

Signals of need in parent–offspring communication and their exploitation by the common cuckoo

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Nestling birds present vivid gapes and produce loud calls as they solicit food, but the complexity of the display is poorly understood. Here we explain the function of reed warbler begging signals and show how they are exploited by the common cuckoo, *Cuculus canorus*, a brood parasite. Reed warbler parents integrate visual and vocal signals from their young to adjust their provisioning rates, and the two signals convey more accurate information about offspring need than either does alone. The cuckoo chick has a particularly striking begging display which has been suggested to be irresistible to host parents. However, we show that the cuckoo, reared alone in the nest, presents a deficient visual display, and elicits the same amount of care as a reed warbler brood only by compensating with its exaggerated vocal display. Therefore the cuckoo succeeds not through mimicry of the host brood begging signals, but by tuning into the sensory predispositions of its hosts.

Many animal displays are highly complex^{1,2}, often built from several component signals of different sensory types^{3,4}. For example, nestling birds beg with a combination of brightly coloured gapes⁵ and repetitive begging calls⁶. Despite their ubiquity, and a range of theoretical models^{7–11}, empirical understanding of multicomponent displays is limited¹². Here we explain why the nestling begging displays of reed warblers (*Acrocephalus scirpaceus*) and their brood parasite, the common cuckoo (*Cuculus canorus*), include both visual and vocal components. Our experiments show that reed warbler parents use both signals to adjust their provisioning rates at the nest. Together, these signals provide parents with more information about their offsprings' need than is available from either signal alone. Moreover, we show that reed warblers follow exactly the same integration rule when provisioning a single cuckoo in their nest as when feeding a brood of their own young. The way in which parents integrate two nestling signals illuminates the function of the cuckoo's extraordinarily rapid begging call¹³. Rather than whipping parents into a feeding frenzy at the nest^{14,15}, the super-normal begging call instead serves to persuade parents to work at their normal rate by compensating exactly for the cuckoo's sub-normal visual display of a single gape.

Information carried by begging signals

We studied a population of reed warblers at Wicken Fen, Cambridgeshire, UK, in the summers of 1996–1998. Nestling reed warblers solicit food from their parents by exhibiting a bright yellow gape and calling repeatedly. Although previous work with other species has established that the various components of the begging display are individually correlated with nutritional state^{5,16,17}, it is not known how they combine to signal food requirements. We investigated whether gape area and begging call rate convey distinct information about the extent of food deprivation (see Methods). Chicks were temporarily removed from the nest at a range of different ages (day 3/4 and day 6/7) in broods of four (the modal brood size). They were fed with chick-rearing mix until they stopped begging, and then kept warm but unfed. Every 10 min, for the next 110 min, we stimulated the brood to beg, recording the begging behaviours on video and audiotape (see Methods). We found that total gape area displayed and begging call rate each varied significantly with both the extent of food deprivation and chick age (Fig. 1). Hence, the different elements of the begging display carried 'multiple messages'¹¹, each element reflecting both age and

hunger^{10,11}. Moreover, because the two elements in the begging display each explained different components of variance, for both chick age and food deprivation, they also functioned as 'back-up' signals (Fig. 1)¹¹.

We checked the robustness of our conclusions by using a separate analysis of a larger data set with a different measure of offspring need, namely the amount of food required to cause the nestling reed warblers to stop begging. Nestlings were temporarily removed from the nest at a range of different ages (day 2 to day 8) and in broods of one ($n = 37$) or four ($n = 12$). They were fed with chick-rearing mix until they stopped begging, and again kept warm but unfed. After 110 min, we induced the brood to beg and recorded the begging behaviours on video and audiotape. Finally, we scored the amount of food eaten by the brood until begging stopped (see Methods). To explain the variance in the amount of food consumed, we used a multiple regression analysis, with total gape area displayed and begging call rate as the two independent factors. We found that each signal explained different components of variance in the broods' nutritional condition. There were significant independent effects of gape area ($t_{48} = 5.63$, $P < 0.0001$) and call rate ($t_{48} = 2.02$, $P = 0.042$) on the amount of food consumed. The regression equation derived was: food consumed (in ml) = 0.002 (gape area displayed (in mm²)) + 0.009 (number of calls per 6 s) – 0.011, and this explained 77.6% of the variance in food consumption. We conclude that multiple begging signals provide parents with a more accurate assessment of offspring need than can be determined from either signal alone.

