



# Nestling cuckoos, *Cuculus canorus*, exploit hosts with begging calls that mimic a brood

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Nestling cuckoos, *Cuculus canorus*, eject host eggs or young from the nest and are then raised alone by the hosts. Using reed warblers, *Acrocephalus scirpaceus*, as hosts, we investigated how the single cuckoo chick can command the same provisioning rate as a whole brood of host young. Large size alone is not sufficient to stimulate adequate provisioning because single blackbird, *Turdus merula*, or song thrush, *T. philomelos*, chicks of the same mass as a cuckoo were fed at a lower rate. Our experiments show that the key stimulus is the cuckoo chick's rapid begging call ('si, si, si, si ...'), which sounds remarkably like a whole brood of host chicks, and which it matched in calling rate. When single blackbird or song thrush chicks were accompanied by loudspeakers that broadcast either cuckoo begging calls or calls of a brood of reed warblers, the hosts increased their provisioning rate to that for a cuckoo chick. We suggest that the cuckoo needs vocal trickery to stimulate adequate care to compensate for the fact that it presents a visual stimulus of just one gape.

**Keywords:** begging calls; brood parasitism; cuckoo; mimicry of calls; reed warbler

## 1. INTRODUCTION

The common cuckoo, *Cuculus canorus*, is a brood parasite, laying its eggs in the nests of various host species and relying entirely on the hosts to incubate its eggs and raise its young to independence. The female cuckoo lays just one egg per host nest. Soon after hatching, the cuckoo chick ejects the host eggs or young, and so it is raised alone. Hosts often reject eggs unlike their own (Davies & Brooke 1989a; Higuchi 1989; Moksnes *et al.* 1991), which has selected for egg mimicry by the parasite (Brooke & Davies 1988). However, there is no evidence that hosts ever reject the common cuckoo's chick, even though it differs in appearance from their own young (Wyllie 1981; Davies & Brooke 1988). Indeed, hosts never interfere as the newly hatched cuckoo ejects their eggs or chicks from the nest and they then labour to feed the impostor even as it grows to eight times their own weight. Reed warbler, *Acrocephalus scirpaceus*, hosts provision a young cuckoo with the same food and at about the same rate as for an average brood (four) of their own young (Brooke & Davies 1989). However, the cuckoo is dependent for longer (17 days in the nest plus 16 days after fledging (Wyllie 1981)) than the host young (11 days nestling plus 12 days fledgling (Cramp 1992)).

Lack of chick discrimination where brood parasites are raised alone may be explained by the cost of mis-imprinting when hosts are parasitized in their first breeding attempt (Lotem 1993). Thus these hosts may do best by accepting any chick in their nest. For example, reed warblers and other hosts of the common cuckoo will accept chicks of other species in among their own brood despite their different appearance (Davies & Brooke

1988, 1989b). This shows that the cuckoo chick does not possess any special stimuli necessary simply for acceptance. But the question remains, given that hosts reduce their provisioning rate as brood size decreases (Brooke & Davies 1989), how can a single cuckoo chick command the same provisioning rate as a whole brood of host young? Previous studies of brood parasite begging have examined cases where the parasite is raised alongside the host young (Redondo 1993; Soler *et al.* 1995; Lichtenstein & Sealy 1998). Here, a major selective pressure on begging is competition within the brood for food (Parker & Macnair 1979; Godfray 1995). Parasites raised alone may reveal how begging signals affect provisioning rates independent of competition in the nest.

We studied how the begging signals of common cuckoo nestlings stimulate host provisioning by reed warblers. Our study site was a breeding population of *ca.* 300 pairs of reed warblers on Wicken Fen and the surrounding fenland, near Cambridge, UK, where cuckoo parasitism varied between years (1985–1997) from 1.6 to 22.5%. The experiments reported here were done in June and July 1996 and 1997. We show that the cuckoo chick's large size alone is insufficient to stimulate adequate host care. Instead, the key feature is its extraordinary vocalizations, which mimic the calling rate of a brood of host young. Our results raise interesting questions concerning how provisioning adults integrate visual and vocal stimuli from begging chicks.

