

Why do Horsfield's bronze-cuckoo *Chalcites basalis* eggs mimic those of their hosts?

N. E. Langmore · R. M. Kilner

Received: 7 July 2008 / Revised: 14 January 2009 / Accepted: 12 March 2009
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Abstract The Horsfield's bronze-cuckoo (*Chalcites basalis*) egg closely matches the appearance of its host fairy-wren (*Malurus* spp.) eggs. Mimicry of host eggs by cuckoos is usually attributed to coevolution between cuckoos and hosts, with host discrimination against odd-looking eggs selecting for ever better mimicry by cuckoos. However, this process cannot explain Horsfield's bronze-cuckoo egg mimicry because fairy-wren hosts rarely reject odd-looking eggs from their nest. An alternative hypothesis is that cuckoos have evolved egg mimicry to disguise their eggs from other cuckoos. Female cuckoos remove one egg from the nest during parasitism and would potentially benefit by selectively removing any cuckoo egg that has already been laid in the nest because otherwise, their egg will be evicted by the first nestling cuckoo along with the host clutch. We used painted, non-mimetic eggs to test whether cuckoos selectively remove odd-looking eggs during parasitism. We found that they were no more likely to remove a non-mimetic egg from a superb fairy-wren *Malurus cyaneus* clutch than would be expected by chance. Thus, our study does not support the cuckoo egg replacement hypothesis to explain mimicry of host eggs by cuckoos.

Keywords Brood parasitism · Cuckoos · Superparasitism · Coevolution · Egg mimicry · Cuckoo egg replacement

Introduction

Many species of cuckoo lay eggs that match the appearance of their hosts' eggs (Davies and Brooke 1988; Higuchi 1998; Davies 2000). In some cuckoo species, the accuracy of mimicry reflects the degree of egg discrimination and rejection by hosts, suggesting that egg mimicry by cuckoos has evolved through coevolution with hosts, in response to egg rejection by hosts (e.g. Honza et al. 2004, Antonov et al. 2006). For example, in Britain, the European cuckoo *Cuculus canorus* has several different races, each of which specialises in parasitising a different host. The various host species are adept at recognising and rejecting odd-looking eggs that are added to their nest (e.g. Davies and Brooke 1988). The cuckoo races lay eggs that differ in appearance, each appropriately mimicking the colouring and patterning of their host's eggs. Most revealingly, only one cuckoo race fails to lay a mimetic egg, and this race parasitises a host, the dunnock *Prunella modularis*, which lacks egg-rejection behaviour (Brooke and Davies 1988).

However, the extent to which cuckoo eggs mimic the host clutch is not always correlated with the host's ability to reject odd-looking eggs (e.g. Edvardsen et al. 2001). The Horsfield's bronze-cuckoo (*Chalcites basalis*) produces a small egg (18×12 mm) for its body size, which is a close match in colour, pattern and width to the delicately speckled eggs laid by their fairy-wren hosts (Langmore et al. 2003). It differs slightly from the fairy-wren egg because it is ~2 mm longer, and the speckling tends to have a more uniform distribution (Langmore et al. 2003). Egg mimicry in Horsfield's bronze-cuckoos is puzzling, because neither

Communicated by M. Soler

N. E. Langmore (✉)
School of Botany and Zoology, Australian National University,
Canberra, ACT 0200, Australia
e-mail: naomi.langmore@anu.edu.au