Parental response to multiple signals

Do parents regulate their provisioning rate in relation to both the rate at which the brood calls and the total gape area displayed? We tested this possibility by subjecting the parents of broods of two and four nestlings, aged 6/7 days old, to playback of begging calls which were broadcast through a small speaker, attached to the side of the nest, every time the nestlings gaped for food. The three treatments were: no playback, playback of one chick calling and playback of four nestlings calling (see Methods). Clearly, the effects of these playbacks on the parents would be confounded if they affected the behaviour of the nestlings. To examine this, we recorded the duration of the brood begging display during each treatment, because in another species this is influenced by sibling vocalizations¹⁸. There was no indication that the playback of

begging calls affected this aspect of chick begging behaviour ($F_{2,32} = 1.17, P = 0.90$), nor did playback alter the likelihood of gaping (Friedman analysis of variance (ANOVA); $\chi^2_2 = 1.63, n = 12, P = 0.43$). Thus by broadcasting begging calls as nestlings displayed, we augmented only the broods' vocal displays (see also below), whereas the manipulations of brood size affected both visual and vocal signals equally. There was a significant effect of both brood size and playback treatment on the rate at which parents delivered food to the nest, and the parental response to playback was independent of brood size (Fig. 2). We have established previously that provisioning rate correlates with nestling weight gain¹³.

In a different analysis, we used data from 59 brood-size manipulations and 52 playback manipulations (see Methods) to investigate the separate effects of visual and vocal signals on provisioning rates to chicks aged 6/7 days old. We used field recordings of broods manipulated to be different sizes to check that the calling rate of individual chicks was not affected by altering the brood size. A strong positive linear relationship between brood size and brood call rate ($R^2 = 0.90, F_{1,15} = 151.6, P < 0.0001$), with a small inter-

cept (1.09), indicated that the mean begging call rate per chick did not vary with brood size. To explain the variance in the rate of parental provisioning, we used a multiple regression analysis with the maximum number of chicks calling per nest (the number of chicks in the brood plus the number of chicks calling on the playback tape) and the maximum number of gapes on display per nest (the number of chicks in the brood) as the two independent factors. We assumed that the whole brood gaped at every visit. Our limited data for broods of two to four chicks show that the mean proportion of the brood that gaped per visit was 0.8 ($n = 13$), but we have no data for larger brood sizes. As before, we checked that the data fitted the assumptions of a linear multiple regression model.

We found that reed warbler parents combined multiple signals from their young to adjust their provisioning rate at the nest. There were significant independent effects of the maximum number of gapes displayed per nest ($t_{110} = 4.42, P < 0.0001$) and the maximum number of chicks calling per nest ($t_{110} = 5.69, P < 0.0001$) on the number of feeds delivered by both parents per hour. Together, both signals explained 62.7% of the variance in nest visit rate ($F_{2,110} = 93.28, P < 0.0001$). The regression equation derived was: feeds delivered per hour = 2.28 (maximum number of gapes displayed) + 2.30 (maximum number of chicks calling) + 8.23. A polynomial regression does not provide a better fit than the linear multiple regression, which indicates that parents probably did not reach their provisioning limit within the range of our experimental treatments.

The regression equation explains parental provisioning rate in terms of the number of chicks displaying visually and vocally 6/7 days after hatching. We studied whether the equation could be expressed more generally to explain provisioning rates to reed warbler nestlings of different ages and in different brood sizes. To generalize the equation from day-6/7 chicks to young of all ages, we

