



Differences in the nestling begging calls of hosts and host-races of the common cuckoo, *Cuculus canorus*

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We compared nestling begging calls of four hosts (reed warbler, *Acrocephalus scirpaceus*; great reed warbler, *A. arundinaceus*; dunnock, *Prunella modularis*; and meadow pipit, *Anthus pratensis*) and the respective host-races of the common cuckoo. Note structure varied between host species, but not between cuckoo host-races, so cuckoos did not vary their call note structure to match that of their hosts' chicks. Call rate increased with age, but there were marked differences between both host species and cuckoo host-races. Dunnock-cuckoos called more rapidly than reed warbler-cuckoos despite growing at the same rate. We suggest this difference reflects how cuckoos tune into the way these host species respond to begging signals from their own young, because dunnock chicks called much more rapidly than reed warbler chicks. Great reed warbler-cuckoos called at a lower rate than reed warbler-cuckoos when young, but at a greater rate when older than 8 days. This could also result from the cuckoo chicks tuning into differences in the way these hosts respond to begging signals. However, great reed warbler-cuckoos grew at a faster rate than the other cuckoo host-races, so they may also call faster to demand higher provisioning rates from this larger host. To test these hypotheses critically, data are needed on how the different host species integrate visual and vocal begging signals from their own broods. We discuss how differences in cuckoo begging might develop, given that cuckoo host-races are restricted to female cuckoo lineages.

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Brood parasites lay their eggs in the nests of other species, and the host adults rear the parasitic chick at a cost of losing all or some of their own brood. These costs to the host have led to the coevolution of sophisticated defences against parasitism by hosts, and subtle trickery by brood parasites to overcome such host defences (Rothstein 1990; Davies 2000). Brood parasites can be broadly divided into two categories: those that are reared alongside the host young ('nonevictors' e.g. cowbirds, *Molothrus* spp., *Vidua* finches and great spotted cuckoo, *Clamator glandarius*), and those in which the hatchling parasite either kills the host chicks or ejects the host eggs and chicks and is then reared alone ('evictors' e.g. *Chrysococcyx* and *Cuculus* cuckoos, including the common cuckoo).

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For the hosts of nonevictor brood parasites, Lotem (1993) showed that in theory it would pay the host adults to learn the characteristics of the chicks in their nest during their first brood, and to discriminate in future broods against chicks that differed from this learnt set. Hence these brood parasites would benefit from mimicry of the host chicks. As predicted, *Vidua* finch brood parasites show extraordinary mimicry of the mouth spot patterns of the chicks of their estrildid finch hosts, with which they are reared (Payne 1973; Nicolai 1974). Vocal mimicry of the host chicks' begging calls has been claimed for great spotted cuckoos, in which the frequency characteristics and note duration of begging calls are different for cuckoo chicks reared by magpies, *Pica pica*, and those reared by carrion crows, *Corvus corone*. In each case they apparently mimic the host chick's calls, which they probably learn (Redondo & Arias de Reyna 1988). Nonevictor brood parasites normally outcompete the host chicks by more vigorous begging (e.g. Redondo 1993; Soler et al. 1995; Lichtenstein & Sealy 1998; Lichtenstein 2001).

In contrast, for evictor parasites which are reared alone, Lotem (1993) predicted that the costs to hosts of

misimprinting on the parasite chick would select against their learning the characteristics of chicks. This is because if a host was parasitized in its first breeding attempt, it would imprint only on the parasite chick and would then reject all of its own offspring in future, unparasitized breeding attempts. These costs exceed the benefits of correct learning, and hence ejector parasites would not be expected to evolve mimicry of the appearance or begging calls of the host chicks. As expected, no examples of visual mimicry of host chicks have yet been described for evictor brood parasites (Davies & Brooke 1988; but see McLean & Waas 1987 and Payne & Payne 1998 for possible examples of vocal mimicry in New Zealand and Australian evictor cuckoos).

However, chicks of evictor brood parasites face different challenges, because they alone have to solicit adequate provisioning by the host adults. Experiments have shown that common cuckoo chicks manipulate their hosts not by visual cues, such as their large size or vivid gape colour, but by their extraordinarily rapid begging calls (Davies et al. 1998; Noble et al. 1999). Adult reed warblers, *Acrocephalus scirpaceus*, integrate information from both visual and vocal components of the begging display of their own chicks to determine how much food to bring to the nest (Kilner et al. 1999). Cuckoos tune into this communication system: they exaggerate their vocal display (calling rate) to compensate for their deficient visual display (gape area) compared with a brood of host chicks (Kilner & Davies 1999; Kilner et al. 1999).

Reed warblers are just one of some 15 favourite host species of the common cuckoo in Europe (Moksnes & Røskaft 1995). This raises the question of whether these hosts differ in their begging calls or in the way that they integrate visual and vocal begging signals from their own young. If so, cuckoo chicks might have to call at different rates to tune into different communication systems in the nests of different host species. However, differences in begging behaviour by cuckoos in different host nests do not necessarily imply that cuckoos must be tuning into different communication systems. Three hypotheses could explain such differences.

(1) Cuckoos adjust their development rate (the rate of functional maturation of tissues; Starck & Ricklefs 1998), and hence daily food requirements, in relation to the provisioning capabilities of their hosts. For the main hosts of the common cuckoo in Europe the modal brood size is four, and the nestling periods are similar (11–13 days), so it follows that larger hosts will bring more food per day to their own chicks, and so will have a greater capacity to provision a cuckoo chick than will smaller hosts. Therefore, this hypothesis predicts that, all else being equal, cuckoo chicks will beg less intensely at any given age when reared by a smaller host, to avoid the costs of begging for provisioning levels that the hosts are incapable of meeting. A further prediction is that as a consequence of developing at slower rates, cuckoo chicks reared by smaller hosts will take longer to fledge.

