Ibis (2000) **142**, 683–686

Short communication

Response to Common Cuckoo *Cuculus canorus* model egg size by a parasitized population of Rufous Bush Chat *Cercotrichas galactotes*

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The different gentes of the Common Cuckoo *Cuculus canorus* are adapted to parasitize different species of passerine birds, the females of each gens laying eggs of constant type and usually similar in coloration to those of the host species (Brooke & Davies 1988, Moksnes & Røskaft 1995). This kind of mimicry apparently results from the hosts' rejection of unlike eggs (Davies & Brooke 1988, Brown *et al.* 1990, Moksnes *et al.* 1990).

Cuckoo eggs are smaller than expected in relation to body mass (Lack 1968, Payne 1974), their size being usually slightly larger than the hosts' (Baker 1942, Lack 1968, Wyllie 1981, Alvarez 1994, Moksnes & Røskaft 1995). The only attempt made to test the response of a Cuckoo host (the Reed Warbler *Acrocephalus scirpaceus*) to egg size showed that giant model eggs coloured like Reed Warbler type Cuckoo eggs were not preferentially accepted or rejected, although they were more likely to be rejected than model eggs similar in size and colour to the eggs of the Reed Warbler Cuckoo gens (Davies & Brooke 1988). This result was interpreted as an adaptation of the small eggs of *C. canorus* and other parasitic Cuculidae to deceive hosts and avoid egg rejection.

The size of Cuckoo eggs, relative to the Cuckoo and to eggs of the host, suggests the action of one or several forces, including the acceptance and rejection of the Cuckoo eggs by potential hosts, and constraints in relation to incubation time (Darwin 1859, Baker 1942), Cuckoo physiology and Cuckoo chick competition.

The Rufous Bush Chat *Cercotrichas galactotes* is regularly parasitized by the Common Cuckoo in southern Spain (27% of the nests in an agricultural area south of Seville), where it lays eggs larger than the host's (Alvarez 1994), and the parasite's egg rejection is carried out by the female of the host pair (Palomino *et al.* 1998).

Although body size of the Iberian and northwestern African race of Common Cuckoo (*C. c. bangsi*) is smaller than other European races (Cramp 1985), egg size of the aforementioned population (Alvarez 1994) is not smaller than that of its northern relatives (Baker 1942, Wyllie 1981, Moksnes & Røskaft 1995). The lower egg size provided by Johnsgard (1997) for *C. c. bangsi* points to the likely existence of different gentes within the subspecies, and in fact, egg volumes of Common Cuckoo and Rufous Bush Chat (Alvarez 1994) fit perfectly in the relationship found by Moksnes and Røskaft (1995) between egg sizes of Common Cuckoos and different host species.

In order to understand better the significance of the greater egg size of the Common Cuckoo, and whether it would contribute to acceptance by the host, I have tried to isolate the Rufous Bush Chat response to model Cuckoo eggs of various sizes.

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MATERIAL AND METHODS

The experiment was carried out in a lowland area in southern Spain during the breeding seasons of 1996–98, during the period when the Cuckoos are present in the area (from the beginning of May to the middle of July).

The study plot (*c.* 1000 ha) is located 20 km southeast of Seville, Spain (37°9′N, 2°14′W), at 12 m asl. This is an agricultural vineyard area, with small patches of kitchen gardens, vegetable growing, interspersed and densely growing fruit trees, greenhouses and a few remnants of the natural vegetation. The density of Rufous Bush Chat breeding pairs was about 0.5/ha.

To determine the Rufous Bush Chat response to the Common Cuckoo egg size, 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 model egg, and its state was subsequently recorded on the first day and then every second day. The introduced model egg was considered to have been accepted if it remained in the nest being incubated with the rest of the clutch (not pushed aside in the nest), and was considered to have been rejected if the birds abandoned their nest or ejected it from the nest.

Since Rufous Bush Chats' rejection of natural or model Cuckoo eggs occurs mainly by nest desertion or, to a lesser extent, by grasping the entire egg with the bill and ejecting it, and never by piercing with the bill and then grasping the shell (Alvarez 1994, 1996, pers. obs. of ejected models or eggs found at a distance from the nest), the previously used model eggs with a thin and soft shell of plaster (Alvarez 1996, 1999) were not used, but rather, they were made of orange wood with some lead pellets inserted in the centre of the model to simulate the ratio of weight:volume of natural eggs (determined empirically, according to Hoyt 1979). All models were painted with acrylic paint to imitate the colour and pattern of natural Common Cuckoo eggs (Alvarez 1994) (background: 10Y 8/1; dark spots: 7.5YR 4/4; light spots: 7.5YR 6/4; Munsell Color 1943) and coated with varnish to obtain a glossy surface similar to that of natural eggs.