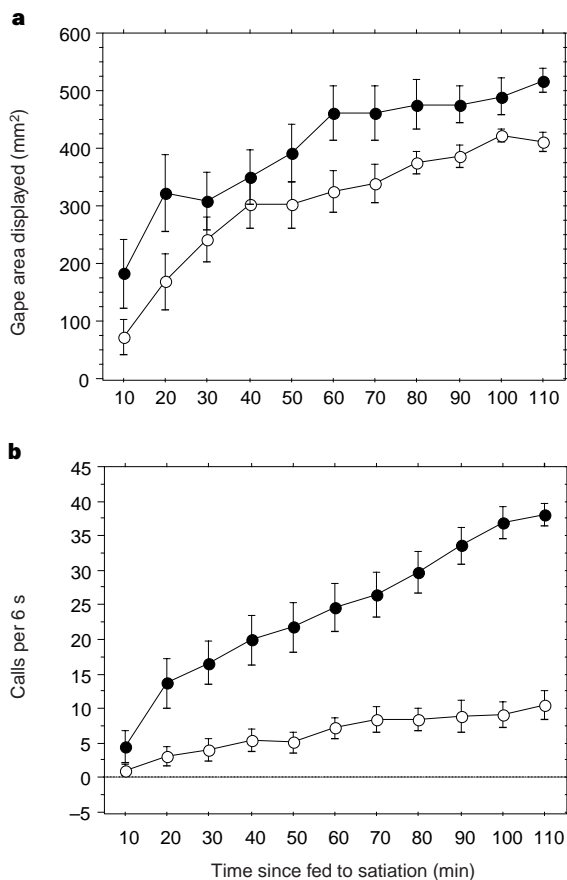


Figure 1 Effect of food deprivation. Effect of food deprivation on **a**, the total gape area displayed by all chicks (see Methods) and **b**, the rate of calling by broods of four reed warblers, on day 3/4 (open circles; $n = 9$) and day 6/7 (filled circles; $n = 10$). Plots show means \pm s.e.m. The data were analysed with a repeated-measures ANOVA, with two within-factors (food deprivation time and type of begging signal) and one between-factor (chick age). There was a significant effect of food deprivation ($F_{10,170} = 28.94, P < 0.0001$) on both begging displays. Moreover, the rate of change in gape area displayed with increasing food deprivation time was significantly greater than the rate of change in begging call rate ($F_{10,170} = 24.80, P < 0.0001$). Older chicks displayed more gape area and called at a higher rate than younger chicks ($F_{1,17} = 6.47, P = 0.021$), and begging call rate changed more with increasing age than did gape area displayed ($F_{1,17} = 3.88, P = 0.065, \text{power} = 0.448$).

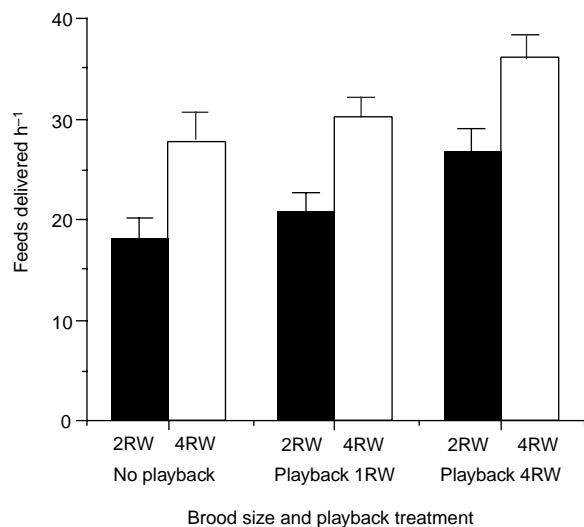


Figure 2 Effect of playback treatments. The effects of the playback treatments at broods of two (2RW; $n = 10$ pairs) and four (4RW; $n = 11$ pairs) chicks on feeds delivered per hour. Bars represent means \pm s.e.m. Each pair of parents was subjected to three treatments: no playback, playback of one reed warbler chick calling (playback 1RW) and playback of four reed warbler chicks calling (playback 4RW). The data were analysed with a repeated-measures ANOVA with one within-factor (playback treatment) and one between-factor (brood size). There was a significant effect of brood size ($F_{1,19} = 13.85, P = 0.0014$) and playback treatment ($F_{2,38} = 13.42, P < 0.0001$) on feeds delivered by both parents per hour, but no interaction between the two ($F_{2,38} = 0.041, P = 0.96$). In a separate analysis, there was no significant effect of pair identity on the response to the treatments with either broods of two chicks ($F_{9,29} = 0.88, P = 0.56$) or broods of four chicks ($F_{10,32} = 1.90, P = 0.10$).