However, Kleven et al. (1999) found that cuckoos reared by reed warblers (a small host, 12 g) and by great reed warblers, *Acrocephalus arundinaceus* (a large host, 33 g), fledged after the same nestling period (18–19 days),

even though the former fledged at significantly lower mass than the latter (68 versus 88 g). This implies differences in growth (mass gain) but not development rates. Cuckoos reared by dunnocks, *Prunella modularis* (an intermediate-sized host, 21 g), also leave the nest at a similar age (18–21 days; Owen 1933). We therefore reject this hypothesis.

(2) Cuckoo development rate is fixed, but the rate of mass gain ('growth') may vary (as in most passerines; Starck & Ricklefs 1998). This hypothesis predicts the findings of Kleven et al. (1999), namely that cuckoos reared by small hosts should fledge at the same age, but at a lower mass, than those reared by large hosts. This could affect begging behaviour in two ways. (a) Cuckoo chicks may be programmed to gain mass at an average feasible rate across all their hosts. Therefore cuckoos reared by small hosts (poorer providers) will be hungrier on average, and hence they will beg more intensely, all else being equal. (b) Alternatively, cuckoo chicks may strategically adjust their demands (and hence begging behaviour) to maximize the rate at which they gain mass (within a fixed developmental time frame) given the provisioning capabilities of their hosts. This would be adaptive because postfledging survival correlates with fledging mass in a range of species (Magrath 1991). This makes the opposite prediction, namely that cuckoos should demand more, and hence beg more intensely, when reared by larger hosts. However, cuckoo chicks would not be expected to demand the entire food supply of the host brood from all hosts, because there are likely to be physiological upper limits to the amount of food that can be assimilated. If the brood food supply for a large host exceeds these limits, then it would not benefit a cuckoo chick to pay the high costs of soliciting such an excessive rate of food supply. The rate of mass gain of a great reed warbler brood greatly exceeds that of a great reed warbler-cuckoo (9.4 versus 5.7 g/day between days 4 and 9; T. Fuisz, unpublished data), which suggests that cuckoos do not exploit the full provisioning capabilities of this large host.

(3) Cuckoo chicks tune into the way that adults of their particular host species integrate visual and vocal begging signals, as described for reed warblers by Kilner et al. (1999). This hypothesis makes no assumptions about development rates, but predicts that at any given age, a cuckoo chick will beg at a rate that compensates for the degree to which its gape is a deficient visual signal compared with that of a host brood, controlling for the degree to which its needs compare to those of a host brood.

These hypotheses are not mutually exclusive: hypothesis 3 could apply in combination with hypothesis 2. The former suggests that cuckoo begging behaviour reflects the chick's demands expressed in the 'language' of its particular host species. Hypothesis 2 is concerned with the nature of these demands, which may be preprogrammed (2a) or flexibly adjusted (2b).

We tested these ideas by comparing the begging behaviour of four common hosts of the cuckoo in Europe: great reed warbler (33 g), dunnock (21 g), meadow pipit, *Anthus pratensis* (18 g), and reed warbler (12 g), and of the four host-races of cuckoos reared by these hosts.

METHODS

Study Sites

We located nests of reed warblers at Wicken Fen and along the adjacent Burwell and Reach Lodes, in Cambridgeshire, U.K. in the summers of 1996–2002, great reed warbler nests in the area of Bugyi, Apaj and Kiskunlacháza in north-central Hungary in spring 2000–2001, dunnoek nests in and around the University Botanic Garden in Cambridge in spring 2000–2001 (see Brooke et al. 1998; Moskát & Honza 2000; Davies 1992; respectively, for further details of study sites) and meadow pipit nests on Ardnamurchan peninsula, Scotland, U.K. in spring 2000 and at Cwm Onnan, near Crickhowell, Wales, U.K. in spring 2000–2001. Each of these four populations was occasionally parasitized by cuckoos, but for dunnocks we boosted our sample sizes by visiting nests located by ringers who responded to an advert we placed in the Ringer's Bulletin of the British Trust for Ornithology. These nests were at widely scattered sites in England between Sussex and Leicestershire. At most nests of all four species we weighed host or cuckoo chicks to the nearest 0.25 g using a Pesola balance. The age of chicks was defined as the number of days after hatching. In a few cases when this was not known with certainty, chick age was estimated from known developmental stages accurate to within 1 day.

Field Recordings

To record host broods and cuckoo chicks we used a Sony ECM-T6 tie-clip microphone attached ca. 10 cm from the nest cup, connected with a 5-m extension lead to a Sony WM-D6C Stereo Cassette-Corder (meadow pipits and dunnocks), a Sony TCD-D3 Digital Audio Tape-Corder (reed warblers), or a Sony PCM-M1 Digital Audio Tape-Corder (great reed warblers). Each nest was recorded for 45–90 min. As we could not standardize the distance of the microphone from the nest, we used a fixed tone producer (Maplins, Cambridge, U.K.) to compare the intensity of chick calls from different recordings made in 2000–2001 (see below). This was momentarily placed in the nest adjacent to the chicks' mouths and sounded twice at the beginning and end of each recording. We had previously determined that the tone produced was highly invariant in amplitude and frequency. To minimize pseudoreplication we recorded each nest at no more than two different ages. For hosts, we used recordings only at nests with modal brood sizes (four for each of the four hosts studied).

