

## Attractive non-mimetic stimuli in Cuckoo *Cuculus canorus* eggs

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Although the Cuckoo *Cuculus canorus* parasitizes various species of passerine birds, as a species it apparently comprises many races or gentes (Baker 1942, Moksnes & Røskoft 1995), the females of each gens favouring just one host species and laying eggs of constant type. Cuckoo hosts have developed rejection of unlike eggs (Davies & Brooke 1989, Brown *et al.* 1990, Moksnes *et al.* 1990). This in turn has resulted in mimicry in the eggs laid by the Cuckoo; these match, more or less accurately, those of their particular hosts (Ali 1931, Brooke & Davies 1988).

Apart from the acceptance of model eggs of their own gens of Cuckoo and the rejection of models of other gentes, with some exception (Brooke & Davies 1988, Davies & Brooke 1988), and the great effect on acceptance of the suitability of the passerine species as hosts (Davies & Brooke 1989, Moksnes *et al.* 1990), no attempt has been made to test the response of hosts to the different stimuli present in the Cuckoo egg.

The fact that Cuckoo eggs do not always mimic the host's egg very closely and are still accepted by the host (Brooke & Davies 1988, Moksnes & Røskoft 1989, Bricambaut 1993) suggests that a copy of the host's egg in every detail may not always result from the evolutionary process leading to acceptance of the parasite's eggs by the hosts.

On the other hand, certain colour features not found in the eggs of another species of Cuckoo, the Great Spotted Cuckoo *Clamator glandarius* (egg coloured plain white or white background with black dots), were found to be more effective than the colour stimuli present in natural Great Spotted Cuckoo eggs; such features released acceptance and incubation by the host (Magpie *Pica pica*; Alvarez *et al.* 1976). This result would suggest a preference more for contrast than for any definite colours of the eggs.

If preference for certain visual stimuli by the host were the main selective force in the process of attaining egg acceptance and if hosts favoured certain unnatural stimuli, then the result of selection (the parasite's egg) would not be exact copies of the host's eggs, but the one producing the highest acceptance.

The Rufous Bush Chat *Cercotrichas galactotes* is regularly parasitized (27%) by the Cuckoo in southern Spain. Here several mechanisms of co-evolution between the two species have been demonstrated (Alvarez 1993, 1994a, 1994b, 1994c, 1996), among them Cuckoo egg rejection (47% of nests naturally parasitized and 61% of those artificially parasitized when the Cuckoos were present in the area) and egg-mimicry.

Although 30% of Cuckoo and Rufous Bush Chat eggs are very similar in background colour, the Cuckoo egg can be readily distinguished by the human observer; it has darker and fewer spots, which give it a paler and more contrasted appearance. Since this colour pattern would suggest an adaptation in the Cuckoo egg not based on mimicry but on response by the host to favoured stimuli, I have tried to isolate some of the factors by testing the response of Rufous Bush Chats to pale and contrasted egg models.

### MATERIAL AND METHODS

The experiment was carried out in a lowland area in southern Spain during the breeding seasons of 1995–97 and during the period when the Cuckoos are present in the area (from the beginning of May to the middle of July).

The study plot (1226 ha) is an agricultural vineyard area, with small patches dedicated to kitchen gardens, vegetable growing, interspersed with densely growing fruit trees, greenhouses and few remnants of the natural vegetation (cork oaks, grasses, forbs and reeds).

The number of female Cuckoos in the study area was probably more than ten and the density of Rufous Bush Chat breeding pairs was about one pair per 2 ha.

To determine the Rufous Bush Chat response to oological characteristics, one of the host's eggs was replaced with a model egg in the afternoon during egg-laying (with at least two eggs in the nest) or in the first 2 days of incubation. Each nest received only one egg model. The state of the nest was subsequently recorded on the first day and then every second day (in total for at least five days). The introduced model egg was considered to have been accepted if it remained in the nest being incubated with the rest of the clutch and was considered to have been rejected if the birds abandoned their nest, damaged the model egg or ejected it from the nest.

Model eggs were of the same size (23 mm × 17 mm), shape and weight (3.3 g) as natural Cuckoo eggs. They were made of silicone, with a thin layer of plaster covered with acrylic paint and coated with varnish to obtain a glossy surface similar to that of natural eggs.

Of the total number of model eggs tested, 20 were 'perfectly mimetic' (their colour and pattern imitated those of Rufous Bush Chat eggs; background: 5.0 Y 8/2; dark spots: 7.5 YR 3/6; light spots: 7.5 YR 5/5; Munsell Color 1943). The results attained in this study were compared with those obtained by Alvarez (1996) in 1993/94 in the same area and following the same procedure during the period of presence of Cuckoos in the area, when 26 model eggs exactly like the ones used in the present study but whose colour was 'partly mimetic', since they imitated that of natural Cuckoo eggs (background: 10 Y 8/1; dark spots: 7.5 YR 4/4; light spots: 7.5 YR 6/4). Out of the 26 nests tested, the Rufous Bush Chats accepted the model egg in ten of them and reject-

**Table 1.** Number and percentage of nests in which Rufous Bush Chats accepted and rejected model eggs of various colours: perfectly mimetic (coloured like Rufous Bush Chat eggs), partly mimetic (coloured like Cuckoo eggs) and non-mimetic (plain white and white background with black spots).

	Mimetic		Non-mimetic	
	Perfectly mimetic	Partly mimetic (Alvarez 1996)	Plain white	White background and black spots
Accepted	18 (90%)	10 (38%)	24 (80%)	20 (83%)
Rejected	2 (10%)	16 (62%)	6 (20%)	4 (17%)

ed it in the other 16 (ns, binomial test). The colour of the other 54 model eggs was 'non-mimetic': 30 of them were plain white (N /9), 24 had a white background (N /9) with black spots (N 0.75/), whose size and distribution on the surface of the egg model imitated those of spots in natural Cuckoo eggs.