divided the 'gape' coefficient by the mean gape area of a day-6/7 reed warbler chick (140 mm²), and divided the 'calls' coefficient by the mean number of calls per 6 s given by an unmanipulated day-6/7 reed warbler chick in the field (12.95 calls/6 s). The regression equation thus derived was: feeds delivered per hour = 0.0162 (gape area displayed (in mm²)) + 0.178 (calls per 6 s) + 8.23. To assess the accuracy of this more general equation, in the field we measured the begging calls produced and gape area displayed by reed warbler young of different ages (day 1 to day 8), in broods of two, three or four, and calculated mean values for broods of each size and age (see Methods). We substituted these means into the regression equation to calculate nine predicted provisioning rates in total. Using data that were not included in the original multiple regression analysis, we compared these predicted values with mean field observations of provisioning rates to broods of two ($n = 1$ day 5 young), three ($n = 2$ day 1/2; $n = 4$ day 3/4; $n = 9$ day 5/6; $n = 4$ day 7/8) and four ($n = 1$ day 1/2; $n = 7$ day 3/4; $n = 10$ day 5/6; $n = 9$ day 7/8) young. If the observations were to match our predictions exactly, the regression of the former on the latter should not differ significantly from the line $y = x$. This is exactly what we found ($t_7 = 1.43, P > 0.1$).

It may seem remarkable that parental provisioning rates for broods of one to eight young, from one to eight days after hatching, can be explained simply as a response to the gape area displayed and the brood calling rate. However, the results of our experiments with chicks in the laboratory indicate that both signals can convey accurate information about chick age, brood size and nutritional state, so perhaps it is not surprising that two signals alone can explain so much of the variance in parental provisioning rate. We suggest that the visual display may provide parents with a crude estimate of how frequently to feed their young, because it is correlated with brood size and chick age, whereas the vocal display may enable parents to fine-tune their provisioning in relation to the brood's level of hunger, because this signal provides more finely graded information about nutritional need. For example, in day-6/7

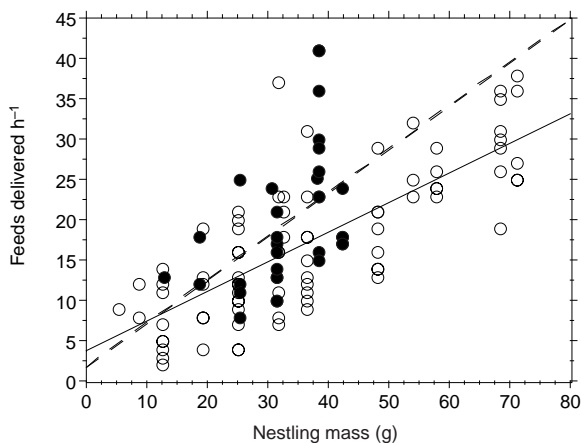


Figure 3 Relationship between nestling mass and feeding rate. The relationship between the mass of young in the nest and the number of feeds delivered per hour by both parents to the nest, for cuckoos (open circles, solid line, $n = 88$ observations of 36 different cuckoo chicks fed by 44 different pairs of hosts; some cuckoo chicks were moved between nests) and broods of four reed warblers (filled circles, dashed line, $n = 34$ different broods fed by their own parents). There was no significant difference between either the elevations ($F_{1,118} = 0.15, P = 0.70$) or the slopes ($F_{1,118} = 1.30, P = 0.26$) of the regression lines for each species. Repeating the analysis using only one randomly selected data point per cuckoo still yielded no significant difference in either the elevations ($F_{1,66} = 0.45, P = 0.51$) or the slopes ($F_{1,66} = 1.27, P = 0.26$). Data were collected in 1985–1986 and 1996–1998 either by using a video camera ($n = 24$ cuckoo observations) or by observing the nest from a distance through binoculars ($n = 64$ cuckoo and 34 reed warbler observations).

chicks the visual signal reaches a plateau 60 min after being fed to satiation, whereas the vocal signal continues to change (Fig. 1).

In theory, the amount of food supplied by parents to young is likely to be the source of a conflict of interests between the two parties, because investment patterns that are optimal for parents can be suboptimal for offspring^{19,20}. Recent theoretical work has suggested that the conflict may be resolved in the parents' favour if provisioning rates are based on costly, and hence reliable, nestling signals of need^{21,22}. The two regression equations that we have derived experimentally (first to relate chick need to their begging signals, and second to relate the begging signals to parental provisioning) allow us to link chick need quantitatively with parental provisioning rates. In principle, this provides a way in which to measure the outcome of parent–offspring conflict, and to test the prediction that parents supply chicks with exactly the food that they demand. At present, this analysis is beyond our reach, because the units of each regression equation are not the same.

