are interconnected in many ways besides the overlapping ranges of their signals. We have already discussed

how they interact through physical competition and how that may have strong effects on their signalling behaviour. In this section, we briefly list three other interconnections that are integral to any explanation of how nestmates affect each other's signalling behaviour.

Unlike physical competition, these effects do not present difficulties for defining signals and hence applying the definition of communication networks to begging. They do, however, illustrate that, in some communication networks, signallers are so mutually dependent on one another that the overlapping transmission ranges of their signals are only one way in which their signalling behaviours are interconnected.

We will list three such relationships among nestlings: genetic relatedness, shared fate and heat transfer. For each category, we touch briefly on their possible implications for signalling. We then discuss perhaps their most interesting implication, which is how all these relationships might combine to give a structure to the communication network within the brood.

Genetic relatedness

Genetic relatedness is perhaps the most important of the relationships among nestlings, because it so heavily influences the fitness consequences of all the other types of relationship. Since nestlings tend to be highly related to one another, relatedness probably affects signalling in this communication network more than in most of the other networks described in this volume. Indeed, for most theoretical models of begging, the main route of sibling effects on begging is through a nestling's inclusive fitness. In general, theory predicts less-exaggerated or less-costly begging the higher the relatedness among nestmates (Johnstone & Godfray, 2002; Price *et al.*, 2002). Consistent with such predictions, interspecific brood parasites, whose relatedness with their host nestmates is zero, such as European cuckoos *Cuculus canorus*, great spotted cuckoos *Clamator glandarius* and brown-headed cowbirds *Molothrus ater*, call more loudly and more frequently than their nestmates (Dearborn & Lichtenstein, 2002; Redondo & Zúñiga, 2002).

Evidence for non-parasitic species, however, is scant. In one comparison across species for which data on genetic parentage was available, begging calls were louder in species with more frequent mixed parentage (Briskie *et al.*, 1994). This result suggests that a species' average level of relatedness within broods might set its average level of begging. A more relevant result for communication networks, however, would be if nestlings within a species could assess their relatedness to broodmates and adjust their levels of competitive signalling accordingly. Nestlings are generally thought to lack the cues by which their nestmates could assess their relatedness (e.g. Whittingham & Dunn, 2001); indeed there may be selection against such cues (Johnstone, 1997). As for kin recognition in birds in general

(Komdeur & Hatchwell, 1999), addressing this issue directly will require more sophisticated experiments than have been applied to date.

Shared fate

Along with relatedness, a fundamental feature underlying nestling interactions is that, like the proverbial eggs in one basket, nestmates often share the same fate. For better or worse, they have the same adults feeding them, share the same local environmental conditions around the nest and, therefore share their chances of survival to a greater degree than participants in most other types of communication network.

This shared fate has inevitable consequences for signalling behaviour; if one nestling begs more loudly, for example, the parents might return more often to feed all the nestlings or a predator might be more likely to find the nest and eat all the nestlings. Thus, both the benefits and the costs of begging by any given nestling are at least partially visited on the whole brood. Indeed, Wilson & Clark (2002) went still further and suggested that broods are subject to a form of group selection which may lead nestlings to signal cooperatively. Aspects of begging that are usually presented as competitive, such as signal characteristics that ostensibly serve to circumvent interference (see below), might instead function cooperatively to coordinate nestmates' signals (Wilson & Clark, 2002). How individual signals fit together to form aggregate brood signals has not been studied yet, but we can safely expect that the shared fate of nestlings will make signalling interactions within their networks differ in interesting ways from those of signallers with more independent fates, such as chorusing frogs.