## RESULTS

The type of egg model (perfect mimetic controls whose colour imitated that of Rufous Bush Chat eggs, partly mimetic controls coloured like natural Cuckoo eggs, non-mimetic plain white and also non-mimetic white background with black spots) is not independent of its acceptance or rejection ( $\chi^2_3 = 10.96$ ,  $P < 0.001$ ; Table 1).

Whereas the partly mimetic egg models were not preferentially accepted or rejected (Alvarez 1996), the perfectly mimetic ones, and the non-mimetic plain white and white with black spots, were accepted significantly more often than rejected ( $P = 0.001$ ,  $P = 0.002$ ,  $P = 0.002$ , respectively; binomial test).

Perfectly mimetic model eggs were more often accepted than the partly mimetic ones ( $\chi^2_1 = 10.53$ ,  $P < 0.01$ ). When the frequencies of acceptance and rejection of control model eggs were compared with those obtained for non-mimetic models, both the egg models coloured plain white and white background with black dots were more often accepted than the partly mimetic models ( $\chi^2_1 = 11.9$ ,  $P < 0.001$ ;  $\chi^2_1 = 12.4$ ,  $P < 0.001$ , respectively), and accepted as well as the perfectly mimetic models (ns, Fisher test). Neither type of non-mimetic model was preferentially accepted or rejected (ns, Fisher test).

## DISCUSSION

Rufous Bush Chats are apparently unable (or almost unable) to distinguish between their own eggs and the perfectly mimetic model eggs, but since approximately the same effect is obtained with definite non-mimetic models, the parasite could take advantage of the hosts' preference for certain visual stimuli and develop non-mimetic but attractive colour patterns on their eggs, rather than matching exactly the hosts' eggs.

The pale and contrasting appearance of natural Cuckoo eggs would suggest that the suggested strategy is at work

for the particular host-parasite system.

If the preference by Rufous Bush Chats towards white and highly contrasting eggs is the only selective force affecting the egg colour of its particular gens of Cuckoo, why has the parasite not developed perfect black dots on a white eggshell?

Among other pressures, predation is the most likely to set an upper limit to background paleness and dot contrast (Cott 1957). Although black dots would also help visually by breaking up the egg surface and outline, a white background and very high contrast would probably attract more attention from potential nest predators than a darker background with brown spots, since both elements would match more closely the reflectance of the mosaic of colour patches in the egg surroundings.

The fact that the two host species that react positively to white and black dots on white egg models (the Rufous Bush Chat and the Magpie) are parasitized by cuckoos (the Cuckoo and the Great Spotted Cuckoo, respectively) that lay eggs paler than the hosts' suggests that the two cuckoo species are using the strategy of producing attractive stimuli, rather than the egg-mimicry strategy. The mechanism will doubtless be different for Cuckoo gentes with eggs darker than their hosts' (four of five gentes analysed by Brooke & Davies 1988). As suggested by the information provided by Brooke and Davies (1988) and in the same way as ground hue of Cuckoo and hosts' eggs is positively correlated (Moksnes & Røskoft 1995), this is probably so for lightness.

Furthermore, the preference for contrasting dots on the eggs is not restricted to host species. Herring Gulls *Larus argentatus* and Ringed Plovers *Charadrius hiaticula* are highly attracted by stimuli consisting of egg models with dark or black dots on a light or white background (Baerends 1962, Koehler & Zagarus 1937 in Tinbergen 1953) and perhaps the preference is not uncommon in birds. If this were the case, parasites laying highly contrasting eggs would have at their disposal a greater array of host species, which would not be available as egg acceptors if the parasite followed the strategy of producing mimetic eggs.

An additional, unresolved question is why birds should prefer contrasting colour patterns in their eggs. The response to highly contrasting stimuli may be quite common in various contexts (e.g. to an unnaturally thin and

contrasted model of a parent head by Herring Gull chicks (Tinbergen & Perdeck 1951).

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## Spatial organization of foraging within a Black-headed Gull *Larus ridibundus* colony

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Group foraging is common in many different animal species (fishes, mammals, birds, insects), and its evolutionary causes have been extensively discussed (Pulliam & Caraco 1984, Ruxton *et al.* 1995, Brown & Brown 1996). One of the main advantages individuals receive from group foraging is the reduced predation risk (Black-tailed Prairie Dog *Cynomys ludovicianus*: Kildaw 1995; Cliff Swallow *Hirundo pyrrhonota*: Brown 1988). This reduced predation risk is often associated with a decrease in vigilance rate (Pulliam & Caraco 1984, Kildaw 1995), which in turn may allow an individual to increase its feeding rate (Valone 1989, Kildaw 1995) and to decrease the variability over time of its food intake (Clark & Mangel 1984, Ekman & Hake 1988, Caraco *et al.* 1995).

In most species, group foraging is associated with communal roosting or colonial breeding. An alleged advantage of communal roosting and colonial breeding in terms of foraging is given by the information centre hypothesis (Ward & Zahavi 1973), according to which animals at a roost or a colony may transfer information about the location of new ephemeral food sources (Ward & Zahavi 1973, Allchin 1992, Barta & Szep 1995, Marzluff *et al.* 1996; but see Bayer 1982, Mock *et al.* 1988, Richner & Heeb 1995). Alternatively, roosts or colonies, as assemblages of many individuals, may facilitate local enhancement (*sensu* Thorpe 1963) to find food (Brown 1988, Buckley 1996). The role of flock foraging in evolution of avian coloniality has thus often been discussed

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