## 2. METHODS AND RESULTS

### (a) Provisioning rates to single chicks

If the cuckoo chick's large size alone is sufficient to stimulate adequate provisioning, then similar-sized chicks of other species should be provisioned at the same rate. We tested this by temporarily replacing a reed warbler brood

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of chicks aged 3–7 d with a single blackbird, *Turdus merula*, chick ( $n=15$ ) or song thrush, *T. philomelos*, chick ( $n=4$ ) aged 3–5 d (their nestlings are very similar). These crouched when the nest swayed in the wind so we tied the supporting reeds to an anchored bamboo cane, after which they begged normally. The provisioning rates to these single blackbird/thrush chicks were compared with those to single cuckoo chicks ( $n=13$ ) aged 5–8 d. Cuckoo and blackbird/thrush ages were chosen to provide chicks of the same mass (mean  $\pm$  s.d.: cuckoo  $25.5 \pm 6.0$  g, blackbird/thrush  $25.5 \pm 6.8$  g). We also compared these provisioning rates with those to single reed warbler chicks ( $n=12$ ) aged 5–6 d, which were much smaller ( $7.8 \pm 1.7$  g). These were recorded from broods temporarily reduced by swapping chicks between nests.

Each chick was tested once at a different nest and recorded for 1 h by video or direct observation (1100–1900, British summer time) after a 2–3 h settling-in period. Data from a sample of chicks recorded for three successive hours showed that this was sufficient time for the chicks and hosts to become accustomed to the recording conditions. First, there was no significant variation over the 3 h in the number of food loads brought per hour to single blackbird/thrush chicks (Friedman test,  $\chi^2_2=2.64$ ,  $p=0.27$ ,  $n=9$ ), single cuckoo chicks ( $\chi^2_2=3.19$ ,  $p=0.20$ ,  $n=7$ ) or single reed warbler chicks ( $\chi^2_2=0.04$ ,  $p=0.98$ ,  $n=12$ ). Second, there was significant variation over the 3 h in the proportion of loads brought which were delivered as feeds to the chicks for the single blackbird/thrushes ( $\chi^2_2=12.19$ ,  $p=0.002$ ) and the single reed warblers ( $\chi^2_2=8.9$ ,  $p=0.012$ ) but not for the single cuckoos ( $\chi^2_2=0$ ,  $p=1$ ). However, this arose entirely because of slightly lower values in the first hour for the blackbird/thrush and reed warbler chicks; there were no significant changes for either from the second to the third hour (multiple comparison tests; blackbird/thrush  $p > 0.6$ , reed warbler  $p > 0.9$ ).

The cuckoos were recorded either in their original nest ( $n=5$ ) or in a new nest where the reed warblers had been tending a brood of their own young ( $n=8$ ). There was no difference in provisioning rate in the two cases ( $t_{11}=0.83$ ,  $p=0.46$ ), nor in another sample of cuckoos spanning a wider age range which were tested both in their original nest and another nest where hosts had been feeding their own young prior to the experiment (matched pairs  $t$ -test,  $t_7=-0.35$ ,  $p=0.74$ ). Therefore, we are confident that the data are not biased by some of the cuckoos being recorded in their home nest. Our previous experiments also show that both hosts and host and cuckoo chicks adapt rapidly to changes in nest contents (Davies & Brooke 1988; Brooke & Davies 1989).