Exploitation by cuckoo chicks

The reed warblers at Wicken Fen are parasitized by the common cuckoo, a brood parasite that relies entirely on its hosts to incubate

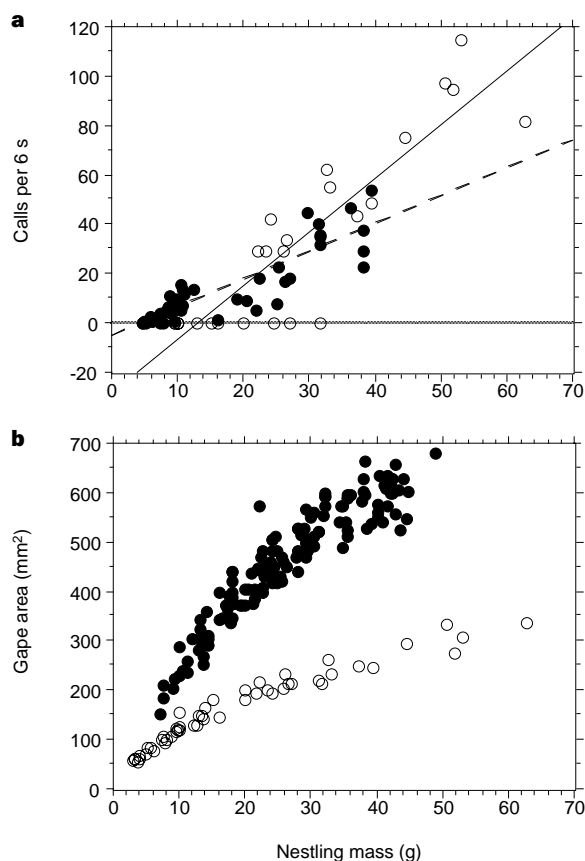


Figure 4 Relationship between nestling mass and begging call rate or gape area. The relationship between nestling mass and **a**, begging call rate, for cuckoos ($n = 25$ measurements) and broods of one and four reed warblers ($n = 49$), or **b**, gape area, for cuckoos ($n = 54$ measurements) and broods of one and four reed warblers ($n = 145$ measurements). Open circles, solid line, cuckoo data; filled circles, dashed line, reed warbler data. Begging displays were measured under standardized conditions of food deprivation in the laboratory (see Methods). The rate of calling by a cuckoo nestling increased at a significantly faster rate with mass than the rate of calling by a brood of four reed warblers ($F_{1,71} = 24.8, P < 0.0001$). We compared the rate of increase in gape area with mass in cuckoos and reed warblers by log-transforming the data, and comparing the elevations of the two resulting regression lines. The gape area displayed by a cuckoo nestling grew at a significantly slower rate than the gape area displayed by a brood of reed warbler chicks ($F_{1,188} = 91.7, P < 0.0001$).

its eggs and rear its young to independence²³. Shortly after hatching, the cuckoo nestling evicts all of the reed warbler eggs and chicks from the nest²⁴, and so becomes the sole beneficiary of parental care. Apparently oblivious to the destruction of their own reproductive success, the pair of warblers then feeds the imposter, even as it grows to eight times their own body weight. By 2 weeks of age, the cuckoo overflows the tiny nest, and the warblers seem to risk being devoured themselves as they perch on the cuckoo's back in order to bow deep into the enormous gape with food.

Our observations show that the rate at which parents provision a single cuckoo chick closely matches the rate at which they provision a brood of four of their own young, of equivalent mass, the modal brood size in this species (Fig. 3). The food brought to the cuckoo is also the same as for their own young²⁵. Previous experiments have established that the cuckoo's success at eliciting care cannot be attributed simply to its relatively large size. When we placed in a reed warbler nest a single blackbird (*Turdus merula*) or song thrush (*T. philomelos*) chick of the same mean mass as a cuckoo nestling, the *Turdus* nestlings were fed at a significantly lower rate. However, their rate of being fed improved markedly when their own begging display was augmented by cuckoo nestling begging calls broadcast from a small speaker at the side of the nest¹³.

Analysis of a larger data set than presented previously¹³ shows that the *Turdus* nestlings accompanied by cuckoo begging calls obtained significantly more food than cuckoos (unpaired $t_{22} = 2.22$, $P = 0.037$). However, when accompanied by playback of four reed warbler chicks calling, *Turdus* young were fed less frequently than a brood of four reed warblers (unpaired $t_{17} = 1.99$, $P = 0.06$, power = 0.454). Both of these results can be explained if we take into account the total gape area displayed during begging. *Turdus* nestlings have a significantly greater gape area than cuckoos of the same mass, and broods of four reed warblers display a greater total gape area than *Turdus* young ($F_{2,41} = 30.7$, $P < 0.0001$). These results provide further evidence that parents integrate visual and vocal nestling signals to decide how frequently to feed their young, and again indicate that the main visual signal is the gape area displayed, and that the main vocal signal is begging call rate.

