

Short communication

**Large Hawk-Cuckoo
Hierococcyx sparverioides
parasitism on the Chinese
Babax *Babax lanceolatus*
may be an evolutionarily
recent host–parasite
system**

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We documented brood parasitism by the poorly studied Large Hawk-Cuckoo on a previously unknown host species, the Chinese Babax. Furthermore, we describe a new egg colour for the Large Hawk-Cuckoo. The parasitism rate of Chinese Babax nests over 4 years was 6.9% (11 of 159 nests), with significant temporal variation. The Large Hawk-Cuckoo laid immaculate white eggs that appeared non-mimetic to the blue Babax eggs, an impression that was confirmed by avian visual modelling. Nevertheless, most Cuckoo eggs were accepted by the host, suggesting that this host–parasite system may be evolutionarily recent.

Keywords: avian visual modelling, breeding success, brood parasitism, cuckoo chick, egg mimicry, egg recognition.

Avian obligate brood parasites reproduce by exploiting the parental care of other bird species, termed hosts (Rothstein 1990). Raising a parasitic chick often results

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in the loss of reproductive output of the host and probably a dramatic loss in fitness. As a consequence, many host species have evolved defences to counter brood parasitism, which in turn selects for corresponding counter-adaptations for better trickery on the part of brood parasites (Brooke & Davies 1988, Davies & Brooke 1989). Thus, hosts and their brood parasites can become involved in evolutionary arms races (Dawkins & Krebs 1979, Davies & Brooke 1989, Stokke *et al.* 2005). Reciprocal adaptations in host–brood parasite systems are best exemplified by recognition and rejection of foreign eggs by the hosts and egg mimicry by the parasites. However, most of the evidence for host-specific adaptations in brood parasite egg types comes from a single exhaustively studied species, the Common Cuckoo *Cuculus canorus*, and its host species in Europe (Moksnes & Røskaft 1995, Davies 2000, Antonov *et al.* 2010). The breeding biology of most of the other species of parasitic Cuculidae is insufficiently studied; for some taxa, for instance the Moustached Hawk-Cuckoo *Hierococcyx vagans* and Dark Hawk-Cuckoo *Hierococcyx bocki*, even the host species remain unknown (Davies 2000, Payne 2005).

Here we document the first records of brood parasitism of the Large Hawk-Cuckoo *Hierococcyx sparverioides* on the Chinese Babax *Babax lanceolatus*, whose breeding ranges overlap in southeastern Asia. The Large Hawk-Cuckoo and its interactions with its host species are poorly understood and many life-history traits including incubation and nestling period remain unknown (Payne 2005). In this study, we investigate brood parasitism of the Large Hawk-Cuckoo on the Babax and determine parasitism rate, egg type, nestling characteristics, host rejection rate of Large Hawk-Cuckoo eggs and Large Hawk-Cuckoo breeding success.

METHODS

The study was performed in Kuankuoshui Nature Reserve (26 231 ha), Guizhou Province, southeastern China (28°10'N, 107°10'E) from April to July in 1999, 2005, 2008 and 2009. The study site is situated in a subtropical moist broadleaved and mixed forest at an altitude of about 1500 m asl (see also Yang *et al.* 2010) and the size of the area that was searched for nests was c. 2400 ha.

The Babax (male: 73.3 g, *n* = 15; female: 70.3 g, *n* = 16) is much smaller than the Large Hawk-Cuckoo (male: 137.5 g, *n* = 2; female: 133.5 g, *n* = 4; Wu *et al.* 1986). It builds open, cup-shaped nests (Fig. 1a) in shrubs, couch grass or bamboo at 1.11 ± 0.69 m (*n* = 169) above the ground. Nests were found by systematically searching all typical and potential nest-sites and by monitoring the activities of adults throughout the breeding season. A special effort was made to find the nests as early as possible to be able to detect Cuckoo

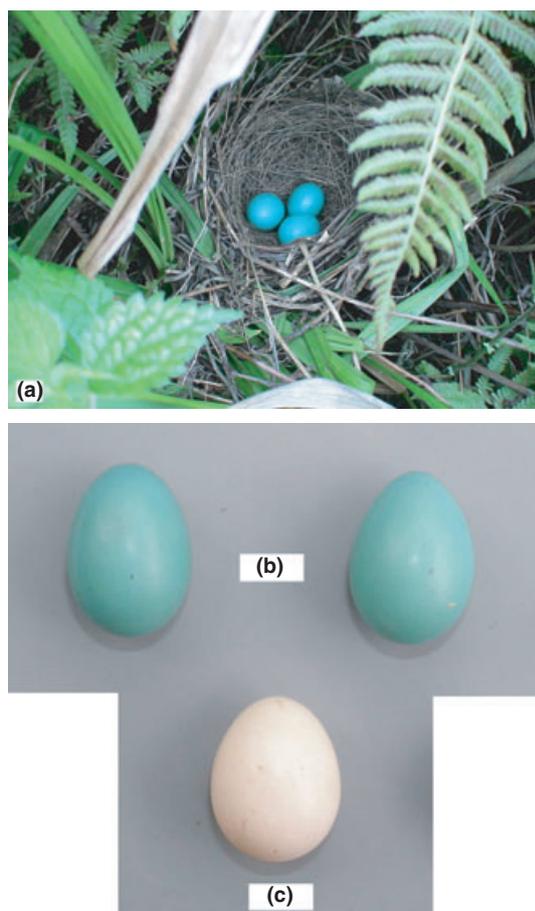


Figure 1. Nest (a) and eggs of the Chinese Babax (b) and Large Hawk-Cuckoo (c). Photographs by C. C. Yang.