Heat transfer

Nestling birds cannot thermoregulate until partway through the nesting period. Before that point, they rely not only on brooding by parents but also on heat from their nestmates. Nests where young hatch asynchronously may consist of older, heat-producing nestlings and younger, heat-consuming nestlings (e.g. Hill & Beaver, 1982). Such thermal relationships among nestlings may increase the variety of their signals and signalling interactions. Specifically, in several species, some aspects of begging, especially begging calls, change when nestlings lose heat and may signal their need for brooding (see above). Nestlings might, therefore, have to compete for attention from nestmates that are sometimes signalling for food and sometimes for warmth, and they might adopt different signalling strategies for each situation. Thermal relationships might also affect signalling through more direct effects on individual signallers. For example, some evidence suggests that house sparrow *Passer domesticus* nestlings lose heat when the stretching and gaping of begging increases their surface area (Ovadia *et al.*, 2002). They might,

therefore, be able to beg more when next to larger nestmates, since any thermal loss during begging would be reduced. Thermal relationships among nestmates are still poorly understood, but, like physical competition and signalling, they are probably readily perceived by nestlings and thus may have immediate and dynamic effects on patterns of signalling within the nest.

Network structure

The net result of all the relationships listed above, including the physical competition also discussed, is that they may lend structure to the communication network within the nest. By 'structure,' we mean a pattern in which not all nestlings have the same sorts of relationship with one another. Most obviously, physical competition can lead to dominance hierarchies, with larger or stronger nestlings suppressing the begging signals of smaller nestlings or displacing them from positions near the parent where their begging signals would attract the parent's attention more effectively (Mock & Parker, 1997).

Hierarchies, however, are only one of a variety of network architectures that might arise. Speaking more generally, Glassey & Forbes (2002b) noted that nestlings can often be divided into 'core' and 'marginal' nestlings (Mock & Forbes, 1995). Survival of core nestlings is usually predictable, whereas marginal nestlings, which may be smaller, in poorer condition, younger, subordinate and/or less able to thermoregulate, survive only if ecological conditions are favourable. This 'structured sibship' (Glassey & Forbes, 2002b) may yield three different sorts of nestling relationships within the brood: core to core, marginal to marginal, and core to marginal (Glassey & Forbes, 2002b).

Variation among species in this underlying structure will affect physical competition and signalling interactions within the nest. For example, one core and one marginal nestling might yield a simple dominance hierarchy, whereas three nestlings in each category might yield two 'cliques' of nestlings, between which there is a dominance hierarchy but within which signalling behaviours are similar and physical competition is equitable. In any case, the underlying structure of relationships within the brood, even though they do not consist of signalling relationships, nevertheless may strongly affect the structure of the overlying communication network – no doubt a recurring theme for most communication networks (e.g. Chs. 10 and 25).

Summary

We have raised three complexities in applying the concept of communication networks to nestling begging. First, characterizing the communication network entails a difficult distinction between signalling and physical interactions. Second, demonstrating some of the more interesting effects of communication

networks entails another difficult distinction: between signalling to the parent and signalling interactions with nestmates. Third, any realistic description of the communication network must include interrelationships among nestmates that do not involve signalling but nevertheless may shape the structure of the network.

These particular issues, of course, have less of an impact on communication in some other kinds of network. Territorial birds singing from their song posts, for example, are far beyond the range of physical interaction, are clearly directing their signals at each other (but see Ch. 14), and are generally unrelated to one another. Nonetheless, the issues we have raised are not unique to begging nestlings. Even territorial birds, for example, can engage in close-range interactions that combine signals with direct aggression, sing in ways that can be seen either as signalling interactions or as attempts to overcome interfering signals, and have dominance relationships that structure their communication network. If communication networks are indeed 'the commonest social environment in which communication occurs' (McGregor & Peake, 2000), then network concepts will inevitably be applied to other systems that do present some of the complications we have discussed to varying degrees. If we are to understand how these networks function, we need to clarify these issues and begging should prove to be a particularly useful system for doing so.

Consequences of the network for begging

We now turn from attempting to characterize the communication network within the nest to exploring how it might affect communication, from both signallers' and receivers' perspectives. Most discussions of communication networks have emphasized two consequences in particular (e.g. McGregor & Peake, 2000; McGregor *et al.*, 2000; see also other chapters in this volume) and we begin with these. First, from the signaller's point of view, signals must be designed to catch the receiver's attention in the face of interference from other signals in the network. Second, receivers, for their part, can more readily compare signallers in a network because they are in transmission range of several signallers at once. A third possible consequence has received less attention: communication networks might reduce error in the information that signals convey. Specifically, as we explain below, nestlings are particularly error prone in deciding when and how intensely to beg. When nestlings partly base these decisions on the behaviour of other nestlings, as they can when signalling within a network of other nestlings, these errors might have less effect on their signals of need.

