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Vocal mimicry of hosts by Great Spotted Cuckoo *Clamator glandarius*: further evidence

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Great Spotted Cuckoo nestlings were shown, after some days in the nest, to have begging calls that differed depending on whether they were being reared by Magpies or Carrion Crows. They also produced calls of a pitch and repetition rate that implied a high level of hunger.

The fact that parent–offspring interactions in altricial species of birds rely on relatively species-specific communication signals creates a selective pressure for brood parasites to evolve mimetic behaviour in order to prevent eviction or abandonment by adult hosts. A high degree of mimicry has been achieved by parasitic grassfinches (Viduinae), which mimic not only visual and acoustic design features of their host's nestlings but also their adult song (Nicolai 1974).

Over the last 20 years, the possibility of vocal resemblance between the young parasite and their hosts' calls has been suggested for at least 11 species of parasitic cuckoos (Courtney 1967, Steyn 1973, Payne 1977, Gill 1982). In most cases, similarity between calls has been judged by merely auditory means, only two papers (Mundy 1973, Morton & Farabaugh 1979) containing sonagraphic evidence. In some instances, the model seems not to be a begging call but an adult (O'Connor 1962, Mundy 1973, see below) or a fledgling (Morton and Farabaugh 1979) contact call. The most complete paper on the subject is that of Mundy (1973) on the Great Spotted Cuckoo *Clamator glandarius* and Striped Crested Cuckoo *C. levaillantii* mimicking, respectively, the nestling begging call and an adult call of their hosts. Both cases refer to only one individual, so intra-species comparison is not possible. All this reveals a marked scarcity of evidence about vocal mimicry of their hosts by parasitic cuckoos.

In this paper, we contribute additional evidence that shows clearly that the nestling begging calls of the Great Spotted Cuckoo are of a different structure when raised by its two main host species in Southern Europe: the Magpie *Pica pica* and the Carrion Crow *Corvus corone*.

Vocalizations

During the 1985 breeding season, we studied Great Spotted Cuckoo parasitism of Magpies and Carrion Crows in Granada (37° 14′ N, 3° 9′ W), Southern Spain, and recorded the begging calls of nestlings. Chicks were induced to beg by auditory or mechanical stimulation. Older cuckoos showed shyness towards humans at first sight but we could make them beg from us willingly after a short period (less than half an

hour) of food-deprivation. Calls were recorded on a Uher 4200 Report Monitor tape recorder through a condenser microphone AKG 568 EB, at 9·5 cm/s speed. Recordings were analysed in a KAI Voice Identification Inc. 700 sound spectrograph using the wide (300 Hz) band filter.

Begging bouts of the Great Spotted Cuckoo chicks were much longer than those of their hosts. Magpie nestlings, when stimulated, emitted a few (2–4) calls and then became silent. Carrion Crow nestlings could utter a higher number of calls (6–9) in series with a mean inter-call interval of 0·31 s. By contrast, hand-fed cuckoos kept on begging until food was delivered to them, holding a continuous, quavering call for as long as 20 s.

Figure 1 shows fragments of begging calls from different individuals of Great Spotted Cuckoo reared by one of the two host species, some days before fledging. At this time, the cuckoos' calls were a long-lasting succession of elements whose

