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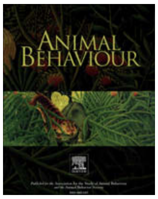

Are dark cuckoo eggs cryptic in host nests?

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The coevolutionary arms race between cuckoos and their hosts has famously yielded cuckoo eggs that evade host recognition and rejection by mimicking the appearance of the host's own clutch. But not all coevolutionary interactions between cuckoos and hosts have followed the same pathway. Several host species do not show egg rejection even when the cuckoo's egg looks entirely unlike their own. For example, hosts of some Australian bronze-cuckoos, *Chalcites* spp., routinely accept olive-brown cuckoo eggs that look very different from the speckled white eggs of their own clutch. Here we investigate the hypothesis that these cuckoo eggs are cryptic, which might explain why hosts do not remove them from their clutch. First, we use a phylogenetic analysis to show that dark bronze-cuckoo eggs are not ancestral, but instead have evolved in a group that parasitizes hosts with dark nests exclusively. Second, we show that dark bronze-cuckoo eggs are laid by two species that parasitize hosts with relatively dark nests, whereas a congeneric bronze-cuckoo species parasitizing host nests with greater ambient light levels lays a mimetic egg. Finally, we use a model of avian visual processing to show that the dark eggs of Gould's bronze-cuckoo *C. russatus* are cryptic in dark host nests. Our results support the hypothesis that some bronze-cuckoo species and their hosts have pursued an alternative coevolutionary trajectory, which has resulted in the evolution of cryptic, rather than mimetic, cuckoo eggs.

Coevolutionary theory predicts that if parasitism is costly, hosts of brood parasites should evolve defences against parasitism and that parasites should evolve reciprocal adaptations to evade these defences. Thus, rejection of foreign eggs by hosts has driven the evolution of egg mimicry in most parasitic cuckoo species; over 60% lay eggs that mimic the eggs of one or more of their hosts (from Johnsgard 1997; Payne 2005). The absence of egg rejection in some host species therefore poses a long-standing theoretical puzzle; why have some hosts failed to evolve egg rejection in response to nonmimetic cuckoo eggs in their clutch despite the high costs associated with parasitism?

Here we focus on one previously untested hypothesis that offers an answer to this question. This is the suggestion that foreign eggs are cryptic when viewed under the nest's ambient light levels, so they simply cannot be seen and therefore cannot be rejected (Marchant 1972; Brooker & Brooker 1989a; Brooker et al. 1990). Marchant (1972) proposed that for cuckoos that parasitize hosts with dark, enclosed nests, a dark, cryptic egg might evade detection even more effectively than a mimetic egg. Brooker and colleagues (Brooker & Brooker 1989a; Brooker et al. 1990) extended this argument by suggesting that if the hosts of these cuckoos build enclosed nests and lay light-coloured eggs, they may never have experienced the visual cues necessary for the evolution of rejecter behaviour. The initial evolution of cryptic eggs could have occurred through (i) selection by an ancestral, rejecter host, (ii) selection by a current host that lost its egg rejection behaviour because of high recognition costs (e.g. Davies et al. 1996) after the cuckoo evolved cryptic eggs or (iii) competition between female cuckoos (Brooker et al. 1990). The last possibility relates to the fact that when cuckoos parasitize a host nest they typically remove one egg from the clutch before laying their own. If the nest has already been parasitized, the cuckoo would benefit by removing the cuckoo egg, which might otherwise hatch first and evict her own egg (Davies & Brooke 1988). However, if the cuckoo egg is not detectable, the second cuckoo would be more likely to remove a host egg instead. Although the hypothesis that some cuckoo eggs are cryptic in the eyes of their hosts has the potential to resolve one of the most long-standing puzzles in the study of coevolution between brood parasites and hosts (Rothstein & Robinson 1998; Davies 2000), it has not been tested previously.

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Here we explore this idea in a group of Australasian cuckoos that lay eggs of colours that are strikingly different from those of their hosts. Several bronze-cuckoos of the genus *Chalcites* lay brown or olive-coloured eggs, quite unlike the immaculate white or speckled white eggs of their hosts (in Australia *C. lucidus*, *C. minutillus*, *C. russatus*; Brooker & Brooker 1989a; Higgins 1999; Fig. 1). The dark colour of bronze-cuckoo eggs is achieved in an unusual fashion among birds; the pigment is deposited in the outer cuticle rather than in the shell itself, as indicated by the fact that it can be rubbed off a freshly laid egg with a fingertip, revealing a pale eggshell underneath (personal observation; McGill & Goddard 1979). Dark eggs may well be cryptic in host nests, because these cuckoos parasitize hosts that build enclosed nests with dim interiors exclusively (Brooker & Brooker 1989a). Bronze-cuckoo chicks are evictors; the nestling cuckoo evicts the host eggs and young from the nest, resulting in complete failure of the reproductive attempt on the part of the host. Despite the high costs of parasitism and the striking difference in colour between host and cuckoo eggs, there is virtually no evidence of rejection of either cuckoo eggs (Gill 1983; Brooker & Brooker 1989b; N. E. Langmore & G. Maurer, personal observation; but see Lord 1931 in Brooker & Brooker 1989a) or model eggs (Brooker & Brooker 1989b; Langmore et al. 2005) by the hosts of these cuckoos.