Laboratory Recordings

To investigate the effect of hunger on chick begging, we temporarily removed single chicks from their nest (under licence from English Nature and Scottish Natural Heritage) and transferred them to the laboratory. We tested 18 meadow pipit chicks (two each from nine nests), and 10 dunnoek chicks (two each from five nests). In the

laboratory we placed each chick into an old nest of its own species, housed in a plastic canary nest pan that was heated from below with an insulated thermos jug of hot water, and placed in a purpose-built wooden box (as described by Kilner & Davies 1998). In the box chicks were videotaped with a Sony CCD-TR840E Hi-8 video recorder and their calls were recorded with a Sony ECM-T6 microphone connected to a Sony WM-D6C tape recorder. We fed chicks to satiation (when they stopped begging) with small balls of Nectarblend rearing mix (produced by Haith's of Cleethorpes, U.K.). We induced chicks to beg at 10-min intervals for 110 min by gently tapping the side of the nest three times. For meadow pipit chicks we analysed responses only at 40, 80 and 110 min. At the end of the experiment we returned chicks to their original nests after no more than 150 min since removal. We checked nests a few days later, and recorded no desertions nor did we find any differences in survival or mass gain compared with nestmates. Our decision to deprive nestlings of food for 110 min after feeding to satiation was based on previous work, which showed that their begging levels did not exceed those recorded under natural levels of hunger in the field (Kilner & Davies 1998).

Sound Analysis

We downloaded recordings on to a Macintosh Power-Book G3 computer using the Canary 1.2.1 software and generated sonagrams using a wide-band filter setting (700 Hz) and a time resolution of 3 ms, with the clipping level set to -120 dB. From these sonagrams we counted the number of notes (defined as a peak on the sonagram trace) per 6 s. In older cuckoo chicks the notes become strung together and are difficult to distinguish by ear, but a clear transition from the separate notes of younger chicks can be seen on sonagrams. We therefore regard the rate of call notes as distinct from call note structure (the shape of the notes when plotted as frequency against time). We selected the first five clearly defined notes that did not overlap with other background noises, or with other notes (in the case of broods of host chicks), and measured maximum and minimum frequency, bandwidth (frequency range), peak frequency (frequency at maximum amplitude) and note duration. We took these measurements on the fundamental frequency, ignoring harmonics. We measured five notes for each of five begging bouts in response to parental feeds, generating 25 measurements for each parameter for each recording, from which we took the mean. To quantify the relative intensity of begging calls we measured the average intensity of the four tone playbacks for each recording (see above), and took the mean. We then measured the average intensity of each of 25 notes per recording (as above), and divided each value by the mean tone intensity for that recording. We took the inverse of this ratio to give a relative measure of intensity standardized to a common reference (the call:tone ratio) on a positive scale (louder calls have higher values).