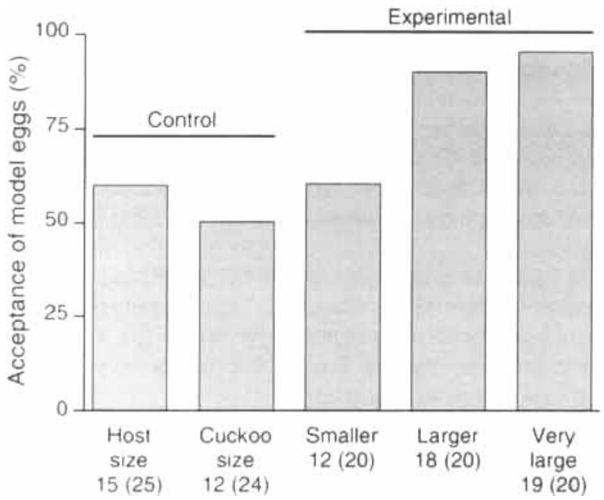

Figure 1. Percentage of nests in which Rufous Bush Chats accepted model eggs of various sizes. The number of egg models accepted are given for each size, with the total number of cases tried given in parentheses. All were coloured like natural Cuckoo eggs. Controls were either the size of host eggs (22 × 16 mm) or the size of Cuckoo eggs (23 × 17 mm). Models of abnormal size were smaller (20 × 15 mm), larger (26 × 19 mm) and very large (34 × 25 mm).

Considering the dimensions of host and Cuckoo eggs in the study area (Alvarez 1994), model eggs of each size type were introduced into 109 nests: 25 controls whose size was the average for Rufous Bush Chat eggs (22 × 16 mm, 2.9 ml), 24 controls whose size was the average of Cuckoo eggs (23 × 17 mm, 3.4 ml), 20 were smaller than normal and below the size of any Cuckoo egg (20 × 15 mm, 2.3 ml), 20 were larger than normal (26 × 19 mm, 4.8 ml) and the other 20 were much larger than normal and of similar size to the eggs of the non-parasitic cuckoos of the same body size as *C. canorus* (34 × 25 mm, 10.8 ml) (Payne 1974, Hoyt 1979).

RESULTS

The overall distribution of acceptance and rejection of the five types of model eggs departs significantly from random (i.e. acceptance or rejection is not independent of the type of model egg: $\chi^2_4 = 16.29$, $P < 0.01$).

Whereas the perfect mimetic model eggs (size like that of host eggs), the partly mimetic ones (size like that of Common Cuckoo eggs) and the non-mimetic model eggs smaller than the controls were not preferentially accepted or rejected (ns, binomial test), the non-mimetic model eggs larger and much larger than the controls were significantly more accepted than rejected ($P = 0.001$, $P = 0.0001$, respectively; binomial test) (Fig. 1).

When the frequencies of acceptance and rejection of the various stimuli were compared with each other, both controls and the smaller than normal egg models were similarly accepted and rejected (host size vs Cuckoo size and smaller, and Cuckoo size vs smaller: ns; χ^2 test), whereas the larger and very large models were more accepted than the smaller, the host size and the Cuckoo size (larger: $\chi^2_1 = 4.80$, $P < 0.05$; $\chi^2_1 = 5.02$, $P < 0.05$; $\chi^2_1 = 8.17$, $P = 0.02$; respectively; very large: $P = 0.002$; $\chi^2_1 = 7.40$, $P < 0.01$; $\chi^2_1 = 10.57$, $P < 0.01$; respectively; Fisher test and χ^2 test). Both the larger and the very large model eggs were similarly accepted (ns, Fisher test).

Rejection of model eggs took place mainly by nest desertion (Table 1). When, for the purpose of analysis, adjacent categories were combined in two groups (1, small size: host, Cuckoo and smaller sizes; 2, large size: larger and very large sizes), the method of rejection by the hosts (either model egg ejection or nest desertion) was in no way related to the size of the models (ns, Fisher test).