We tested three key assumptions of the hypothesis that dark bronze-cuckoo eggs have evolved for crypsis. A recent phylogenetic comparative analysis (Fig. 1 in Kilner 2006) suggests that the ancestral egg colour of the Cuculidae was immaculate and white. This implies that the dark pigment of bronze-cuckoo eggs is the result of selection at some stage of their evolutionary history, but we do not know when. We started by using a phylogenetic analysis to investigate the stage in the evolutionary history of these cuckoos at which dark eggs evolved.

Next, we used a comparative approach to test whether dark eggs have evolved for crypsis in dark nest environments. We compared the host nest environment of two bronze-cuckoos that lay dark eggs, *C. lucidus*, shining bronze-cuckoo, and *C. minutillus*, little bronze-cuckoo, with a congener, *C. basalis*, Horsfield's bronze-cuckoo, which is unique among the Australian bronze-cuckoos in laying a mimetic, white speckled egg (Langmore et al. 2003; Langmore & Kilner 2009). We predicted that if dark eggs have evolved to be cryptic in poorly illuminated nests, the hosts of the cuckoos that lay dark eggs should have darker nests than the hosts of *C. basalis*. We tested this prediction by comparing the light intensity in the interiors of the nests of two biological hosts (sensu Brooker & Brooker 1989a) each for *C. basalis*, *C. lucidus* and *C. minutillus*.

Figure 1. A triple-parasitized *Gerygone magnirostris* clutch from Cairns, showing the host egg (top) and the range of egg colours laid by *C. russatus*. Most eggs were of the brown form (right). Sixteen percent ($N = 25$) of parasitized *G. magnirostris* nests at our Cairns site contained multiple cuckoo eggs, and two of these clutches contained three cuckoo eggs. Genetic analysis (mtDNA) of cuckoos from two of these nests indicated that multiple parasitism can be attributed to multiple females rather than repeat laying by a single female (N. E. Langmore, G. J. Adcock, G. Maurer, R. M. Kilner, unpublished data). Photo: E. Rosenfeld.

Finally, we used visual modelling to test whether the eggs of *C. russatus*, Gould's bronze-cuckoo, are more similar to the nest lining (i.e. cryptic) than are the eggs of its host *Gerygone magnirostris*, large-billed gerygone, in the eyes of both the hosts and the cuckoos themselves, when viewed in the dark environment of the host nest. Visual modelling is ideal for such an analysis for three key reasons. First, the detectability of an object depends not only on properties of the object itself, but also on the perceptual abilities of the receiver (Endler 1990), and it is well known that avian vision differs from human vision (Bennett et al. 1994). Unlike mammals, birds have both single and double cones in their retinas, and the single cones comprise four, rather than three (or two), types (Cuthill 2006); in addition to long-, medium- and short-wavelength cones, birds also have an ultraviolet-sensitive cone. Therefore, we quantified egg colour using reflectance spectrophotometry and analysed colour taking into account avian perceptual abilities using a model of avian visual processing (Vorobyev & Osorio 1998; Vorobyev et al. 1998).

The second reason for using visual modelling is that the detectability and discriminability of an object is also particularly influenced by the light environment in which it is perceived (Endler 1990). Nest luminosity affects host perception of cuckoo egg mimicry (Avilés 2008) and the incidence of egg rejection abilities in hosts (Langmore et al. 2005). Visual modelling allows us to investigate whether the birds can discriminate their eggs in the poor lighting conditions within their nests.

Finally, visual modelling also enables us to consider a potentially more important feature of detectability in dark environments, which is the luminance of the object relative to its background (Vorobyev & Osorio 1998), or its brightness contrast. Colour vision is greatly reduced in dark environments, and in very dim environments many vertebrates have ineffective colour vision (Dusenbury 1992). Nevertheless, they can still distinguish light from dark (Kelber et al. 2003). Therefore we also modelled the luminance of cuckoo and host eggs relative to the nest background.

METHODS

Phylogenetic Analysis

We used a recent phylogeny of the cuckoos (Sorenson & Payne 2005) and the Mesquite software package for phylogenetic analyses (Maddison & Maddison 2007) to reconstruct the ancestral form of the colours of bronze-cuckoo eggs, using the parsimony reconstruction method. Descriptions of egg colours were obtained from Payne (2005).

Field Methods

We studied parasitism of *Acanthiza chrysorrhoa*, yellow-rumped thornbill, and *A. reguloides*, buff-rumped thornbill, by *C. lucidus* in Campbell Park, Canberra, southeastern Australia (149° 9′E, 35° 16′S) from 1999 to 2007; parasitism of *G. magnirostris* and *G. levigaster*, mangrove gerygone, by *C. minutillus* in Darwin, Northern