Design to catch receiver attention

McGregor and Peake (2000) suggested that the main effect of networks on signal design arises through competition for receiver attention, as each signaller

attempts to circumvent the interference caused by competing signals in the network. Perhaps no other communication system is more obviously a competition for receiver attention than a brood of noisy nestlings. Given the interest in the exaggeration of this signal and its role in nestmate competition, however, there are surprisingly few studies that specifically address how begging signals are designed to overcome interference from nestmates. Our understanding of begging and nestling competition might be considerably enhanced by thinking of begging nestlings as a communication network.

In particular, we suspect that many of the most striking characteristics of the begging display may be designed for overcoming interference. If so, then the conspicuousness and complexity of the display, which seems unnecessarily extravagant for such a short-range signal, may, in fact, be a proportionate response to signal interference (Dawkins & Guilford, 1997; Horn & Leonard, 2002). Here we briefly discuss how selection for overcoming interference might account for a few of the more obvious features of begging (see also Horn & Leonard, 2002).

High output

The most straightforward way to overcome any background noise is to increase the amplitude or duty cycle of one's signal. There is ample evidence that nestlings respond in this way to signalling by nestmates (Budden & Wright, 2001; but see Cotton *et al.*, 1996). For example, nestlings in some species beg more intensely when placed near a begging nestmate (Leonard & Horn, 1998) and call at higher rates when they can hear a nestmate calling (Leonard & Horn, 2001c).

Locatable signals

Surprisingly small apparent angular separation between stimuli can significantly enhance a receiver's ability to tell them apart (Ch. 20). Thus design features that enhance the locatability of nestlings are likely to enhance how well they stand out from competing signals and so focus parental attention on an individual nestling. The visual components of begging, brightly coloured gapes in particular, seem designed to be readily locatable targets for parental attention. These gapes have particularly bright outlines in species that nest in cavities, most likely so that the location of each nestling's gape is distinct despite the darkness (Kilner & Davies, 1998; Heeb *et al.*, 2003).

Begging calls, in contrast, do not seem as obviously suited for locating nestlings because they are broadcast noisily throughout the nest. Also, there is little evidence so far that their structures are individually distinct in ways that would make them easy for parents to distinguish (Leonard & Horn, 2001c; but see Popp & Ficken, 1991). Indeed, some theoretical models suggest that they should not be individually distinct because that would risk rejection by the parent (Beecher, 1991; Johnstone, 1997).

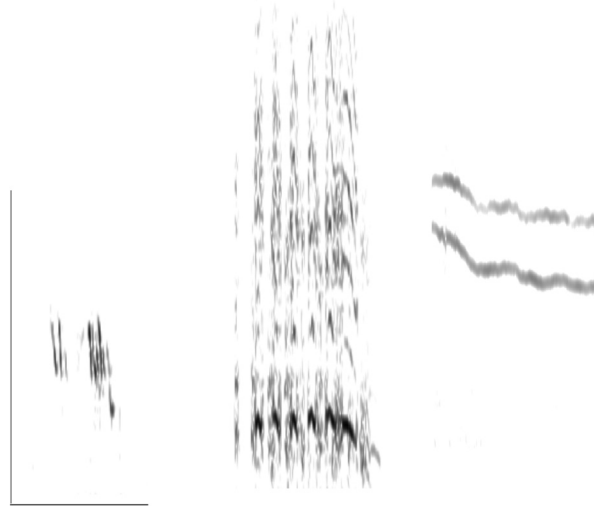


Fig. 9.1. Spectrograms of three nestling begging calls: tree swallow *Tachycineta bicolor*, hairy woodpecker *Picoides pubescens* and white-browed scrubwren *Sericornis frontalis*. Vertical bar is 10 kHz, horizontal bar is 500 milliseconds and filter bandwidth is 700 Hz.