The control model eggs whose colour and size were like Cuckoo eggs were accepted or rejected in similar proportion to equivalent models in Alvarez (1996) (ns, χ^2 test). The preferred larger and very large model eggs in the present study were also preferred equally highly to the two kinds of non-mimetic model eggs sized like natural Common Cuckoo eggs, one of them coloured plain white (larger and very large; ns, Fisher test) and the other with white background and black spots (larger and very large; ns, Fisher test) in Alvarez (1999). The over-sized model eggs of the present study were also preferred equally to the perfect mimetic ones, of Cuckoo egg size and coloured like the host's eggs (Alvarez 1999) (larger and very large; ns, Fisher test).

DISCUSSION

The mechanism to attain egg acceptance by the Common Cuckoo is apparently based on mimicry in egg size for certain host species or populations (the case of Reed Warblers discriminating between eggs of different size, Davies & Brooke 1988). On the other hand, the high

Table 1. Number of rejections by Rufous Bush Chats by the modalities of model egg ejection or nest desertion toward Cuckoo model eggs of different size.

	Host size (22 × 16 mm)	Cuckoo size (23 × 17 mm)	Smaller (20 × 15 mm)	Larger (26 × 19 mm)	Very large (34 × 25 mm)
Model egg ejection	2	4	2	0	0
Nest desertion	8	8	6	2	1

acceptance by Rufous Bush Chats of non-mimetic models which are larger or much larger than normal indicates an effect of attraction, large size apparently compelling the birds to incubate Cuckoo eggs.

It therefore seems that the particular mechanism of Cuckoo egg acceptance may vary between pairs of Cuckoo and host species, and may also be opportunistic in the sense of taking advantage of the abilities of the different hosts.

The mechanism of stimulus attraction in the acceptance of Cuckoo eggs by Rufous Bush Chats is not limited to egg size, and their response towards light and contrasted coloration in the Cuckoo egg (Alvarez 1999) points in the same direction.

The positive response towards larger eggs shown by Rufous Bush Chats and perhaps other hosts (apparently also the Magpie *Pica pica* parasitized by the Great Spotted Cuckoo *Clamator glandarius*, Alvarez & Arias de Reyna 1974, Alvarez *et al.* 1976), and probably used by the Cuckoo to its own benefit, may correspond to a general attraction exerted by large egg size also towards non-host bird species. Larger than normal eggs are known to be more attractive to nesting Greylag Geese *Anser anser*, Herring Gulls *Larus argentatus*, Oystercatchers *Haematopus ostralegus* (Tinbergen 1951, 1953) and Pied Flycatchers *Ficedula hypoleuca* (Haartman 1981).

Apparently, to a great extent due to limited variation in Cuckoo egg size and to the common choice of host species with small eggs, Cuckoo eggs are usually larger, although relatively smaller when the chosen host species lays larger eggs. Examples are the Great Reed Warbler *Acrocephalus arundinaceus* and Red-backed Shrike *Lanius collurio* in Europe (Baker 1942, Wyllie 1981, Moksnes & Røskaft 1995) and Azure-winged Magpie *Cyanopica cyana* in Japan (apparently a recent host, Yamagishi & Fujioka 1986). This, together with inconclusive evidence about Cuckoo egg size varying significantly with host egg size (negative results in Baker 1942, Brooke & Davies 1988, positive results in Moksnes & Røskaft 1995), points to mimicry in egg size not extending to most host–parasite dyads.

If the mechanism of attaining acceptance by large egg attraction were not uncommon, the Cuckoos would not need to rely so much on mimicry (and thus to specialize in certain host species). So, by laying relatively larger eggs, they may have a greater array of passerine species available as secondary hosts (Moksnes & Røskaft 1995).

The fact that the Cuckoo has not developed much larger eggs demonstrates the existence of factors other than host preference for large eggs affecting the evolution of egg size. The answer may in part be in the known direct relationship between egg size and incubation time (Rahn & Ar 1974), and the need on the part of the Cuckoo to adjust the incubation period of its eggs to that of the host, as noted by Darwin (1859). There is not, however, a fine adjustment of Cuckoo incubation time to that of particular hosts.

In relation to this, although the slightly larger Cuckoo egg size (relative to the host egg) in the study area does not apparently accord with its shorter incubation period (Cuckoo: 12 days, Lack 1968, pers. obs.; Rufous Bush Chat: 14 days, pers. obs.), some kind of phylogenetic inertia (Cuculidae as a whole tend to have short incubation periods, those of parasitic species being only slightly and non-significantly shorter than non-parasitic species, Payne 1977) and retention and pre-incubation of the Cuckoo egg in the female body prior to laying (Perrins 1967, Lack 1968) may help produce an incubation period shorter than the host's.