R. M. Kilner
Department of Zoology, University of Cambridge,
Downing St.,
Cambridge CB2 3EJ, UK

splendid fairy-wrens (*M. splendens*; Brooker and Brooker 1989b) nor superb fairy-wrens (*M. cyaneus*, Langmore et al. 2003) reject Horsfield's bronze-cuckoo eggs from their nests. Furthermore, both host species show very low rates of ejection and desertion of model eggs that match host eggs in size but differ in appearance (Brooker and Brooker 1989a; Langmore et al. 2003). The lack of model egg rejection cannot be explained as a constraint of small bill size because superb fairy-wrens did not use puncture ejection to reject painted real eggs either (Langmore et al. 2003). The failure of fairy-wrens to reject cuckoo eggs and non-mimetic experimental eggs appears to be related to poor visibility in the dim interiors of the dome-shaped nests typical of most Australian bronze-cuckoo hosts (Langmore et al. 2005). The only evidence of egg discrimination by hosts is that superb fairy-wrens are more likely to abandon a clutch containing a large (20 × 15 mm) non-mimetic egg than a fairy-wren sized non-mimetic egg, perhaps using tactile cues. This suggests that the small size of cuckoo eggs has been selected by host discrimination (Langmore et al. 2003).

An alternative explanation for egg mimicry, the 'cuckoo egg replacement' hypothesis, could explain the evolution of egg mimicry in this species (Davies and Brooke 1988; Brooker and Brooker 1989a; Brooker et al. 1990; Davies 1999). Cuckoos of the genera *Cuculus* and *Chalcites* remove one egg from the nest before adding their own. Soon after hatching, their offspring complete the destruction of the host's breeding success by evicting any unhatched eggs, and newly hatched young from the nest (e.g. Honza et al. 2007). Davies and Brooke (1988) proposed that if more than one female cuckoo parasitises the same nest, it would pay the second cuckoo to remove the existing cuckoo egg so that her own offspring is not evicted later by the first cuckoo in the nest. According to this hypothesis, adult female cuckoos should preferentially remove the oddest-looking egg from the nest before adding their own egg to the clutch. Mimetic cuckoo eggs could, therefore, evolve in response to cuckoo discrimination, as a strategy for concealing eggs amongst the host clutch to avoid detection by a second cuckoo female visiting the host nest.

Previous tests of this hypothesis have yielded equivocal results. Davies and Brooke (1988) and Davies (1999) found that 14% of reed warbler *Acrocephalus scirpaceus* nests parasitised by a European cuckoo were subsequently parasitised by a second cuckoo. However, second cuckoos were no more likely to remove a real cuckoo egg than a host egg from the existing clutch. At other nests, Davies and Brooke played the part of the first cuckoo themselves, adding model eggs painted either to resemble a reed warbler egg or to differ in appearance. When these nests were subsequently parasitised, the female cuckoo tended to remove the model egg more frequently than a host egg, but she was no more likely to remove a non-mimetic model

than one that matched the host eggs. Davies (1999) concluded that there was no strong support for the cuckoo egg replacement hypothesis in this system.

Even if European cuckoo females had selectively removed odd-looking eggs, their behaviour is unlikely to have driven the evolution of egg mimicry in reed warbler-cuckoos, which instead is far more likely to have been selected by host discrimination (Davies 2000). This is because parasitised populations of reed warblers have good egg discrimination abilities and are able to reject between 27% and 69% of non-mimetic eggs (Stokke et al. 2008). If only 14% of parasitised reed warbler nests are parasitised by a second cuckoo, a badly matching cuckoo egg has a 27–69% chance of being removed by a reed warbler, compared to a 14% chance, at most, of being removed by another cuckoo. However, in the absence of host discrimination against odd-looking eggs, cuckoo egg replacement could cause the evolution of cuckoo egg mimicry (Davies and Brooke 1988). Brooker and Brooker (1989a) and Brooker et al. (1990) have, therefore, proposed that cuckoo egg replacement is a likely explanation for the mimetic eggs of the Horsfield's bronze-cuckoo.

We tested this hypothesis by painting model and real eggs so that they looked unlike host eggs, placing them in host superb fairy-wren nests and observing which egg was removed from the clutch by Horsfield's bronze-cuckoos in subsequent parasitism events.

Methods

Study site

Experiments were performed in Campbell Park and the Australian National Botanic Gardens, Canberra, Australia, between September and January in 1999, 2000 and 2001. We located the nests of colour-banded superb fairy-wrens during nest building and checked them every second day for host and cuckoo eggs.