Nonetheless, many calls do display features thought to enhance locatability, including abrupt onsets and offsets, broad frequency ranges and use of frequencies to which parents are most acutely tuned (Horn & Leonard, 2002; Fig. 9.1). Whether these features really do enhance locatability within the confines of a nest has not been tested directly. Comparative evidence, however, suggests that begging calls do display some of these features, except when subject to counteracting selective pressure from predators that use locatable calls to find and depredate nests (Haskell, 2002; Horn & Leonard, 2002).

Multiple components

Which features of signals stand out from the noise of competing signals will depend on the situation, and the multiple components of the begging display may allow nestlings to signal effectively in each of these different situations. For example, a nestling competing with a nestmate in the front of a cavity nest might gain more from gaping wider and posturing more intensely than a nestling stuck in the back of the nest, because the nestling in the front is plain sight of the parent. In contrast, a nestling in the back of the box cannot be clearly seen by the parent and would probably gain more from large increases in call rate than from any changes in the visual signal (Leonard *et al.*, 2003). Therefore, in addition to the numerous other psychological advantages of multimodal components (Rowe, 1999), they may provide nestlings with a toolbox of ways to make their signal stand out despite changing conditions.

Precedence

Precedence effects, the tendency of receivers to take more notice of signals that occur first, may favour signallers that signal before their competitors do (McGregor *et al.*, 2000). Note that such effects, as shown in insect and frog choruses, for example, may (Greenfield, 2002) or may not (Gerhardt & Huber, 2002) be the result of certain psychological effects also known as precedence (for which Dent & Dooling (2003a,b) provide an avian example). Begging may provide a particularly good example of this effect on signalling. Parents in a wide range of species are more likely to feed nestlings that beg before their nestmates (Budden & Wright, 2001) and nestlings appear to have been selected for hair-trigger responses to the first sign of the parent's arrival (Leonard & Horn, 2001d). The importance of precedence effects may vary considerably among species, providing interesting opportunities for comparative tests of their effects on signalling. For example, they may be less important in species in which parents spend more time assessing begging signals at each visit (e.g. Krebs, 2002) or in which hasty responses by nestlings might waste energy or attract predators (Leonard & Horn, 2001d).

Signal suppression

All the aspects of signal design we have outlined so far can overcome signal competition by enhancing the signaller's own signal. Signallers might also, however, overcome competition by suppressing the signals of competitors. For example, nestling whydahs *Vidua* spp. spread their wings to block their parents' view of nestmate signals (B. Mines, personal communication) and dominant nestlings of many non-passerine species aggressively punish subordinate nestmates that beg in their presence (Drummond, 2002; Roulin, 2002). Subtler versions of such direct approaches to signal competition may be widespread and should be looked for in other species.

Comparison among signals

A second consequence of communication networks is that they allow receivers to compare information from several signallers at once. Social eavesdropping, extracting information from a signalling interaction (Ch. 2), is a particularly interesting special case of such comparisons. However, receivers might also benefit from the network simply by being able to compare signals simultaneously rather than having to assess each signaller in succession (Chs. 7 and 14).

Surprisingly, how or even whether parents compare begging signals to decide which nestling to feed is still poorly understood. Many studies, using various measures of begging intensity, have shown that more intensely begging nestlings are more likely to be chosen, but such evidence is only correlational. Only a few recent studies have experimented on parental choice in sufficient detail to separate

the roles of non-signalling and signalling components of begging, or to demonstrate preferences based on individual components of the begging display (Horn & Leonard, 2002; Kilner, 2002a,b). Demonstrating whether parents use information from signalling interactions among nestlings will require still more refined experiments (see above).

Interestingly, recent models suggest that parents *must* assess interactions among nestlings if begging is to evolve as a signal at all (Rodríguez-Gironés *et al.*, 2001; Royle *et al.*, 2002). Specifically, if parents simply select the most obvious signal, then the information content of begging becomes irrelevant and begging consists merely of a scramble for the parents' attention. If, however, parents can calibrate the information in the signals to correct for competitive differences among nestlings, whether those are expressed via signalling (e.g. Roulin, 2002) or physical competition, then begging can indeed convey information on need (Rodríguez-Gironés *et al.*, 2001; Royle *et al.*, 2002). Under this scenario, a network environment may have been of central importance in the evolution of begging.

