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Cuckoos in raptors' clothing: barred plumage illuminates a fundamental principle of Batesian mimicry

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A fundamental principle of Batesian mimicry is that it pays to look like a local harmful species that is recognizable to other local species (receivers). Mimicking an allopatric species confers no benefit, as it is not recognizable to local species. It is thought that the common cuckoo, *Cuculus canorus*, is a Batesian mimic of the Eurasian sparrowhawk, *Accipiter nisus*, predominantly via its barred plumage, which facilitates access to host nests to deposit eggs. Barring is widespread in five genera of Old World cuckoos, unlike nonparasitic cuckoos, and evolved after the evolution of parasitism. Although barred plumage is predominant in parasitic cuckoos, it is unclear whether it may have a widespread function in cuckoo–hawk mimicry. If widespread, there should be a visual similarity between all five genera of Old World parasitic cuckoos and sympatric raptors. In addition, given that it pays to look like a local harmful species, sympatry should predict the degree of similarity. We compared barred plumage from all five genera of parasitic Old World cuckoos and up to eight sympatric raptors using digital image analysis. Cuckoos predominantly matched most raptors for at least one pattern attribute. In addition, three out of five cuckoos closely resembled a sympatric raptor for all barred pattern attributes examined, and potential model species were not confined to sparrowhawks. Habitat did not appear to influence plumage pattern similarity in most species studied. Finally, the barred plumage of sympatric species was more similar in appearance than those in allopatry. Together this demonstrates that cuckoos look like a local harmful species, which is congruous with Batesian mimicry.

In Batesian mimicry, a harmless species mimics an unpalatable or a harmful one. For example, *Dismorphia* butterflies (mimics) vary their colour pattern according to the local species of toxic Neotropical *Heliconius* butterflies (models; Bates 1862). By looking like a familiar unpalatable model, the mimic avoids detection. Therefore, a fundamental principle of Batesian mimicry is that there is an advantage to looking like a local unpalatable or harmful species that is recognizable.

Parasitic cuckoos are an extraordinary example of mimicry with diverse strategies to trick hosts into rearing their young (Davies 2011). Some cuckoos closely mimic the eggs of their hosts (Brooke & Davies 1988; Moskát et al. 2008; Spottiswoode & Stevens 2010, 2011; Stoddard & Stevens 2010), and others mimic host nestlings (Langmore et al. 2011). Studies of brood parasitism in cuckoos have predominantly focused on egg as well as chick mimicry, and have highlighted the drastic impact on host reproductive potential that has set the scene for a well-documented coevolutionary arms race (Moyer 1980; Davies et al. 1996; Davies 2000, 2011; Soler & Soler 2000; Langmore et al. 2003; Grim 2006; Spottiswoode & Stevens 2011). However, given that parasitism begins with depositing eggs in a host nest, blocking access to the nest has the greatest potential to minimize reproductive costs (Moksnes et al. 2000; Davies & Welbergen 2009; Feeney et al. 2012). As a consequence, brood-parasitic cuckoos appear to have evolved a range of strategies to gain access to host nests. For example, in the genera *Clamator*, *Eudynamys* and *Scythrops* it is reported that males elicit a mobbing response to distract hosts while females discreetly lay their eggs in host nests (Gaston 1976; Davies 2000). However, given the costs that hosts can impose on parasitic cuckoos, inconspicuousness should be favoured to evade detection (Moyer 1980; Davies & Brooke 1988; Langmore et al. 2003; Davies & Welbergen 2008; Pozgayová et al. 2009).