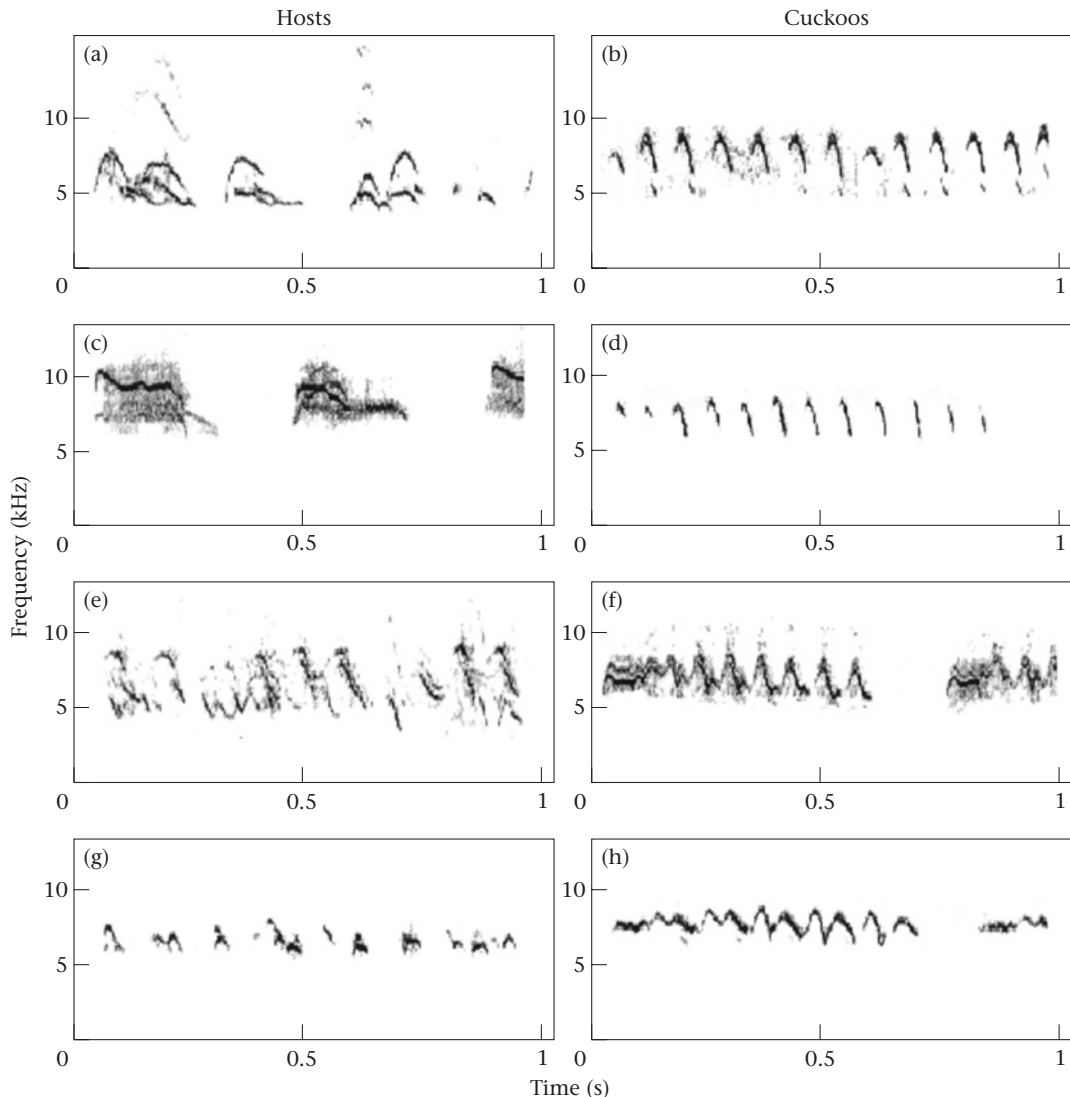


Figure 1. Sonograms of begging calls recorded in the field for 8-day-old chicks of broods of four (a) reed warblers, (c) great reed warblers, (e) dunnocks and (g) meadow pipits, and for 8-day-old cuckoo chicks reared by each of these hosts (b, d, f, h, respectively).

Statistical Analysis

For each host and cuckoo host-race we carried out separate regressions to determine the effects of age on various begging call parameters. Our previous work had identified call rate as a key variable in the begging displays of chicks that varied with chick demand and influenced provisioning by parents (Kilner et al. 1999). Therefore we used ANCOVAs to see whether the relation between call rate and age varied between hosts or cuckoo host-races. We then examined aspects of the structure of calls (frequency characteristics and duration) using MANCOVAs. As our sample sizes for relative intensity measures were considerably smaller, we compared this parameter in a separate ANCOVA test. For post hoc tests in ANCOVAs we used Scheffé's tests (Zar 1999) to determine significant differences between hosts or cuckoo host-races.

RESULTS

Variation with Age

Figure 1 shows typical sonograms of 8-day-old chicks for four host species and the four host races of cuckoos that parasitize them. The key change in begging calls with age was that older host and cuckoo chicks gave notes at a faster rate (Table 1). For host chicks the frequency of these notes also increased with age, and in at least two cuckoo host races this was also the case. For both hosts and cuckoos there was some evidence that the relative intensity of notes increased with age. Overall, the age-related changes in begging call parameters were similar for hosts and cuckoos (Table 1).

Variation with Hunger

We examined the begging calls of 10 single dunnock chicks, aged 3–4 days, at 10-min intervals for 110 min

Table 1. Regressions of seven begging call parameters against age for four hosts and four cuckoo host-races

	N	Rate	Frequency			Band-width	Note duration	Relative intensity
			Minimum	Maximum	Peak			
Brood of host chicks								
Reed warbler	31	↑	↑	—	—	—	↑	—
Great reed warbler	17	↑	↑	↑	↑	↓	—	↑
Dunnock	10	↑	↑	↑	↑	—	—	—
Meadow pipit	26	↑	↑	↑	↑	—	—	↑
Single cuckoo chick								
Reed warbler-cuckoo	32	↑	↑	—	—	↓	↑	↑
Great reed warbler-cuckoo	19	↑	↑	↑	↑	↓	—	↑
Dunnock-cuckoo	10	↑	—	—	—	—	—	—
Meadow pipit-cuckoo	8	↑	—	—	—	↓	↑	—

Parameters were measured from sonagrams made from field recordings of the begging calls of broods of four host chicks (the modal brood size for each of the hosts) and from single cuckoos. Arrows indicate the direction of significant results, which either increase with age (upward arrows) or decrease with age (downward arrows; $P < 0.007$ with Bonferroni corrections applied). Large arrows indicate $P < 0.001$, and small arrows indicate nonsignificant trends ($0.007 < P < 0.05$). Sample sizes differed from the figures given in the second column for rate (great reed warbler: 19; meadow pipit: 30; great reed warbler-cuckoo: 21; meadow pipit-cuckoo: 9) and for relative intensity (reed warbler: 11; dunnock: 5; reed warbler-cuckoo: 7; dunnock-cuckoo: 7; meadow pipit-cuckoo: 5).

after feeding to satiation. Hungrier chicks called at significantly higher rates (Friedman test: $\chi^2_5 = 37.10$, $P < 0.0001$), and this was not because satiated chicks did not beg at all (for 50–110 min after satiation, when all but one chick begged: $\chi^2_6 = 16.93$, $P < 0.01$). There were no significant differences in minimum, maximum and peak frequency, bandwidth, duration or intensity (50–110 min after satiation, Friedman tests: $1.55 < \chi^2 < 7.89$, $0.23 < P < 0.97$).

We analysed the begging calls of 18 meadow pipit chicks, aged 6–7 days, in a slightly different way, by comparing begging call rates at 40, 80 and 110 min after feeding them to satiation. Again we found that hungrier chicks called at significantly higher rates (Friedman test: $\chi^2_2 = 12.54$, $P = 0.002$). For the other call parameters too few individuals begged at 40 min after satiation to permit the same comparisons, but there were no differences between begging calls at 80 and 110 min after satiation for any other parameter (Wilcoxon tests: $-1.48 < Z < -0.06$, $0.13 < P < 0.96$). Call rate also increases with hunger for reed warblers and reed warbler-cuckoos (Kilner & Davies 1999).