At 6–8 days of age, a cuckoo nestling's begging call closely matches the rate of calling of a brood of four reed warblers¹³. However, as the cuckoo grows, its begging call becomes increasingly more rapid, far faster than the rate of calling achieved by a brood of

four reed warblers (Fig. 4a). Conversely, despite its enormous gape, the total gape area displayed by the single cuckoo is much less than that of a brood of four reed warblers, and the difference becomes more pronounced with increasing chick mass (Fig. 4b). This is an inevitable consequence of the fact that adult cuckoos have relatively small bills in relation to mass compared with adult reed warblers²⁶, so a single cuckoo will never match the gape area of four reed warblers of the same total mass (Fig. 5).

If reed warblers follow the same integration rule when feeding a cuckoo as when feeding their own young, we can use our regression equation to test whether the increasingly supernormal begging call of older cuckoo nestlings serves to compensate exactly for their increasingly subnormal visual stimulus, compared with a brood of four reed warblers. Using the equation: feeds delivered per hour = 0.0162 (gape area displayed (in mm²)) + 0.178 (calls per 6 s) + 8.23, we calculated predicted begging call rates for cuckoos. We measured the gape areas of cuckoo nestlings at different stages of development ($n = 26$ measurements of 20 different cuckoos), as well as their hourly provisioning rates by both parents ($n = 74$ observations of 28 cuckoos fed by 36 different pairs) and calculated mean values for cuckoos on days 4–11, 13 and 15 (see Methods). We substituted these mean scores into the regression equation to calculate the predicted begging call rate at different stages of development.

When we compared our predictions with measurements of unmanipulated cuckoo begging call rates in the field, we found no significant difference between the two (Fig. 6). Therefore reed warblers do indeed use exactly the same provisioning rules when feeding cuckoos and when feeding their own brood (Fig. 7). The increase in the cuckoo's calling rate with age is exactly what we would expect if it is to offset the disadvantage of displaying a single gape. Furthermore, the close match between our predictions and observations (Figs 6, 7) indicates that any cues other than gape area and call rate must play a minor role in determining host provisioning rate. For example, our experiments show that gape colour has no effect on provisioning rate²⁷. A key point is that the cuckoo does not mimic the begging displays of a brood of reed warblers precisely, but instead tunes into the way in which the host parents integrate visual and vocal cues from their young²⁸, exaggerating the latter to

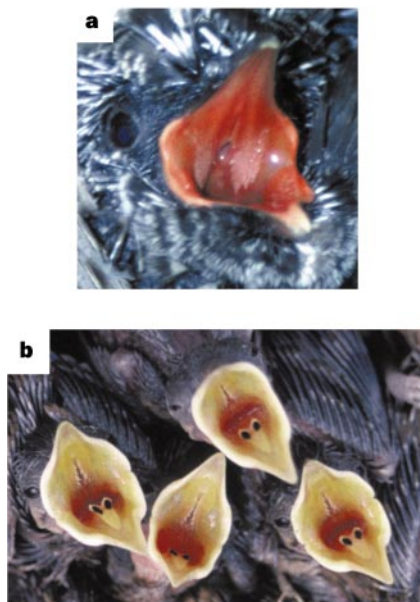


Figure 5 Chick gapes. **a**, A nestling cuckoo, day 11/12; **b**, a brood of four reed warblers, day 6/7. The two pictures are at roughly the same magnification.