Two Horsfield's bronze-cuckoo eggs were found in the same nest in three out of 114 parasitised nests (2.6%). Assuming that an individual cuckoo would not adopt the maladaptive behaviour of laying twice in the same nest, this suggests that competition between female cuckoos could select cuckoo eggs that mimic hosts eggs in this species.

Preparation of non-mimetic eggs

Model eggs were made of Alumilite Super Plastic cast in silicone moulds. We also used real eggs that were obtained either from fairy-wren clutches that were freshly deserted or from captive zebra finches, which lay an egg (mean [range] length × width = 15.1 [13.2–17.35] × 10.9 [9.57–12.7] mm,

(Zann 1996)) similar in size to a small superb fairy-wren egg (mean [range] length×width=16.09 [15.1–18.2]×12.4 [11.1–13.4] (Rowley 1965)). Real eggs were used for experiments within 14 days of laying, sometimes in two different nests, and then discarded.

Model eggs were the same size as fairy-wren eggs (16×12 mm) and were painted with bright blue (cobalt turquoise 153) Daler-Rowney acrylic paint. Real eggs were painted either the same blue as the plastic eggs, a similar olive-brown (mix of ‘coffee bean,’ ‘moss green’ and ‘parchment’ Plaid acrylic paint) to the egg of the shining bronze-cuckoo *Chalcites lucidus* (an occasional fairy-wren parasite) or off-white (‘parchment’ Plaid acrylic paint) with large brown (‘buckskin brown’ Plaid acrylic paint) spots.

Artificial parasitism experiments

Due to the unpredictability and generally low rates of parasitism by cuckoos, a large number of host nests must be found and parasitised with experimental eggs in order to obtain an adequate sample of nests that are subsequently parasitised by cuckoos. We parasitised 89 superb fairy-wren nests (52 with blue plastic eggs, 16 with blue real eggs, 12 with spotted real eggs and nine with brown real eggs) during the laying period of the host, usually on the day the first egg was laid. Thereafter, nests were usually checked daily for evidence of cuckoo parasitism. Although superb fairy-wrens breed from September to January/February, all experiments were conducted prior to mid-December to avoid potentially confounding seasonal effects. Clutch abandonment is exceedingly rare in superb fairy wrens and mainly occurs late in the season (0.6% of nests, $N=3,114$ clutches, A. Cockburn pers. comm.). Experiments were approved by the Australian National University Animal Experimentation Ethics Committee (Protocol No. F. BTZ.99.99). Model and real painted eggs were left in the nest for five full days and removed on the sixth day if they had not been ejected by the host. This meant that there was only an extra egg in the clutch for the first 2–4 days of the incubation period, and there was no impact on the hatching success of clutches.

Statistical analysis

To test whether female cuckoos removed the non-mimetic egg more often than would be expected by chance, we needed to know the number of eggs in the clutch at the time that they made their choice. Brooker et al. (1988) observed that Horsfield’s bronze-cuckoos lay their eggs within 2 or 3 h of sunrise, shortly after the host had laid her egg. Therefore, we assumed that the cuckoo never laid before the host had laid her egg for the day. For example, a cuckoo laying on the second day of the laying period of the host,

after we had added a non-mimetic egg, would be faced with a choice between two host eggs and one non-mimetic egg. For five nests, we did not know the exact number of eggs at the time that the cuckoo parasitised the nest because 2 or 3 days elapsed between nest checks. We followed the procedure used by Davies and Brooke (1988) and assigned these nests an intermediate clutch size. For example, if the cuckoo parasitised a nest containing either three or four eggs, we assigned a clutch size of 3.5. The data were analysed both including and excluding these five nests.

For each clutch size, we calculated the expected proportion of nests in which the cuckoo would remove the non-mimetic egg, if she selected eggs for removal at random. For example, cuckoos faced with two host eggs and one painted egg would be expected to remove the painted egg from 33% of nests. At each clutch size, we tested whether the observed number of nests in which the cuckoo removed a host egg differed significantly from the expected number using a χ^2 test.