Differences Between Host Species

The relation between the calling rate of a brood ($N = 4$ chicks in each case) and age was significantly different for the four hosts (ANCOVA: $F_{3,82} = 20.25$, $P < 0.0001$; Fig. 2), with dunnock broods calling at the highest rate followed by meadow pipit, reed warbler and great reed warbler broods. All pairwise comparisons of slopes were significant ($P < 0.05$) using Scheffé's tests, apart from reed warbler versus great reed warbler.

A comparison of the relation of five other call parameters (maximum, minimum and peak frequencies, bandwidth and note duration) with age revealed a significant difference between species overall (MANCOVA:

Roy's greatest root = 0.795, $F_{5,74} = 11.76$, $P < 0.0001$). There were significant effects of species on minimum frequency ($F_{3,76} = 11.86$, $P < 0.0001$), maximum frequency ($F_{3,76} = 3.84$, $P = 0.013$), peak frequency ($F_{3,76} = 3.23$, $P = 0.027$) and bandwidth ($F_{3,76} = 8.97$, $P < 0.0001$). For minimum frequency, the relation was steepest for great reed warbler broods, followed by meadow pipit, reed warbler and dunnock broods (Fig. 3), with a similar pattern for the other frequency parameters. There was no

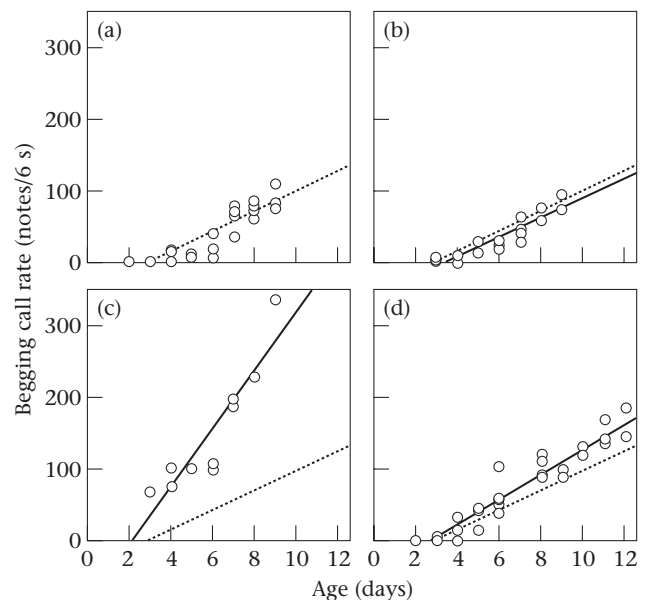


Figure 2. Begging call rate against age for broods of four (a) reed warblers ($N = 31$), (b) great reed warblers ($N = 19$), (c) dunnocks ($N = 10$) and (d) meadow pipits ($N = 30$). Dotted lines in each case show the linear regression for reed warblers for comparison. Rates were measured from sonagrams derived from field recordings.

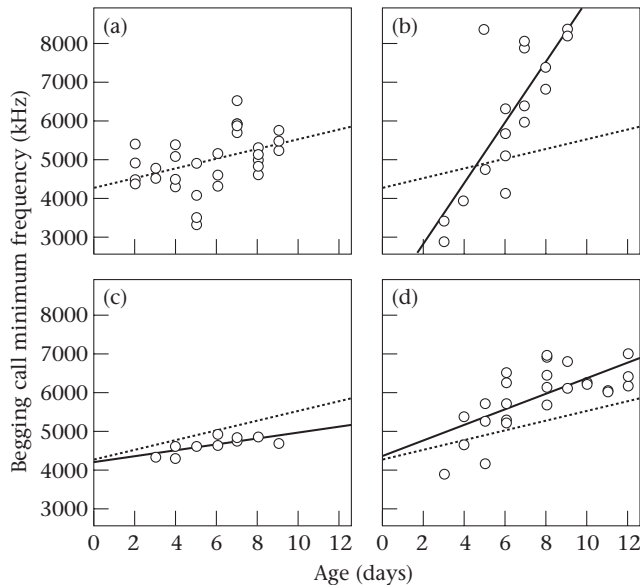


Figure 3. Minimum frequency of begging call notes against age for broods of four (a) reed warblers ($N=31$), (b) great reed warblers ($N=17$), (c) dunnocks ($N=10$) and (d) meadow pipits ($N=26$). Dotted lines in each case show the linear regression for reed warblers for comparison. Minimum frequencies were measured from sonagrams derived from field recordings.

significant effect of species on the relation between relative intensity of calls and age (ANCOVA: $F_{3,51}=2.44$, $P=0.075$, power=0.57).

Differences Between Cuckoo Host-races

The relation between calling rate and age was significantly different for the four cuckoo host-races (ANCOVA: $F_{3,64}=7.10$, $P=0.0003$; Fig. 4). It was steepest for great reed warbler-cuckoo, followed by meadow pipit-cuckoo, dunnock-cuckoo and reed warbler-cuckoo. All pairwise comparisons of slopes were significant ($P<0.05$) using Scheffé's tests, apart from dunnock-cuckoo versus reed warbler-cuckoo. The relation for these two differed significantly in elevation, with dunnock-cuckoos calling more rapidly than reed warbler-cuckoos (Scheffé's test: $S_{1,42}=3.488$, $P<0.005$).