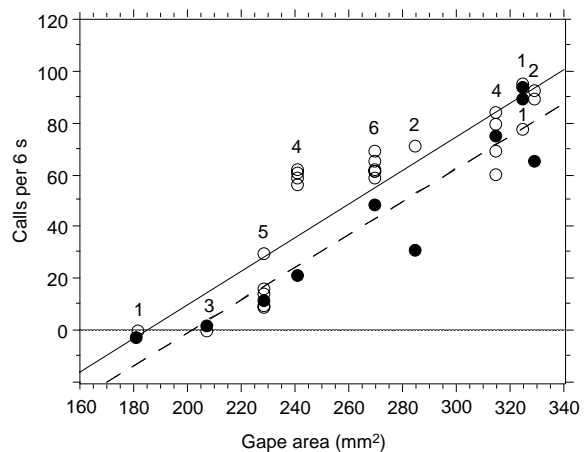


Figure 6 Comparison of observed and predicted begging call rates. Observed cuckoo begging call rate (open circles, solid line) is compared with the predicted cuckoo begging call rate (filled circles, dashed line) that should accompany the display of a particular gape area, assuming that reed warblers use the same rules to feed both a cuckoo nestling and their own young. Numbers refer to sample sizes of cuckoos measured at each age. Both lines increase significantly in relation to gape area ($F_{1,35} = 24.8$, $P < 0.0001$), but there is no significant difference between them in either their slope ($F_{1,35} = 0.018$, $P = 0.89$) or their elevation ($F_{1,35} = 0.77$, $P = 0.78$). Each predicted value corresponds to a particular day of the cuckoo's nestling period (from left to right, day 4–11, day 13 and day 15).

compensate for deficiencies in the former. There is an analogy here with the way in which males can exploit female sensory systems in mate choice²⁹. This sensory exploitation differs from the deception practised by aggressive mimics such as *Photurus* fireflies and *Bolas* spiders³⁰ which, respectively, mimic exactly the visual or chemical cues of their prey.

Theoretically, we would expect the cuckoo to demand a much higher provisioning rate than a brood of reed warblers, because it has no genetic stake in the future breeding success of the parents^{31,32}. However, far from being an irresistible narcotic lure¹⁴, the cuckoo chick apparently struggles to induce parents to feed it at the rate at which they would provision a brood of their own young. Rather than demanding a higher provisioning rate, the cuckoo instead exploits hosts by forcing them to provide care for longer (17 days in the nest plus 16 days after fledging, compared with 11 days in the nest plus 12 days after fledging for reed warbler young)³³. Parents can certainly be made to work much harder in the short term²⁵, so why don't cuckoos solicit a higher rate of provisioning? It has previously been argued that this would not benefit the cuckoo because it might exhaust hosts before the end of the cuckoo's dependent period²⁵. But the data shown here suggest another explanation. By evicting the reed warbler chicks from the nest at the start of its nestling life, the cuckoo gains the benefit of receiving all the food brought to the nest, but pays the cost of being solely responsible for dictating the rate at which it is provisioned. Constrained by its visual display of a single gape, the cuckoo may be unable to solicit a higher rate of feeding, perhaps because there is an upper limit to the rate at which calls can be produced or perceived.

Other species of brood parasite that are reared alongside the hosts' own young may show a different solution to the same problem. These species might suffer the cost of sibling competition for food at each nest visit^{34,35}, but at least they gain the benefit of assistance in soliciting a high visit rate. In short, the constraints of eliciting a high provisioning rate alone, or of losing food in sibling competition, may mean that we never see brood parasites being fed at the high rate we might predict. □

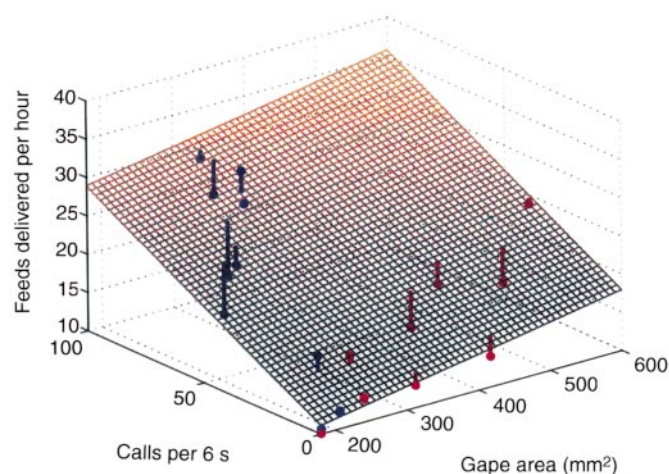


Figure 7 Comparison of predicted and observed provisioning rates. Predicted provisioning rates, derived from our experiments with reed warbler nestlings, are shown by the plane, which represents the regression equation: feeds delivered per hour = 0.0162 (gape area displayed (in mm²)) + 0.178 (calls per 6 s) + 8.23. Observed provisioning rates of cuckoo young are shown in blue, and of reed warbler broods in red. Each point represents mean gape area, number of calls per 6 s and feeds delivered per hour for chicks of different ages and/or broods of different sizes. Lines connect to points that lie above or below the plane. Cuckoos display a relatively small gape, but call at a relatively high rate, while the reverse is true for reed warbler broods. However, the provisioning rates of both fall close to the predicted plane, showing that reed warbler parents follow the same integration rule when feeding cuckoos and their own brood.