Brood-parasitic cuckoos dupe hosts into treating the parasite as if it is something it is not by looking like either a harmless species (aggressive mimicry) or a harmful species (Batesian mimicry). Aggressive mimicry is suspected among drongo cuckoos (*Surniculus* spp.) that form foraging flocks with multiple species of small passerines, and contribute to the flock by acting as a predator sentinel (Feeney et al. 2012). Batesian mimicry in cuckoos has been suspected since the time of Aristotle owing to their remarkable resemblance to raptors, especially *Accipiter* hawks (Wallace 1889). Their striking visual similarity is derived from their yellow eyes and legs, their size

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and shape, flight patterns and barred underparts (Payne 1967; Honza et al. 2006; Davies & Welbergen 2008; Davies & Welbergen 2009; Welbergen & Davies 2011; Trnka et al. 2012). In addition, it has been suggested that the rufous morph of the common cuckoo, *Cuculus canorus*, might represent mimicry of the Eurasian kestrel, *Falco tinnunculus* (Voipio 1953; Trnka & Grim 2013). Some species additionally possess polymorphisms in the colour of their barred plumage to thwart hosts that can see past the cuckoos' disguise. These polymorphic species are likely to possess multiple hawk-like features demonstrating that the host–parasite arms race probably also occurs in the adult phenotype of parasites (Voipio 1953; Thorogood & Davies 2012, 2013; Trnka & Grim 2013) and the alternative morph may represent frequency-dependent mimicry for an additional model, the Eurasian kestrel (Honza et al. 2006; Thorogood & Davies 2012; Trnka et al. 2012; Trnka & Grim 2013).

In Old World cuckoos, barred plumage evolved within the context of host–parasite coevolution, suggesting that it is an adaptive strategy to facilitate access to host nests (Krüger et al. 2007). This type of plumage pattern covers most of the ventral surface and is composed of within-feather alternating light and dark pigmentation, transversal to the feather's axis (Fig. 1; Payne 1967, 2005; Bortolotti 2006; Gluckman & Cardoso 2010). Studies of Batesian mimicry in parasitic cuckoos have focused on the common cuckoo, which is thought to mimic the Eurasian sparrowhawk, *Accipiter nisus* (Davies & Welbergen 2008; Davies & Welbergen 2009; Welbergen & Davies 2011). Field experiments measuring host responses to models of the common cuckoo demonstrate that barring can constrain host aggression at close range and that polymorphisms in barred plumage coloration can thwart detection by hosts (Voipio 1953; Moksnes et al. 1991; Honza et al. 2004, 2006; Grim 2005a; Thorogood & Davies 2012; Trnka et al. 2012; Trnka & Grim 2013). By looking like a harmful model, the common cuckoo can facilitate access to host nests in which to place its eggs and when hosts learn to discriminate, altering the phenotype can be a successful strategy.

In Old World parasitic cuckoos (Cuculidae) 35 species out of 58 have barred plumage, which is also common in both sparrowhawks (*Accipiter*) and other raptor genera (Ferguson-Lees & Christie 2001; Payne 2005). Given that resembling a local dangerous species has allowed the common cuckoo to flourish, Batesian mimicry via barred plumage patterns may be widespread in Old World cuckoos to facilitate access to host nests, and many types of raptors may be the dangerous model.

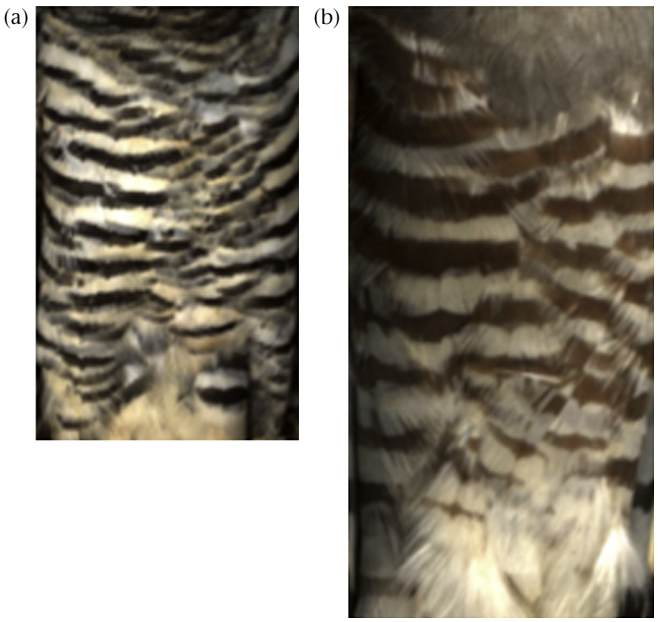

Figure 1. Barred plumage patterns. Although barred plumage is a common and easily identifiable pattern, it can vary extensively as shown on the same scale in (a) *Cuculus saturatus* and (b) *Aviceda cuculoides*. Photographs of plumage within the figure are copyright of the Natural History Museum and were taken by Thanh-Lan Gluckman.