We also tested whether cuckoos and fairy-wrens differed in their propensity to remove an experimental egg from the clutch using a logistic regression, as this would indicate which species is more likely to have selected for egg mimicry by cuckoos. The response variables were ‘reject’ (including rejection of an experimental egg and desertion of the whole clutch) or ‘accept’, and the factors included in the model were ‘species’ (superb fairy-wren or Horsfield’s bronze-cuckoo), ‘treatment’ (blue, brown or speckled egg), type of egg (real or plastic), the year in which the experiment was conducted and the interaction between species and treatment.

Results

Eighteen of 89 nests containing non-mimetic eggs were subsequently parasitised by a Horsfield’s bronze-cuckoo (Table 1). Each cuckoo was faced with between two and four host eggs and one painted egg at the time she parasitised the nest. Cuckoos removed the non-mimetic egg from four nests and a host egg from 14 nests. Cuckoos did not remove the non-mimetic egg any more than would be expected by chance ($\chi^2=0.37$, $df=3$, $P>0.9$). The result did not differ when we excluded the five nests for which the exact clutch size at the time of parasitism was unknown ($\chi^2=0.16$, $df=2$, $P>0.9$).

Extrapolating from this result, we can calculate the probable incidence of parasitism by two cuckoos at the same nest. Two Horsfield’s bronze-cuckoo eggs were found in the same nest in three of 114 parasitised nests. If the second cuckoo removes the cuckoo egg from about 22% of previously parasitised nests (as suggested by our experimental results), then we are likely to have missed a second

Table 1 Nests parasitised with painted eggs that were subsequently parasitised by a cuckoo, showing the number of host and painted eggs removed by the cuckoo for each type and colour of experimental egg and the number of host eggs in the nest at the time the cuckoo laid

Treatment	No. of host eggs	Cuckoo removed	
		Painted egg	Host egg
Blue plastic egg	2	1	1
	3	2	7
	3.5	0	3
	4	0	2
Real spotted egg	4	1	0
Real brown egg	3	0	1
Total		4	14

parasitism event (due to removal of the first cuckoo egg by the second cuckoo) at one nest at most, giving a predicted total of 3.85 cases of double parasitism out of 114, or 3% of parasitised nests and 0.5% of all superb fairy-wren nests. Interspecific competition between cuckoos is unlikely to have driven the evolution of mimetic Horsfield's bronze-cuckoo eggs, because no fairy-wren nests ($N=715$ nests in which eggs were laid between 1999 and 2006) were parasitised by any of the other four cuckoo species at our study site, even though two of these species, the shining bronze-cuckoo and the fan-tailed cuckoo *Cacomantis flabelliformis* are reported to be occasional fairy-wren parasites (Brooker and Brooker 1989b).

Horsfield's bronze-cuckoos and superb fairy-wrens did not differ significantly in their propensity to remove an odd-looking egg from the clutch (Nominal logistic model, $\chi_7^2=8.33$, $P=0.3$, Likelihood ratio tests of species effect; $\chi_1^2<0.001$, $P=0.99$, treatment effect; $\chi_3^2=2.78$, $P=0.25$, egg type effect; $\chi_1^2=2.45$, $P=0.12$; Year effect $\chi_1^2=2.55$, $P=0.11$, Species*Treatment effect $\chi_1^2=0.02$, $P=0.99$).

Discussion

2.6% of parasitised superb fairy-wren nests contained two Horsfield's bronze-cuckoos eggs, suggesting that intraspecific competition between female cuckoos for hosts does occur, albeit at a low rate, in our study population. A similar rate of multiple parasitism by Horsfield's bronze-cuckoos was found in an Australia-wide compilation of nest records (2.7%, $N=1,012$ parasitised nests, Brooker and Brooker 1989a). Although even a low rate of multiple parasitism could result in selection for cuckoo egg replacement, we found no evidence to support the prediction that Horsfield's bronze-cuckoos preferentially remove odd-looking eggs from the host clutch when parasitising the