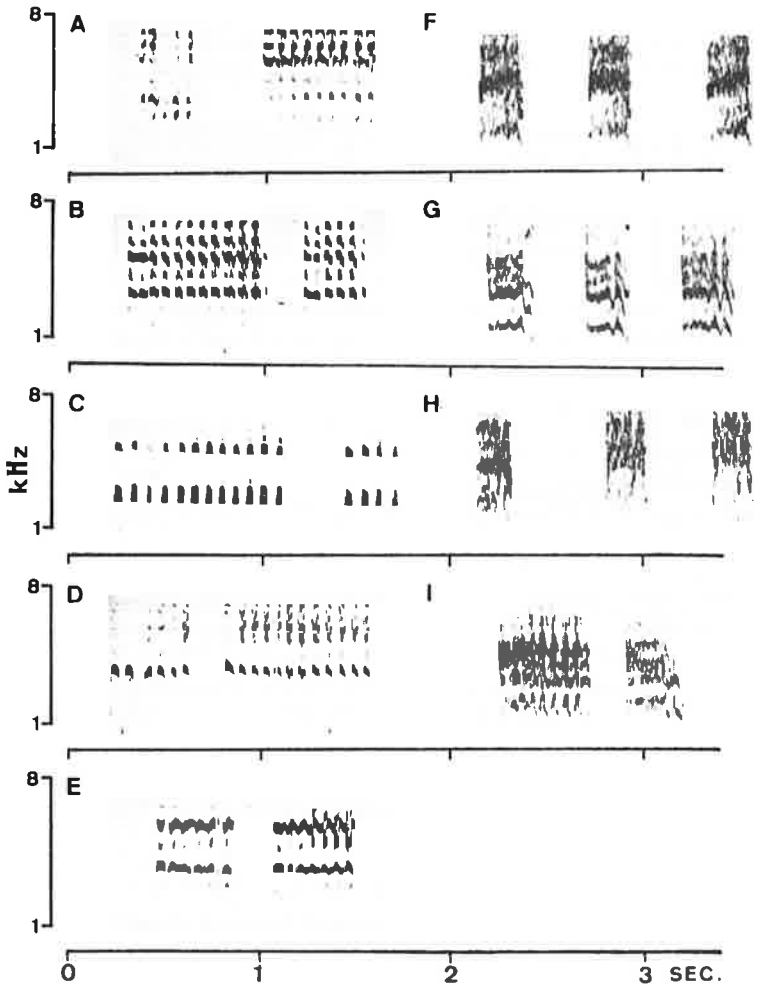

Figure 1. Fragments of begging calls of different Great Spotted Cuckoo individuals several days before fledging (15–20 days old). A–E: cuckoos raised by Magpies. F–H: cuckoos raised by Carrion Crows. I: cuckoo raised by Carrion Crows, 11 days old.

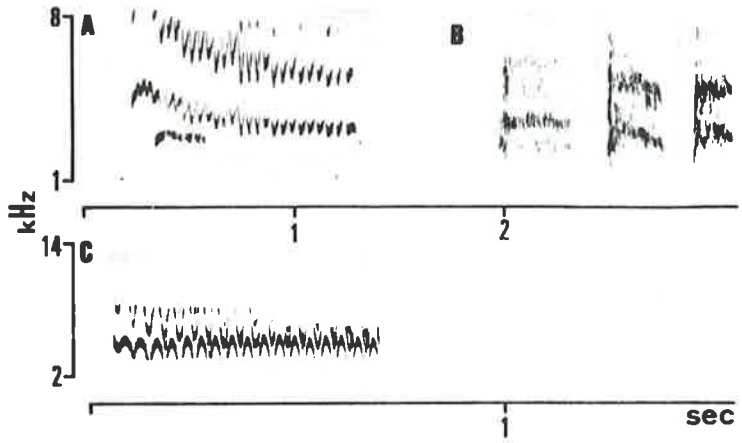

Figure 2. Begging calls of hosts. A: call of a Magpie nestling, 10 days old. B: three calls of Carrion Crow nestlings, 15 days old. C: call of a Magpie nestling, 15 days old, at half speed.

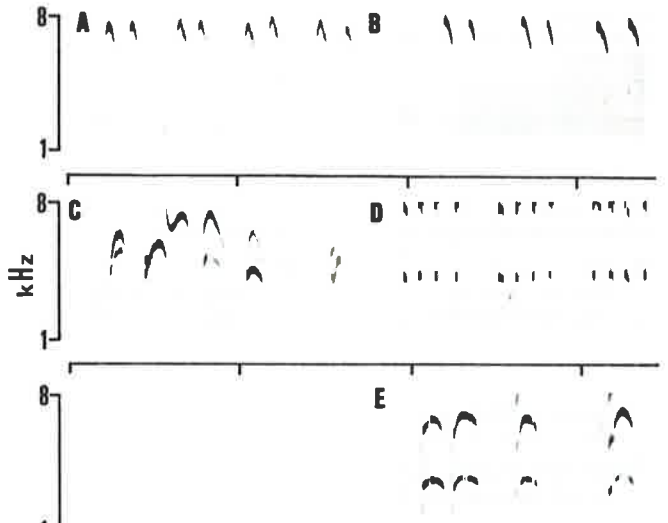

Figure 3. Early begging calls of parasites and hosts. A,B: fragments of Great Spotted Cuckoo (3–4 days old) calls (A: raised by Magpies; B: raised by Carrion Crows). C: six calls of Magpie nestlings, 2 days old. D: fragment of a call of a Great Spotted Cuckoo raised by Carrion Crows, 7 days old. E: four calls of Carrion Crow nestlings, 3 days old.