Although Fig. 1 appears to suggest that there may also be differences between cuckoo host-races in the structure of call notes, a comparison of the relation of five call parameters (maximum, minimum and peak frequencies, bandwidth and note duration) with age revealed no significant difference between host-races (MANCOVA: Roy's greatest root=0.16, $F_{5,59}=1.92$, $P=0.09$). Furthermore, there was no effect of host-race on the relation between relative intensity of calls and age (ANCOVA: $F_{3,30}=2.20$, $P=0.11$).

To summarize, rate appears to be the most important begging call parameter that varies with age, hunger, host species and cuckoo host-race. Next we tested whether cuckoos grew at different rates in the nests of different host species, and whether this could explain the differences we found between cuckoo host-races in the relation between call rate and age.

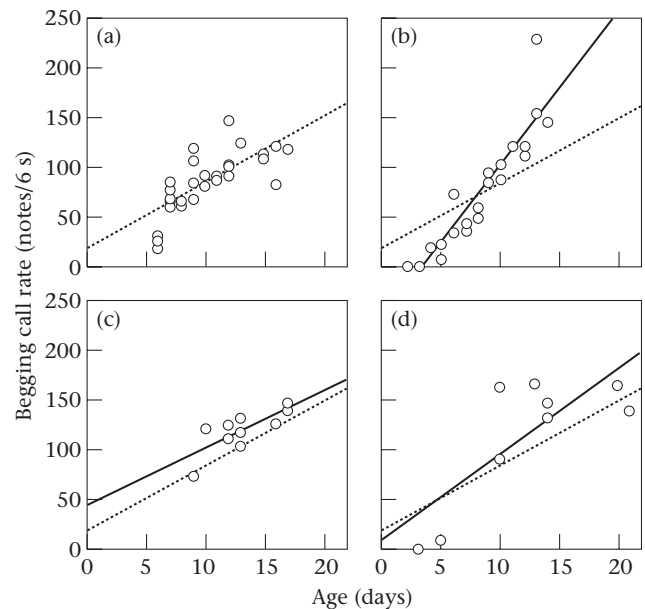


Figure 4. Begging call rate against age for (a) reed warbler-cuckoos ($N=32$), (b) great reed warbler-cuckoos ($N=21$), (c) dunnock-cuckoos ($N=10$) and (d) meadow pipit-cuckoos ($N=9$). Dotted lines in each case show the linear regression for reed warbler-cuckoos for comparison. Rates were measured from sonagrams derived from field recordings.

Cuckoo Growth Rates

We found significant differences between the growth (rate of mass increase with age) of reed warbler-cuckoos, great reed warbler-cuckoos and dunnock-cuckoos (ANCOVA: $F_{2,73}=17.83$, $P<0.0001$; there were too few data to include meadow pipit-cuckoos in the analysis). This difference may have arisen because we had a wider range of ages of reed warbler-cuckoos (0–16 days) than great reed warbler-cuckoos (4–12 days) or dunnock-cuckoos (3–13 days), and the data points from older and younger chicks fell on the flatter parts of the sigmoid growth curve. However, the result was still significant when we balanced the age range of the samples (data from chicks aged 3–13 days: $F_{2,56}=8.59$, $P=0.0006$; Fig. 5). The difference was due to great reed warbler-cuckoos having a significantly steeper relation than reed warbler-cuckoos ($F_{1,49}=19.04$, $P<0.0001$). There was no difference between the growth rates of reed warbler and dunnock-cuckoos ($F_{1,36}=2.55$, $P=0.18$, power=0.33).

Cuckoo Growth Rates and Begging Calls

Because great reed warbler-cuckoos grew at a faster rate than reed warbler-cuckoos and dunnock-cuckoos, the differences we found between their begging calls may simply have resulted from mass differences. Therefore we repeated our comparisons of call parameters, but entered mass as a covariate in the model in addition to age. For cuckoo recordings where the cuckoo mass was not known, we predicted masses from logistic growth curves fitted to the raw mass data (reed warbler-cuckoos: $Y = -11.45 + 97.6 / (1 + \exp(-0.233(X - 7.63)))$;

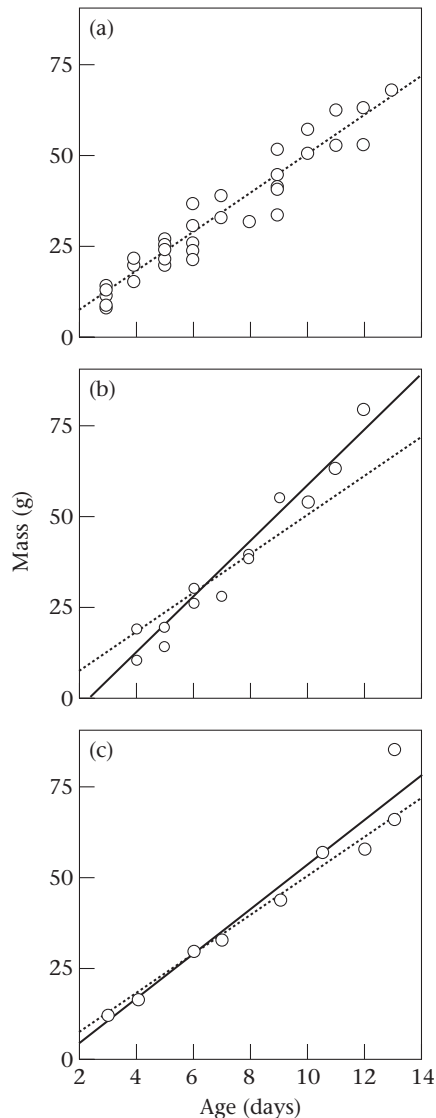


Figure 5. Growth rates for (a) reed warbler-cuckoos ($N=40$ measurements from 35 individuals), (b) great reed warbler-cuckoos ($N=13$ measurements from 7 individuals) and (c) dunnock-cuckoos ($N=9$ measurements from 7 individuals) aged 3–13 days. Each individual contributed no more than two data points. Dotted lines in each case show the linear regression for reed warbler-cuckoos for comparison.

great reed warbler-cuckoos: $Y = -90.51 + 10.051 / (1 + \exp(-0.0597(X - 80.5)))$; dunnock-cuckoos ($Y = -162.6 + 21600 / (1 + \exp(-0.030(X - 161.5)))$). There were inadequate data for masses of meadow pipit-cuckoo chicks to generate a logistic growth curve, so they were excluded from the following analyses.