nest. Rather, our data suggest that Horsfield's bronze-cuckoos select eggs for removal at random. Our results concur with other studies that have tested this prediction with a different cuckoo species (Davies and Brooke 1988; Davies 1999). Further, Horsfield's bronze-cuckoos did not differ significantly from superb fairy-wrens in their propensity to remove an odd-looking egg from the nest, so there does not appear to be any stronger selection for egg mimicry due to intraspecific competition between cuckoos than due to host egg discrimination—both were weak in this study. Three possible non-exclusive explanations for the failure of cuckoo females to have evolved selective removal of cuckoo eggs are; (1) intraspecific competition between Horsfield's bronze-cuckoo females for nests is largely avoided by the maintenance of exclusive breeding territories in this species (Langmore et al. 2007), (2) egg discrimination is constrained in dome-nesting hosts by the dimly lit nest interiors (Langmore et al. 2005) and the same visibility constraints should apply to cuckoos and (3) selective egg removal is too costly for cuckoos, because nest abandonment is more likely if the host sees the cuckoo at the nest (Davies and Brooke 1988; Langmore et al. 2003) and a cuckoo that remains at the nest for the extra time required to examine the host clutch might increase the chance of being 'caught in the act' by the host.

The puzzle of how egg mimicry has evolved in Horsfield's bronze-cuckoos, therefore, remains unsolved. Grim (2005) proposes six possible explanations for a similarity between host and cuckoo eggs. Of these, three hypotheses could potentially explain the similarity between the eggs of Horsfield's bronze-cuckoos and their hosts. First, host and cuckoo eggs might resemble one another by chance alone. Second, egg mimicry may have been selected by cuckoo discrimination at some point in their evolutionary history, but this behaviour has now been lost. Cuckoos may have lost the ability to recognise and remove odd-looking eggs if it takes longer to discriminate a cuckoo egg with increasing accuracy of mimicry of host eggs, and if (as is the case in superb fairy-wrens, (Langmore et al. 2003)) hosts use a cuckoo's presence near the nest as a cue for egg ejection or desertion (Davies and Brooke 1988). Finally, cuckoo egg mimicry may have evolved through discrimination by a past host that is no longer parasitised, by a current host that has not yet been tested experimentally or by a current host that has lost its egg recognition abilities due to high recognition costs (Davies et al. 1996).

How can we distinguish between these different hypotheses, which require descriptions of lapsed or lost behaviours? One approach might be to simulate extraordinarily high levels of parasitism by placing stuffed cuckoos near fairy-wren nests to see if egg rejection of odd-looking eggs can then be induced. This technique might also fool cuckoos that there is a greater risk of double parasitism,

increasing the likelihood that they will discriminate against odd-looking eggs during parasitism.

Alternatively, an indirect approach could be used to detect evidence of discriminatory abilities that have been lost, either by fairy-wrens or cuckoos. If Horsfield's bronze-cuckoo eggs are no longer recognised by their appearance, then their colouring and patterning is likely to be subject to random drift. For example, when compared with eggs laid by a race of its African congener, the Diederik cuckoo *C. caprius*, which are subjected to intense discrimination by its red bishop *Euplectes orix* hosts (Lawes and Kirkman 1996), Horsfield's bronze-cuckoo eggs should appear far more variable. Preliminary evidence in support of this possibility is that the eggs of Horsfield's bronze-cuckoos in our population differed sufficiently between females to allow identification of which female had parasitised a nest on the basis of egg morphology (Langmore et al. 2007). However, although this approach can potentially tell us whether Horsfield's bronze-cuckoo egg mimicry has been selected by discriminatory behaviours in the past, it cannot identify the agent of discrimination.

Acknowledgements We thank S. Butchart, N. Davies, J. Gardner, S. Hunt, G. Maurer and A. Peters for invaluable help in the field and A. Cockburn for providing data on superb fairy-wren clutch abandonment rates in undisturbed nests. NEL was supported by an Australian Research Council Fellowship. RMK was supported by a Royal Society University Research Fellowship. We are grateful to Environment ACT and the Australian National Botanic Gardens for permission to work on the study sites. Experiments comply with the current laws of the country in which they were performed.

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