Another factor which may presumably hinder increase of Cuckoo egg size is the need to allocate maternal stores to small eggs, as a strategy to increase the number of eggs laid (Haartman 1981).

I am grateful to M. Vázquez, José and Juan Ayala and J. Bernal for help in the field, and to E. Aguilera, J. A. Amat, R. B. Payne and T. Redondo for valuable comments. Financial support was provided by DGICYT (PB92-0115, PB95-0110) and Junta de Andalucía (RNM 0105).

REFERENCES

Alvarez, F. 1994. A gens of Cuckoo *Cuculus canorus* parasitizing Rufous Bush Chat *Cercotrichas galactotes*. *J. Avian Biol.* **25:** 239–243.

Alvarez, F. 1996. Model Cuckoo *Cuculus canorus* eggs accepted by Rufous Bush Chats *Cercotrichas galactotes* during the parasite's absence from the breeding area. *Ibis* **138:** 340–342.

Alvarez, F. 1999. Attractive non-mimetic stimuli in Cuckoo *Cuculus canorus* eggs. *Ibis* **141:** 142–144.

Alvarez, F. & Arias de Reyna, L. 1974. Mecanismos de parasitación por *Clamator glandarius* y defensa por *Pica pica*. *Doñana, Acta Vert.* **1:** 43–65.

Alvarez, F., Arias de Reyna, L. & Segura, M. 1976. Experimental brood parasitism of the magpie (*Pica pica*). *Anim. Behav.* **24:** 907–916.

Baker, E.C.S. 1942. *Cuckoo Problems.* London: Witherby.

Brooke, M. de L. & Davies, N.B. 1988. Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature* **335:** 630–632.

Brown, R.J., Brown, M.N., Brooke, M. de L. & Davies, N.B. 1990. Reactions of parasitized and unparasitized populations of *Acrocephalus* warblers to model cuckoo eggs. *Ibis* **132:** 109–111.

Cramp, S. 1985. *The Birds of the Western Palearctic,* Vol. 4. Oxford: Oxford University Press.

Darwin, C. 1859. *The Origin of Species.* London: Murray.

Davies, N.B. & Brooke, M. de L. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. *Anim. Behav.* **36:** 262–284.

Haartman, L. von 1981. Co-evolution of the Cuckoo *Cuculus canorus* and a regular Cuckoo host. *Ornis Fenn.* **58:** 1–10.

Hoyt, D.F. 1979. Practical method of estimating volume and fresh weight of bird eggs. *Auk* **96:** 73–77.

Johnsgard, P.A. 1997. *The Avian Brood Parasites.* Oxford: Oxford University Press.

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds.* London: Methuen.

Moksnes, A. & Røskaft, E. 1995. Egg-morphs and host preference in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *J. Zool., Lond.* **236:** 625–648.

Moksnes, A., Røskaft, E., Braa, A.T., Korsnes, L., Lampe, H.M. & Pedersen, H.C. 1990. Behavioral responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour* **116:** 64–89.

Munsell Color 1943. *Munsell Book of Color.* Baltimore, Maryland: Kollmorgen Instruments Corporation.

Palomino, J.J., Martín-Vivaldi, M., Soler, M. & Soler, J.J. 1998. Females are responsible for ejection of cuckoo eggs in the rufous bush robin. *Anim. Behav.* **56:** 131–136.

Payne, R.B. 1974. The evolution of clutch size and reproductive rates in parasitic cuckoos. *Evolution* **28:** 169–181.

Payne, R.B. 1977. The ecology of brood parasitism in birds. *Annu. Rev. Ecol. Syst.* **8:** 1–28.

Perrins, C.M. 1967. The short apparent incubation period of the Cuckoo. *Br. Birds* **60:** 51–52.

Rahn, H. & Ar, A. 1974. The avian egg: incubation time and water loss. *Condor* **76:** 147–152.

Tinbergen, N. 1951. *The Study of Instinct.* Oxford: Oxford University Press.

Tinbergen, N. 1953. *The Herring Gull's World.* London: Collins.

Wyllie, I. 1981. *The Cuckoo.* London: Batsford.

Yamagishi, S. & Fujioka, M. 1986. Heavy brood parasitism by the Common Cuckoo *Cuculus canorus* on the Azure-winged Magpie *Cyanopica cyana*. *Tori* **34:** 91–96.

Received 13 April 1999; revision accepted 27 October 1999