Figure 1 summarizes the provisioning rates to the three chick types. Although the reed warblers readily accepted the blackbird and thrush chicks, they brought food at a significantly lower rate than to a cuckoo chick of the same weight. In fact, the rate to single blackbird/thrush chicks was not significantly higher than to the single reed warbler chicks that were only one-third of their mass. The food brought was mainly single large items (e.g. flies, damselflies, moths and caterpillars) or billfuls of smaller prey, and there was no difference among the three chick types (% billfuls: Kruskal–Wallis,  $p > 0.2$ ). Provisioning rate (loads per hour) was positively correlated with

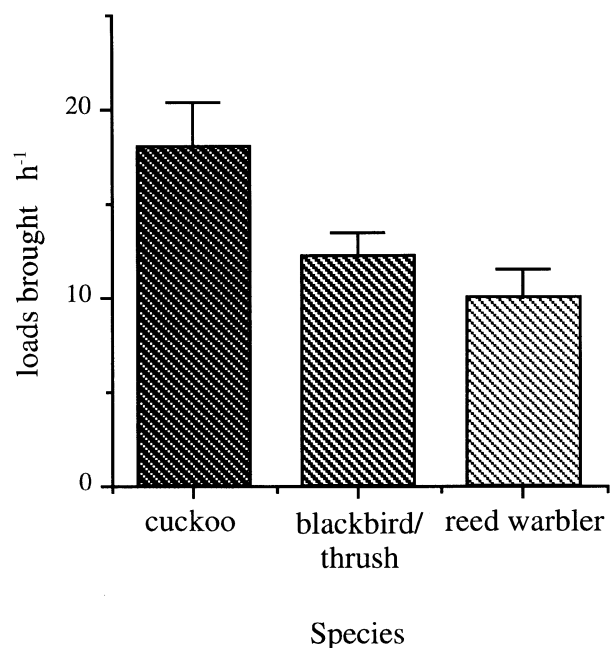


Figure 1. Number of food loads (mean  $\pm$  1 s.e.) brought per hour by pairs of reed warblers to single cuckoo chicks ( $n=13$ ), single blackbird or song thrush chicks ( $n=19$ ) the same mass as a cuckoo, and single reed warbler chicks ( $n=12$ ). Comparing the three groups,  $F_{2,41}=5.36$ ,  $p=0.0085$ . Cuckoo rates were higher than to blackbird/thrush ( $p < 0.05$ ) and reed warbler ( $p < 0.05$ ) but there was no significant difference between the latter two (Fisher PLSD tests).

weight gain per hour for both cuckoos and blackbirds/thrushes (ANCOVA,  $F_{1,17}=6.25$ ,  $p=0.023$ ; no difference between the two, interaction  $F_{1,17}=0.414$ ,  $p=0.53$ ). Thus, provisioning rate was a reasonable measure of amount of food delivered. The mean weight gain for blackbird/thrush chicks was  $0.18 \text{ g h}^{-1}$ , well below that of healthy young of these species in their home nests ( $0.57 \text{ g per provisioning hour in Magrath (1989)$ ; one-sample  $t$ -test,  $t_8=-7.59$ ,  $p < 0.001$ ). Therefore, the fact that the reed warblers were confronted with a large and hungry chick was not sufficient to raise their feeding rate.

#### (b) *The cuckoo chick's begging call*

We conclude that the cuckoo chick must provide other stimuli that elicit adequate host care. An obvious candidate is its unusual begging call, a continuous and rapid 'si, si, si, si...', quite unlike that of a single reed warbler or blackbird/thrush chick's slower 'tsip, tsip', and sounding to our ears remarkably like a whole brood of chicks.

To control for hunger, we removed chicks from their nests for a short time and recorded begging calls in the laboratory. In cases where we removed whole broods or cuckoo chicks, temporary replacements were added to the nest so the host adults did not desert. We placed the chicks in an artificial nest, consisting of a plastic canary nest pan lined with felt and wrapped with aluminium foil underneath. This was supported on a wooden stand and heated from below with an insulated jar of hot water. The chicks were supported and covered with sanitary nesting material for insulation. We induced chicks to beg by removing the covering material and lightly tapping the box with plastic forceps. The chicks were fed balls of Nectarblend