The differences between cuckoo host-races in call rates remained significant when age and mass were both entered as covariates in the model (ANCOVA: $F_{2,57}=5.77$, $P=0.006$). Hence the relation we found for call rate against age (with great reed warblers showing the steepest relation) cannot simply be explained by differences in the masses of cuckoo chicks of the same age reared by different hosts.

A comparison of the relation of five other call parameters (maximum, minimum and peak frequencies, bandwidth and note duration) with mass and age as covariates revealed no significant difference between species (MANCOVA: Roy's greatest root=0.142, $F_{5,46}=1.75$, $P=0.14$). However, for relative intensity, there was a significant effect of species (ANCOVA: $F_{2,21}=5.63$, $P=0.011$).

DISCUSSION

Begging Call Note Structure

The structure of the begging call notes produced by chicks of the four cuckoo host-races did not differ: there were no significant differences in minimum, maximum and peak frequency, bandwidth, duration and intensity, despite differences between the host species in all four frequency parameters. This is not surprising given that the costs of misimprinting select against hosts of evictor cuckoos learning chick characteristics, so there is no selection for evolution of visual or vocal mimicry by the parasite chick (Lotem 1993).

Among North American wood warblers (Parulidae), Haskell (1999) found that ground-nesting species (whose nests are more vulnerable to predators) had begging calls with higher frequencies (which render them less locatable by predators). Briskie et al. (1999) found that species subject to greater nest predation also had higher-frequency begging calls, and these were of lower intensity. Therefore it might be expected that meadow pipits, which nest on the ground and are therefore more vulnerable to predation, should have higher-pitched and lower-intensity begging calls than the other three host species, which all nest above the ground. However, for chicks older than 5–6 days, meadow pipit chicks called at significantly lower frequencies than great reed warbler chicks, and at higher intensities than dunnock or reed warbler chicks (although these differences were not significant). This suggests that selection on begging calls to reduce locatability to predators is not the only factor influencing their acoustic structure and intensity.

Various frequency characteristics of begging calls increased with age for most hosts and cuckoo races. This is perhaps surprising given that adult body size is positively correlated with the mass of song-producing structures (Morton 1975; Ryan & Brenowitz 1985): smaller adult birds produce higher-pitched vocalizations both within (e.g. Schubert 1976) and between species (e.g. Wiley 1991; Badyaev & Leaf 1997). However, in humans at least, fundamental frequency is positively correlated with vocal effort and hence intensity (Lienard & Di Benedetto 1999). For those hosts and host-races for which we had adequate sample sizes, relative intensity increased with chick age, so the increase in call frequency with age may simply be because older chicks gave louder calls.

Differences Between Cuckoo Host-races

We found that begging calls of cuckoo host-races and hosts varied with age, hunger and species/host-race, with

call rate being the key parameter that varied. Older and hungrier chicks called at faster rates. Host species differed in calling rate (with dunnocks calling fastest, followed by meadow pipit, reed warbler and great reed warbler). Cuckoo races also differed in call rates (with the relation with age being steepest for great reed warbler-cuckoos, followed by meadow pipit-cuckoo, dunnock-cuckoo and reed warbler-cuckoo). Given that experimental work has shown that host adults attend to begging call rate (Kilner et al. 1999), it is perhaps not surprising that the key differences we found between the begging of cuckoo host-races were differences in calling rate. However, the explanation for the size and direction of these differences is more difficult to elucidate. We return to the hypotheses suggested in the Introduction, of which we have already rejected hypothesis 1.

Hypothesis 2a suggests that cuckoo development rate is fixed, so cuckoo chicks will be hungrier and hence call at a higher rate at any given age in nests of smaller hosts, which provision the cuckoo less well. The finding that both dunnock-cuckoos and meadow pipit-cuckoos (>6 days) called at higher rates than reed warbler-cuckoos despite being reared by larger hosts (21, 18 and 12 g, respectively) is strong evidence against this hypothesis.

Hypothesis 2b suggests that cuckoo development is fixed, but cuckoos strategically adjust their demands and hence their begging behaviour in relation to the provisioning capabilities of their hosts. This predicts that cuckoo chicks call at higher rates and gain mass faster when reared by larger hosts. The result that older great reed warbler-cuckoos (>8 days) called at higher rates than reed warbler-cuckoos, and that great reed warbler-cuckoos gained mass at faster rates is consistent with this hypothesis. However, the hypothesis cannot explain why dunnock-cuckoos called more rapidly than reed warbler-cuckoos, despite growing at the same rate.

Hypothesis 3 proposes that a cuckoo chick tunes in to the way that host adults integrate visual and vocal begging signals, and begs at a rate that compensates for the degree to which its gape is a deficient visual signal, controlling for the degree to which its needs are comparable to those of a host brood. The finding that dunnock-cuckoos called at higher rates than reed warbler-cuckoos, but grew at the same rates, could be explained by this hypothesis, given that dunnock broods called more rapidly than reed warbler broods.