structure differed depending on which species fostered them. Elements of calls uttered by chicks reared in a Magpie nest were of greater duration and narrower frequency range than those of chicks coming from a Carrion Crow nest. The same general differences appeared when comparing the begging calls of almost fully-grown nestlings of the hosts (Fig. 2). Calls of Magpie nestlings were tonal, frequency-modulated signals lasting, on average, $0{\cdot}53 \pm 0{\cdot}33$ (s.d.) s ($n = 34$). Energy

was concentrated in several bands, harmonically related, whose intense frequency modulation resulted in series of brief segments of harsh quality. The frequency of the fundamental band ranges between 1·5 and 5 kHz. On the other hand, calls of nestling Carrion Crows tended to be shorter (0·28 ± 0·11 s, $n = 34$), harsh structures ranging from 2 to 4 kHz. Calls of cuckoos raised by Magpies had elements with a duration (0·59 ± 0·28 s, $n = 13$), significantly greater than those of calls from cuckoos reared by Carrion Crows (0·34 ± 0·14 s, $n = 13$) (Two-tailed Student's t-test, $t = 2·78$, d.f. = 24, $P < 0·05$). Conversely, differences in duration between elements of cuckoo calls and calls of their hosts did not differ significantly for the Magpie ($t = 0·64$, d.f. = 45, n.s.) nor for the Carrion Crow ($t = 1·65$, d.f. = 45, n.s.).

Calls of very young cuckoos did not match those of host nestlings of a similar age (Fig. 3). They consisted of a long sequence of very brief elements almost uniformly distributed in time which were rearranged in older nestlings' calls to give them their characteristic structure. Typically, calls of cuckoos were higher-pitched than calls of hosts of a similar weight.

Discussion

Structural similarities between calls of parasites and hosts of a given species do not affect the duration of a bout of elements, which is longer in cuckoos. Rather, development implies that cuckoos change the temporal patterning of individual call elements to clump them into clusters of a similar duration to that of a single host call. These new elements also become affected in their distribution of energy along the frequency range, matching that of the hosts' calls.

Begging calls of Cuckoo *Cuculus canorus* nestlings consist of a long series of brief, repetitive elements (Glutz & Bauer, in Cramp & Simmons 1985). Persistent calls may be the result of selective pressures acting on young parasites to induce adult hosts to collect food for them at a high rate (as in the Cuckoo) or to compete advantageously with their nest-mates (as in the Great Spotted Cuckoo and other non-evicting species). Chicks of Yellow-billed Cuckoo *Coccyzus americanus*, a non-parasitic member of the Cuculinae, beg for food silently (Potter 1980), so extremely long begging calls seem to be an adaptation to parasitism rather than a characteristic of the group.

Another feature of parasites' calls which would enhance their effectiveness as feeding releasers is their high frequency. Both traits, frequency of the call and rate of emission, positively correlate with the chick's level of hunger in some species studied (Collias 1952, Hartby 1969, Chamberlain & Cornwell 1971, Morton 1977, O'Brien & Dow 1979). In this sense, repetitive, high-pitched calls may be considered to be deceptively mimicking the call of a very hungry nestling.

The tendency of parasites to evolve super-stimulant calls may be constrained by the degree in which species-specific parameters in a call are needed for it to trigger appropriate responses in the adult host. Great Spotted Cuckoo nestlings seem to have overcome such a constraint by reorganizing individual elements of their long call into clusters which resemble host nestling calls in time and energy distribution patterning, but of a higher pitch and repetition rate, thus mimicking the structure of individual host begging calls while maintaining the deception of a high level of hunger.

Courtney (1967), when considering the causal implications of host–parasite vocal resemblance, emphasized the role of imitation by learning for those species of cuckoo which are raised with their host's chicks. Mundy (1973) suggested that, since parasites often hatch before the host nestlings, they could begin by imitating the

'food-arrival' call of the adult. Our results suggest that this probably does not occur. Begging calls of newly-hatched birds are simpler structures than those of older nestlings and are very similar throughout a wide range of species (Korbut 1982), probably as a result of the immature state of voice production mechanisms. Perhaps adult host discrimination at these stages is not enough for it to create a selective pressure against non-mimetic calls of the parasite. Unfortunately, we could not perform cross-fostering experiments in order to determine whether learning was actually involved, as the breeding seasons of Carrion Crow and Magpie only slightly overlap in our study area. Nevertheless, sonagrams seem to indicate that vocal mimicry of hosts' calls is achieved as a consequence of experience. The most dissimilar call within cuckoos reared in Carrion Crow nests is that of the youngest individual (Fig. 1 I). Host nestlings in Magpie nests eventually starve, only the cuckoos fledging at the end. This fact may account for the greater variability and less striking resemblance between the calls observed in these two species.

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