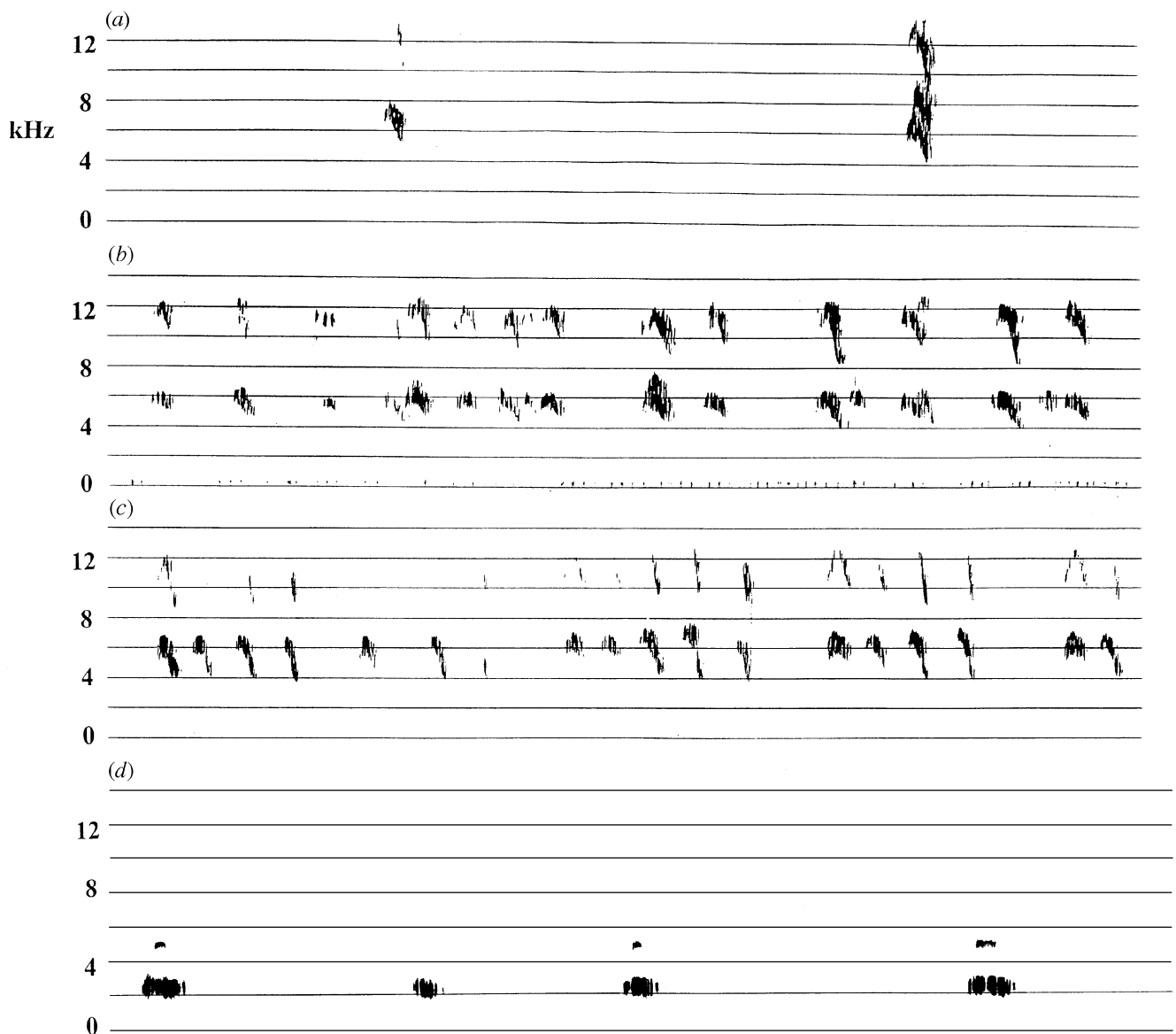


Figure 2. Sonograms (2.5 s) of the begging calls, recorded 60 min after feeding to satiation, of (a) a single reed warbler chick, (b) a brood of four reed warblers, (c) a single cuckoo chick and (d) a single blackbird chick.

rearing mix (egg, honey and ground seed) until they stopped begging, presumably having reached satiation. They were then stimulated to beg 60 min later and their calls were recorded with a Sony Datman set at recording level 6, with the microphone 20 cm from the chicks. The calls were analysed with the Canary 1.2.1 application on a Macintosh computer.