Methods

Measurement of nestling gape area, mass and call rate in the field. For all species, we used Vernier callipers to measure the distance between the proximal outer corners of the mouth flange to the nearest 0.05 mm (gape width), and the distance between the proximal corner and the tip (gape length) and calculated the product (gape area, assuming the usual fully open gape). For broods, total gape area displayed was the sum of the individual gapes. We found it impossible to handle cuckoo chicks older than day 11 and be certain that they would settle back in the nest. Therefore gape areas for cuckoo chicks on days 13 and 15 were estimated from the extrapolated polynomial regression of gape area on nestling weight, using published masses of common cuckoos in reed warbler nests at these ages³². We measured nestling mass in the field to the nearest 0.25 g using a 50 g Pesola spring balance, and in the laboratory to the nearest 0.005 g using a Sartorius electronic balance. We recorded the vocalizations emitted by unmanipulated cuckoos at different ages and reed warblers of different ages and in different brood sizes onto digital audiotape (DAT), using a Sony ECM-T6 tie-clip microphone attached to the side of the nest, and then recorded these calls onto a Macintosh computer. We scored the number of calls produced during the first 6 s of each nest visit (the shortest nest visit duration) using the sonograms produced by the application Canary 1.2.1.

Measurement of begging displays and food consumption in the laboratory. To standardize levels of food deprivation, we recorded the begging displays of chicks in the laboratory in June–July 1996–1998. Chicks were temporarily removed from the nest at a range of different ages (reed warblers day 2–8, cuckoos day 2–11) and in broods of one (reed warblers $n = 37$, cuckoos $n = 25$) or four ($n = 19$) chicks. They were kept warm⁵ and fed with Nectarblend rearing mix until they stopped begging. We considered this to be the moment of satiation. The broods of four chicks were induced to beg every 10 min for the next 110 min, and all chicks were induced to beg after 110 min. Repeated testing had no effect on begging behaviour^{5,17}. Begging was induced in the box apparatus described in ref. 5. Vocalizations were recorded as above. After begging at 110 min, we recorded how many small balls of Nectarblend all nestlings (except seven broods of four reed warblers) consumed until they stopped begging, and then returned them to their nests in the field. To standardize each test for comparison between species, we measured how many balls of food displaced 1 ml water.

Parental response to nestling visual and vocal signals. In June–July 1996–1998, we performed 111 treatments using 63 different pairs of parents when chicks were 6/7 days old. For each treatment we scored total feeds delivered per hour at the nest by both parents. Data were collected either by using a video camera ($n = 20$) or by observing the nest from a distance through binoculars ($n = 91$). Twenty-four pairs of parents, with brood sizes ranging from two to four chicks ($n = 10$ broods of 2; $n = 3$ broods of 3; $n = 11$ broods of 4) were each tested in three different treatments: playback of no vocalizations, playback of a single chick calling, and playback of four chicks calling. We rotated the sequence of testing between each pair of parents. Whether we used one randomly selected treatment per pair or the total number of treatments as independent data points, the outcome of our analysis was the same. Using each pair as a data point, there were significant independent effects of the number of gapes displayed ($t_{62} = 3.66$, $P = 0.0005$) and the number of chicks calling ($t_{62} = 4.36$, $P < 0.0001$) on parental provisioning rate.

Manipulation of brood size. We manipulated brood sizes so that they ranged from one to eight nestlings ($n = 59$). For broods of more than five chicks, old *Turdus* nests were placed over the top of the reed warbler nest and the enlarged brood was placed inside. Parents and chicks were given 1 h to adjust to the manipulation, which we have shown previously to be sufficient^{13,25}, and provisioning rate was measured for the next hour.

Playback manipulation. We broadcast the vocalizations of either a single reed warbler chick ($n = 28$) or a brood of four reed warblers ($n = 24$) through a speaker attached at the side of the nest at brood sizes ranging from two to five ($n = 52$). We played back recordings of 20 different single reed warbler chicks ($n = 14$ recorded in the laboratory, $n = 6$ recorded in the field) and 18 recordings of different broods of four reed warblers ($n = 8$ recorded in the laboratory, $n = 10$ recorded in the field). Details of playback technique and recordings of vocalizations are given elsewhere¹³.

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