Manipulative begging calls by parasitic cuckoo chicks: why should true offspring not do the same?

The long-standing puzzle of how cuckoo chicks deceive their foster parents[1–4] continues to challenge evolutionary biologists. Although the host's inability to discriminate among nestlings can be explained as a result of an evolutionary lag[1–3] or learning constraints[5], the tendency to feed any nestling at the nest does not explain how the single chick of the common cuckoo (*Cuculus canorus*) extracts food from its foster parents at a rate comparable to that of a whole brood of host young[6].

A new study[7], using reed warbler hosts (*Acrocephalus scirpaceus*), suggests that cuckoo chicks trick their foster parents by using begging calls that mimic the sound of a whole brood. This finding provides an exciting explanation for how the cuckoo deceives its host but also challenges our view of nestling begging as honest signals of offspring need[8,9]. If cuckoo chicks can use manipulative begging calls, why have normal chicks not evolved similar adaptations to exploit their parents? Although there are certain hints in the literature that suggest possible answers, the issue is still unresolved.

The common cuckoo is an obligate brood parasite that lays a single egg in the nests of several passerine host species. Soon after hatching, the cuckoo nestling ejects the host eggs or young from the nest and is thus raised alone. Previous studies have shown that a single cuckoo chick raised by a small passerine, such as the reed warbler, is fed at the same rate as, and for a longer period than, a brood of four host young[6]. One suggestion to explain the success of the cuckoo chick in eliciting parental care was that its large size, bright gape and intense begging provided the parents with a super normal stimulus[1] or with an image of an especially high quality offspring[4]. However, evidence in support of these hypotheses is not sufficiently unambiguous and mostly concerns systems in which the parasite is raised alongside the host young and has to compete with them for food[4,10]. The new study by Davies *et al.*[7] provides a different answer to the problem.

Initially, Davies *et al.* showed that large size alone was insufficient to stimulate adequate provisioning. When they replaced a reed warbler brood with a single blackbird chick (*Turdus merula*) or a song thrush (*T. philomelos*), which are similar in size to the cuckoo chick, the rate of food delivery was significantly smaller than to a single cuckoo chick and similar to a single reed warbler chick. Further exploration suggested that the stimuli used by cuckoo chicks to elicit host care are their unusual begging calls, which, to human ears, sound remarkably like the begging calls of a whole brood of reed warblers. Indeed, on a sonogram, the cuckoo begging calls and those of a whole brood of reed warblers are very alike. Each individual cuckoo begging call is similar to that of an individual reed warbler, but the cuckoo rate of calling is much faster. Whereas a single reed warbler chick sounds like 'Si,...Si,...Si,…' at a rate of about 0.3 calls per second and a whole brood of warblers can produce about 3.6 calls per second, a single cuckoo chick produces an intense 'Si,Si,Si...' at a rate of 5.6 calls per second, sounding just like a group of hungry warbler chicks. In contrast, blackbird and thrush chicks have calling rates of only about one call per second, which could explain their inability to elicit the same provisioning rate as a single cuckoo, despite being the same size.

To test their idea experimentally, Davies *et al.* used playbacks of begging calls and showed that when single blackbird or thrush chicks were accompanied by loudspeakers, which broadcast either cuckoo begging calls or calls of a brood of reed warblers, the host increased its provisioning rate to that for a cuckoo chick. Finally, to confirm that the increase in provisioning rate was not an artefact of using playbacks, the researchers compared the effect of a playback of a single reed warbler chick with that of a cuckoo call or a whole brood. Although a playback of a single reed warbler did not cause an increase in the provisioning rate to natural broods, a playback of cuckoo calls or a brood of reed warblers did cause an increase, as expected.

Davies *et al.* concluded their study by suggesting that the cuckoo chick needs vocal trickery to compensate for the fact that it presents a visual stimulus of just one gape. Extending their point, it can also be said that the cuckoo's way of deceiving its host is to pretend to be a group of several offspring rather than appearing as a single high quality one. This strategy makes adaptive sense in the light of our current understanding of parent–offspring conflict and communication. The gain in parental fitness from feeding a single offspring increases with offspring need until it reaches an asymptote, which is higher for higher quality offspring[8,11]. On the one hand, because there is no increase in parental fitness after reaching the asymptote, parents might not have evolved to provide extra care in response to begging levels that are greater than those of the highest quality host chick at the greatest possible need. Accordingly, there is no point in the cuckoo exaggerating begging behaviour beyond this level. On the other hand, parental increase in fitness from allocating resources to a group of four chicks might reach a higher asymptote, at a later stage, thus justifying a higher level of food provisioning (i.e. the asymptotic fitness of four average chicks is likely to be higher than that of a single high quality chick). Therefore, by mimicking a whole brood of host young, the cuckoo can potentially exploit more host care than by providing the stimulus of a single large chick.

If begging calls that mimic a brood are so effective, why have normal chicks not evolved a faster calling rate to exploit their parents? Although true offspring are expected to be less selfish than the parasite, because they are genetically related to their parents[12,13], the existence of parent–offspring conflict allows some level of manipulative begging calls to benefit the offspring[14]. Recent models suggest that such manipulative begging calls could be selected against if begging is a costly 'handicap' and, therefore, an honest signal of offspring need[8,9,14]. However, given that a high calling rate is not too costly for the cuckoo, why would a blackbird chick of the same size not increase calling rate, at least to some extent? One possible answer is that producing frequent calls is especially cheap of the cuckoo. For example, if frequent calling is easier to produce in a squat begging posture, which is typical of the cuckoo[7], blackbird chicks, which must stretch their neck to compete with other siblings, might not be able to afford the extra effort. Hence, one direction for further research is to look for asymmetries in the cost of the signal[12,15] that permit dishonesty only for the cuckoo.

Another approach would be to assess asymmetries in the benefits gained from signalling. Because the cuckoo chick is raised alone, it receives all the benefits from the increase in provisioning rate. However, a chick in a brood of four that uses a similarly enhanced begging call pays the full cost of the extra begging but receives only part of the benefits. Moreover, such a chick is likely to do worse than its competing siblings because they share the benefits but pay nothing for the signal. Therefore, using begging components that stimulate food delivery to the entire brood,

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but not specifically to the chick that produces them, may be a luxury that only a single cuckoo chick can afford.

The idea that begging components, such as call rate, stimulate food delivery to the whole brood, whereas others, such as posture, are concerned with competition once food has arrived[7,9], should be a major target for further experimental research. If true, chicks with a better competitive ability (who therefore secure a greater share of the food brought to the nest) might do even better by behaving more like the cuckoo and mimicking a brood. Alternatively, small chicks that fail to compete and are, therefore, generally more hungry might gain more from cuckoo-like begging, despite obtaining only a small portion of the food brought to the nest.

The possibility that the costs and the benefits resulting from a collective brood signal are not equally shared among brood members will greatly complicate parent–offspring communication and could allow some level of dishonesty to evolve. Perhaps, to some extent, there is a 'hidden cuckoo chick' within each normal nest.

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Arnon Lotem

Dept of Zoology,
Faculty of Life Sciences,
Tel-Aviv University, Tel-Aviv 69978, Israel
(lotem@post.tau.ac.il)

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