Figure 2 shows sample sonograms of the begging calls. Calling rates of chicks aged 3–7 d (measured during 12 s periods of active begging) differed between single reed warblers (mean  $\pm$  s.e. calls per 12 s =  $4.3 \pm 0.96$ ,  $n=6$ ), single blackbird/thrush chicks ( $12.4 \pm 1.29$ ,  $n=8$ ), single cuckoos ( $67.8 \pm 12.9$ ,  $n=6$ ) and broods of four reed warblers ( $43.7 \pm 5.6$ ,  $n=7$ ; Kruskal–Wallis,  $H_3=26.89$ ,  $p<0.001$ ). Multiple comparison tests showed that there was no significant difference between a single reed warbler and a single blackbird/thrush ( $p>0.3$ ), but both called at a significantly lower rate than the cuckoo ( $p<0.001$ ). The cuckoo's rate did not differ from that of a whole brood of reed warblers ( $p>0.6$ ). Although the calling rate of a single reed warbler

increased with food deprivation, it never matched that of the cuckoo chick (R. M. Kilner *et al.*, unpublished data). There were no significant differences in call amplitude of single reed warblers or blackbird/thrushes ( $p>0.45$ ) and both were of significantly lower amplitude than the cuckoo ( $p<0.01$ ). Cuckoo and reed warbler brood calls did not differ in amplitude ( $p>0.45$ ).

#### (c) Playback experiments

If the cuckoo's begging call is the key stimulus for adequate provisioning, then playbacks of cuckoo begging calls next to a single blackbird/thrush chick should increase the host provisioning levels to that of a cuckoo. Furthermore, if mimicry of brood vocalizations is involved, the cuckoo playback should be equally effective as playback of brood calls, which are known to increase provisioning rate in several species of birds (von Haartman 1953; Bengtsson & Ryden 1983).

We tested these predictions with another experiment, again temporarily replacing a reed warbler brood with a

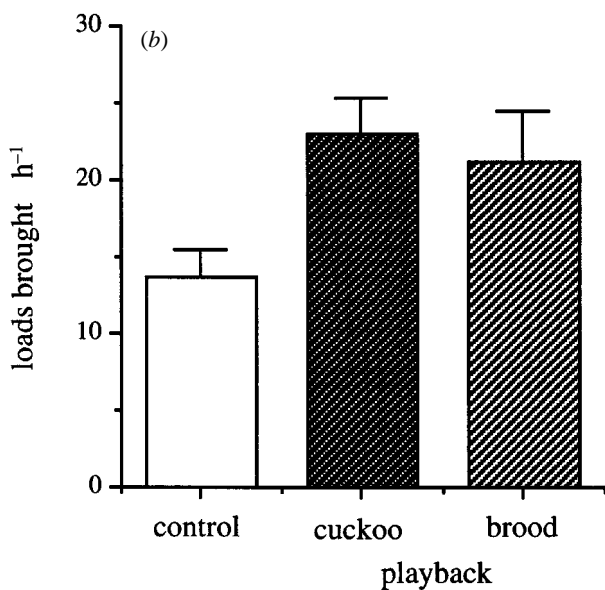


Figure 3. (a) Blackbird chick in a reed warbler nest with speaker in position. (b) Reed warbler provisioning rate (mean  $\pm$  1 s.e.) to single blackbird ( $n=6$ ) or song thrush ( $n=3$ ) chicks, each tested under three conditions: control (no playback), playback of cuckoo begging calls or calls of a brood of four reed warblers. Each chick was tested once in a different nest, except for one thrush tested twice on successive days in two different nests, hence  $n=10$  experiments. Comparison of the three treatments: repeated measures ANOVA,

single blackbird/thrush chick, but this time accompanied by a small loudspeaker next to the nest (figure 3a). After the same 2–3 h settling-in period, we observed the nest through binoculars from ca. 6 m for three successive hours, one where we broadcast cuckoo begging calls every time the chick begged, one where we broadcast calls of a brood of four reed warblers, and one control hour with no broadcast. The sequences were varied at successive nests. The hosts behaved normally throughout the watches and seemed unperturbed by the speaker or playbacks.