Error reduction

The last possible consequence of communication networks that we will discuss has received little attention, although it seems simple in principle and broad in implications. Specifically, because information in a network is transferred via not just one but several signals, the impact of error from any given signal might be reduced. To explain this possibility, we first outline some possible sources of error in begging displays and then discuss how the communication network may reduce this error.

Begging by individual nestlings may be considerably error prone for at least two reasons (Clark, 2002; Horn & Leonard, 2002). First, nestlings may be poor at assessing their own needs, especially since doing so requires integrating their current condition with their future requirements and their likely returns from begging, both of which are partly under control of their parents, their nestmates and the vagaries of the environment (Clark, 2002). Second, nestlings are often poor at distinguishing the parent's arrival at the nest from other sights and sounds and, therefore, often beg in response to irrelevant stimuli. In older tree swallow *Tachycineta bicolor* nestlings, for example, while nestlings often simply start begging after their nestmates do, many of the initial begging responses are to events other than the parent, like the wind blowing through the trees or the bump of another bird species landing by the nest (Leonard & Horn, 2001d; Horn & Leonard, 2002). Conversely, nestlings apparently hold back on begging when they are unsure whether the parent actually has arrived and so may miss the parent's arrival or may send an inappropriately weak signal (Clark, 2002). From the nestling's point of view, these are errors in how they deliver the begging signal. From the parent's

point of view, however, such errors corrupt any information that the parent might obtain from the begging signal.

Begging in a network may buffer such errors, because each nestling bases its decision of when and how intensely to beg partly on the begging of its nestmates (e.g. Leonard & Horn 1998, 2001c). This influence of nestmates should reduce the influence of the errors that each nestling would make if it were begging on its own; from the parent's point of view, it would provide a more reliable signal of offspring need (Clark, 2002).

This argument could, of course, be reversed. Specifically, one might argue that the more links in the information chain from nestlings to parents, the less accurate and reliable information will be (Royle *et al.*, 2002). Determining whether networks reduce or increase error requires modelling of information flow through the network. A nestling's decision of when to beg, to take the first step in the chain as an example, may be seen as a game of signal detection, in which the nestling can either try to be the first to detect the parent's arrival, at the risk of more false alarms (as shown above for tree swallows), or can free-ride by eavesdropping on the responses of nestmates, at the risk of begging later than its nestmates (Erev *et al.*, 1995). Notwithstanding the promise of such models, probably the most pressing need for understanding information flow through networks, indeed for all the possible consequences of the begging network surveyed above, is for more empirical research on how parents assess begging signals.

Summary and future directions

In this chapter we have tried to show that begging by nestling birds is a promising system for clarifying fundamental aspects of communication networks, particularly the grey but conceptually fruitful areas between physical acts and signals, between signalling competitively and interacting, and between communication and other functional relationships among signallers. Theoretical work on the evolution of begging has already started exploring each of these areas, but it has been inspired more by field workers' insistence that begging behaviour is complex than by any attempt to treat begging as a communication network. In the future, theoretical work would likely benefit from a more explicit application of network concepts, much as studies of economics and cooperation in humans have benefited from models of social networks (e.g. Slikker & van den Nouweland, 2001). Conversely, those studying other communication networks will likely benefit from staying abreast of theoretical developments in the study of begging.

Perhaps the greatest opportunities for future work, however, are in empirical studies that focus on signalling and nestmate interactions in more detail. Despite

enormous variation in the form of begging calls within and across species, for example (Popp & Ficken, 1991), only a handful of studies have addressed the function of this variation in any detail (Horn & Leonard, 2002; see also Kilner (2002b) for the display as a whole). Similarly, despite a long history of interest in intrabrood competition in birds (Mock and Parker, 1997), few studies have tried to identify the specific functions of the various behaviours that nestlings use in competition, especially what information they might convey to both parents and nestmates (Clark, 2002; Roulin, 2002). Perhaps most importantly, how, or even whether, parents choose which nestling to feed remains largely unknown because the requisite experiments have not been done (Royle *et al.*, 2002). Hopefully, greater appreciation that nestlings communicate within a network of signallers, with all its attendant challenges and opportunities, will inspire more research on all of these fundamental questions.

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