Therefore we favour a combination of hypotheses 2b and 3. However, three factors make it difficult to derive predictions about the precise rate at which cuckoo chicks should beg in the nests of different host species. First, cuckoos reared by different hosts have to elicit varying proportions of the normal feeding rate to a host brood, because hosts vary in size. For example, a 6-day-old cuckoo chick weighs the equivalent of 3.6 reed warbler chicks, 2.5 dunnock chicks, 2.1 meadow pipit chicks and 1.7 great reed warbler chicks of the same age. Hence a great reed warbler-cuckoo will require a much smaller proportion of the host brood requirements at any given age than a reed warbler-cuckoo chick. Second, we have shown that cuckoos grow at different rates with different hosts, so their food demands at a particular age will vary

according to host species. Third, hosts may differ in the way they integrate calling and gaping to determine provisioning rates. For example, dunnock chicks call at significantly higher rates than the other hosts, perhaps because they are less constrained by kin selection, as they are less related on average to their nestmates, owing to their polyandrous mating system (Davies 1992; Briskie et al. 1994). To avoid being exploited by their more selfish chicks, dunnock parents may have evolved a reduced sensitivity to calling rate in their assessments of begging displays. These three factors mean that it is possible to predict how cuckoos should beg in nests of different host species only by determining growth rates of cuckoos and host broods, and by carrying out an experimental determination of provisioning rules as Kilner et al. (1999) did for reed warblers and reed warbler-cuckoos.

In the absence of such data we can only qualitatively compare begging call rates for the four cuckoo host-races. In summary, the finding that dunnock-cuckoos called at higher rates than reed warbler-cuckoos, despite similar growth rates, is probably because cuckoo chicks tune into the way that their host species integrate visual and vocal begging signals. The steeper and overlapping relation between call rate and age for great reed warbler-cuckoos than for reed warbler-cuckoos may also be explained by this hypothesis. Older great reed warbler-cuckoos may call faster than reed warbler-cuckoos to exploit the greater provisioning capacity of their larger hosts.

Development of Cuckoo Begging

Host-races of the common cuckoo are restricted to female cuckoo lineages, with cross-mating by males maintaining the cuckoo as one species (Marchetti et al. 1998; Gibbs et al. 2000). Therefore it has been suggested that the distinctive egg types laid by each host-race (which usually match the eggs of their respective hosts) are under maternal genetic control; otherwise cross-mating by male cuckoos would disrupt host-egg mimicry. However, this mechanism of genetic control cannot explain host-race differences in begging calls, because then only daughter cuckoos would beg differently in the nests of different host species.

The differences could be mediated by female control of hormone levels in the egg yolk (Schwabl 1993). For example female dunnock-cuckoos could put more testosterone into their eggs, which could cause their offspring to beg more rapidly than those of reed warbler-cuckoos. However, Kleven et al. (1999) transferred 1-day-old great reed warbler-cuckoos to reed warbler nests and found that they grew at the same rate as reed warbler-cuckoos in reed warbler nests. Similarly, reed warbler-cuckoos transferred to great reed warbler nests grew at the same rate as great reed warbler-cuckoos. Assuming that the equal growth rates of both types of cuckoos when reared by the same host species are a result of similar begging behaviour (not measured by Kleven et al. 1999), then differences between the host-races cannot be a result of maternal hormone levels in the eggs.

Instead, differences between cuckoo host-races in begging behaviour are most likely to arise through a learning mechanism. Cuckoo chicks cannot learn from the host chicks, of course, as these are ejected before or shortly after they hatch by the young cuckoo chick. However, begging behaviour may be modified through a trial and error process in response to provisioning by the host adults.

Evidence that nestlings can indeed learn to beg differently is provided by great spotted cuckoos in which the chicks mimic the begging calls of the different host species' chicks with which they are reared (Redondo & Arias de Reyna 1988). Another example is provided by Major Mitchell cockatoos, *Cacatua leadbeateri*, which sometimes take over galah, *Cacatua roseicapilla*, nest holes, but fail to remove the galah's eggs before laying their own. The fostered galah chicks give galah begging calls immediately after hatching, but quickly learn to give those of the host species (Rowley & Chapman 1986, 1991; Bradbury & Vehrencamp 1998). In both cases it is not known whether the chicks learn to call appropriately by mimicking their nestmates or through positive feedback from parental responses. A mechanism of learning by trial and error and responding to positive feedback has been described for brown-headed cowbirds, *Molothrus ater*, in which naïve yearling males tend to repeat song types to which a female gives a visual response (West & King 1988). For cuckoo chicks, adjusting the rate at which notes were repeated in the begging call in response to provisioning behaviour by the host adults would be an even simpler developmental task.

Kedar et al. (2000) claimed to show that house sparrow, *Passer domesticus*, chicks learned within a few hours to adjust their begging displays to suit the likelihood of receiving food. Evidence of an environmental influence on calling behaviour during begging comes from an experiment by Kölliker et al. (2000). They cross-fostered great tit, *Parus major*, chicks so that half of each brood came from a foreign nest, and found that a common rearing environment could explain some of the variation in the energy flux density of nestling begging calls. Chicks therefore seem capable of modifying their calling behaviour in response to parental provisioning. We predict that if cuckoos were cross-fostered between host species, the cuckoo chicks could flexibly modify their calling in the nest to suit the host that provisioned them.

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