Playback tapes were made by recording a sequence lasting 20 s from broods of four reed warblers or from a single cuckoo either under natural field conditions or in the laboratory 60 min after feeding to satiation, which produced calling rates matching those in the field. The sequences were edited with the SoundEdit application of a Macintosh computer, with a high-pass filter to remove background noise. The resulting sequence (ca. 15 s) was then re-recorded onto metal audiotapes as a continuous 10 min loop and broadcast at natural amplitude (there was no significant difference in amplitude or calling rates for the two playbacks) using a Sony Professional Walkman. A different brood and cuckoo recording was used for each of the ten experiments.

The results showed that both cuckoo and brood playbacks caused a similar, marked increase in provisioning rates compared to the control period (figure 3b), as expected if the cuckoo calls mimicked those of a begging brood. There was no difference across the three periods in type of food delivered (% billfuls, Friedman test,  $p=0.53$ ). Nor was there a difference in time spent begging (Friedman test,  $p=0.69$ ), so it seems likely that the playbacks stimulated the hosts directly rather than via a change in chick begging behaviour. The accompaniment of the cuckoo or brood playback increased the provisioning rate of the single blackbird/thrush so that it now did not differ significantly from that of a cuckoo chick (figure 1;  $t_{21}=1.468$ ,  $p>0.1$ ). In this experiment, all hosts were confronted with the same large novel chick type, so any differences in their provisioning rate must be due to the playback.

It could be argued that any playback would increase host provisioning rate. However, in a second experiment, playbacks of calls from a single reed warbler chick did not increase provisioning rate to natural broods (2–5 young) compared with control periods (Wilcoxon matched pairs test,  $n=11$ ,  $p=0.66$ ), even though both cuckoo and brood call playbacks caused significant and similar increases in provisioning rate, just as they did to the single blackbird/thrush chicks (R. M. Kilner *et al.*, unpublished data). In this experiment the calls were broadcast at natural amplitude (there was no significant difference between brood and cuckoo playbacks but both were louder than the single reed warbler,  $p<0.01$ ). It is possible, therefore, that hosts responded more to cuckoo and brood playbacks because of their greater amplitude. However, in a third

$F_{2,18}=17.28$ ,  $p<0.0001$ . There was no difference between cuckoo and brood playbacks but both differ from controls ( $p<0.01$ , Fisher PLSD tests). If the second recording of the thrush tested twice is omitted ( $n=9$  experiments) to avoid possible pseudoreplication, the significance levels remain the same.

experiment there was no difference in provisioning rate to natural broods when accompanied by playback of single reed warbler calls at natural amplitude versus the louder amplitude of cuckoo begging calls (Wilcoxon test,  $n=10$ ,  $p=0.72$ ). The lack of effect here is not because reed warblers feed their natural broods at a maximal rate that cannot be exceeded; an increase in brood size beyond the normal size can lead to provisioning rates double the usual rate, at least in the short term (Brooke & Davies 1989). We conclude that the effectiveness of the cuckoo call is not due simply to its amplitude.

### 3. DISCUSSION

In some species of brood parasites, the parasitic chicks are raised along with the host's young. In these cases they may mimic the gape patterns of the host's young (e.g. *Vidua* finches (Nicolai 1964)) or their begging calls (e.g. *Clamator* cuckoos (Mundy 1973; Redondo & Arias de Reyna 1988)). They may also have louder and more persistent calls than the host young (Redondo 1993; Briskie *et al.* 1994) or special gape stimuli that increase the chance that they are fed (Soler *et al.* 1995). All these features are likely to enhance competitive success in the brood once the parents arrive with food, and exaggerated begging compared to the host's chicks is what would be expected from the fact that the parasite has no genetic stake in its nestmates (Harper 1986).