Barred plumage may have multiple functions in brood parasitism. It has been well documented that avian brood parasites monitor host nests discreetly from nearby perches (Alvarez 1993; Hauber & Russo 2000; Begum et al. 2011). At a distance, barred plumage may provide camouflage while the parasite is searching for and watching potential hosts, but when detected at close range it may contribute to hawk mimicry and constrain aggression; however, it has also been suggested that it may increase aggression by some hosts towards parasites (Payne 1967; Marshall 2000; Honza et al. 2006; Davies & Welbergen 2008; Welbergen & Davies 2011; Trnka et al. 2012). Barred plumage can vary extensively in size, spacing, contrast and relative importance of the main marking size to the overall pattern (Fig. 1). If barred plumage patterns function in mimicry in brood-parasitic cuckoos, recognition of local raptors as predators by hosts (i.e. host discrimination and response) should drive a similarity in plumage pattern attributes to be geographically specific (Bates 1862; Briskie et al. 1992; Lindholm & Thomas 2000; Hale & Briskie 2007; Pfennig & Mullen 2010).

Recent studies of egg patterning employing digital image analysis to quantify patterning objectively with respect to avian vision have revealed new levels of subtlety in host–parasite interactions in cuckoos (Spottiswoode & Stevens 2010, 2011; Stoddard & Stevens 2010). Such methods have not yet been applied to barred plumage in cuckoos and raptors, so it is currently unknown whether the patterning of parasitic cuckoos is indeed similar to that of local raptors, and whether distribution overlap drives pattern similarity. No study to date has objectively quantified pattern similarity in sympatric populations of parasitic cuckoos and raptors. We examined whether the barred plumage of Old World parasitic cuckoos may function in Batesian mimicry from an avian perspective. If Batesian mimicry is widespread and sparrowhawks are not the only model, plumage pattern attributes of all genera of Old World parasitic cuckoos will match those of raptors in *Accipiter* and other genera. In addition, if barring does confer a widespread advantage, we predicted that overlap in geographical distribution (sympatry) will predict plumage pattern similarity.

METHODS

We sampled representatives of Old World parasitic cuckoos with barred plumage on the basis of taxonomy and geographical distribution. According to Howard & Moore (2003) there are six genera containing parasitic cuckoos with barred plumage: *Cuculus*, *Chrysococcyx*, *Eudynamys*, *Cacomantis*, *Cercococcyx* and *Scythrops*. The genus *Scythrops* has limited barring on the lower part of the ventral surface and, given its orientation when the bird is flying towards hosts, the barring is unlikely to function in mimicry; we thus removed this genus from further consideration. We focused our sampling efforts on cuckoos and raptors with a restricted distribution range in the tropics of Africa and Oceania (Asia and eastern Australia), where parasitic cuckoos are concentrated (Yom-Tov & Geffen 2005). North and South American species are not represented in this study as only a few brood-parasitic cuckoos are found on these continents and they do not have barred plumage (Payne 2005). To assess overlap of distributions we scanned maps from *Raptors of the World* (Ferguson-Lees & Christie 2001) and *The Cuckoos* (Payne 2005) for comparison by eye. For the purposes of this study it was important to establish approximate geographical range overlap, but not precise estimates of the extent of overlap. Therefore, we scored the overlapping distribution of raptors on the basis of up to 25%, 50%, 75% and 100% of that of cuckoos (Table 1). We aimed to sample all sympatric raptors for the cuckoos

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