When parasites are raised alone, because they have ejected or killed the host chicks, they do not face the problem of competition once food arrives, only that of stimulating an adequate rate of host feeding visits to the nest. At first sight, exaggerated begging is also expected because the lone parasite has no genetic interest in the host's future reproduction. However, it may not pay to overstimulate the hosts if this means relying on a provisioning rate that the hosts have not evolved to sustain. This may explain why host provisioning rates to a cuckoo are about the same as for an average brood of their own young, even though in the short-term hosts can be stimulated to work at a higher rate if their brood size is increased (Brooke & Davies 1989).

Our results show that the extraordinary brood-mimicking vocalizations of the common cuckoo chick are the key stimulus that leads to adequate host provisioning. Parasitic honeyguides, *Indicator indicator*, which use mandibular hooks to kill host nestlings, have also been reported to sound like several young (Fry 1974), so vocal mimicry of a brood may be widespread in cases where parasitic chicks are raised alone. Further experiments are needed to identify the precise features of the begging call which affect host provisioning rate. It is possible that some components of begging signals (e.g. call rate) are involved in stimulating food delivery rate to the nest, whereas others (e.g. postures) are concerned with competition once food has arrived (Kacelnik *et al.* 1995; Kilner & Johnstone 1997). A comparative study of parasites raised alone and those raised together with host young may help to resolve this issue.

It will also be interesting to discover whether the cuckoo chick's call is host-specific, or whether it simply mimics general features of passerine brood calls, which would be effective for a range of hosts. This is particularly relevant

for the common cuckoo, where coevolution with hosts has resulted in host-specific strains (gentes), each laying eggs that match, to varying degrees, those of its particular host (Chance 1940; Brooke & Davies 1988; Moksnes & Røskaft 1995). In at least one case where the parasitic chick is raised alone (the diederick cuckoo, *Chrysococcyx caprius*, which also has gentes (Reed 1968)), begging calls differ between chicks raised by different hosts. Remarkably, in two other cuckoos, *Eudynamys taitensis* and *Chrysococcyx lucidus*, which eject host eggs or chicks, the young cuckoo even mimics the structure of the begging calls of the host young (McLean & Waas 1987). In this case it does not have the opportunity to copy the host young, so its calls must either be genetically programmed or develop through host parent conditioning to match calls that are most effective in stimulating host care (for an analogous case in the calls affecting mate choice in a brood parasite, see King & West (1983) and West & King (1988)).

In our experiments the playback of the cuckoo's begging call elevated the hosts' provisioning rate to a single blackbird/thrush to that of a cuckoo chick. This suggests that the call is the major or perhaps even the only cause of the difference in host care in the two cases and seems to leave no role for another obvious cuckoo feature, the vivid orange-red gape (blackbirds/thrushes have pale yellow gapes like those of reed warbler chicks). Experiments in which we painted the gapes of either one chick of a brood or of whole broods of reed warblers also suggested that an orange-red gape colour did not affect provisioning rates (D. G. Noble *et al.*, unpublished data). In some other species, however, redder gapes do stimulate parental feeding (Kilner 1997; Götmark & Ahlström 1997).

Why does the common cuckoo nestling need vocal trickery to stimulate adequate provisioning? It seems unlikely that this is just to counteract host discrimination against its odd appearance (Redondo 1993) given that hosts will accept a variety of foreign chicks (Davies & Brooke 1988, 1989b). Alternatively, the calls may help to compensate for the cuckoo's reduced begging postures, which are probably restricted because of its large size. The cuckoo squats low and still and simply opens its gape; if it stretched up on extended tarsi like the host young it would risk falling out of the nest. However, our results do not support this idea: when blackbirds and thrushes (which do stretch for food when they beg) were accompanied by the cuckoo playbacks they did not receive significantly more food than a cuckoo. Another possibility is that hosts calibrate their provisioning rate partly by the number of begging mouths they see. The cuckoo's vocal mimicry of a brood may compensate for the fact that it presents a visual stimulus of just one gape.

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