parasitism. In the egg-laying period, nests were checked every day and every 3–5 days during incubation. For each nest, we recorded egg-laying date, clutch size, egg colour, egg size and the occurrence of brood parasitism. That an egg was that of a Large Hawk-Cuckoo was confirmed by the presence of a large nestling (see Fig. 4) and further molecular analysis (Yang *et al.* 2010). Large Hawk-Cuckoo eggs were regarded as rejected by hosts when Cuckoo eggs were ejected or in cases in which nests containing Cuckoo eggs were deserted: no non-parasitized nests were deserted (0 of 51 nests in 1999). Hatching success of the Large Hawk-Cuckoo was defined as the proportion of eggs hatched relative to the number of eggs laid; only nests found before or during the egg-laying period were included. Fledging success was defined as the number of young fledged relative to the number of eggs hatched. Breeding success was defined as the number of fledglings relative to the number of eggs laid; only nests found before or during the egg-laying period were included (Kleven *et al.* 2004).

We determined the reflectance of the eggs using a spectrophotometer (Avantes-2048; Avantes, Apeldoorn, the Netherlands) and measured one randomly selected egg per clutch, summarizing its reflectance as the mean of six measurements per egg (two at the blunt end, two at the middle and two at the sharp end of the egg). Only eggs found in 2005 and 2008 were measured for reflectance. In total, eggs from 27 clutches of Babax and two Large Hawk-Cuckoo eggs (one in 2005 and another in 2008) were measured. Because human and avian vision differ greatly (Cherry & Bennett 2001), we analysed egg colour using Goldsmith's tetrahedral colour space (Goldsmith 1990), a strongly advocated visual model for studies of colour patterns as processed by tetrachromatic visual systems (Stoddard & Prum 2008). We used the average spectral sensitivity curves for UVS-type avian retinas provided by Endler and Mielke (2005). Each spectrum is represented by a point in a tetrahedron, in which the vertices correspond to exclusive stimulation of the ultraviolet- (UV), blue- (B), green- (G) and red- (R) sensitive cones. Each colour point can be described by its spherical coordinates (θ , φ , r), where angles θ and φ represent the horizontal (RGB) and vertical (UV) components of hue, respectively, and r is the length of the colour vector and represents chroma (colour saturation). To visualize hue distributions independently of chroma, we mapped colours onto a unit sphere centred on the achromatic origin using Robinson projection, where θ [$-\pi$; π] corresponds to longitude, and φ [$-\pi/2$; $\pi/2$] to latitude (Stoddard & Prum 2008). As a measure of achromatic brightness, we calculated normalized brilliance following the methods of Stoddard and Prum (2008).

Visual modelling was processed by the TETRACOLORSPACE software (Stoddard & Prum 2008). Statistical analyses were performed in SPSS 13.0 for Windows (SPSS Inc., Chicago, IL, USA). Data are presented as means \pm sd.

RESULTS

Parasitism rates of Babax nests differed significantly among years ($\chi^2 = 10.23$, $df = 3$, $P = 0.017$; Table 1). Babax mean clutch size was 3.05 ± 0.55 eggs ($n = 40$).

Table 1. Large Hawk-Cuckoo parasitism and egg rejection rate in the Chinese Babax.

Year	Number of nests found	Number of nests parasitized	Parasitism rate (%)	Rejection rate (%)
1999	60	9	15.00	44.44
2005	20	1	5.00	0.00
2008	51	1	1.96	0.00
2009	28	0	0.00	—
Total	159	11	6.92	36.36

Egg dimensions (length \times width) of the Babax and Large Hawk-Cuckoos were $27.11 \pm 1.20 \times 20.30 \pm 0.73$ mm ($n = 36$) and $27.89 \pm 2.17 \times 21.17 \pm 0.70$ mm ($n = 3$), respectively. Babax egg colour appeared to be a uniform blue to the human eye, with little intra- or inter-clutch variation (Fig. 1b). The Large Hawk-Cuckoo laid immaculate white eggs (Fig. 1c) that appeared non-mimetic in relation to host eggs. All parasite eggs were white in colour and to the human eye appeared similar to each other. An objective analysis of egg colour confirmed that Babax eggs were indeed very different from those of the Large Hawk-Cuckoo, and variation in the horizontal (trichromatic) component of hue in the Babax was low (Fig. 2). Large Hawk-Cuckoo and host eggs showed no overlap in hue, chroma or brilliance (Fig. 2). The Large Hawk-Cuckoo eggs were much less saturated in colour and brighter than Babax eggs (chroma: $t = 3.00$, $df = 27$, $P = 0.009$; brilliance: $t = -7.36$, $df = 27$, $P < 0.0001$). These analyses clearly indicate that results from avian visual modelling agreed well with the human eye assessment of Large Hawk-Cuckoo eggs appearing non-mimetic.

Despite the low level of mimicry, Babax hosts accepted seven of 11 Large Hawk-Cuckoo eggs. Of the

seven cases in which Cuckoo eggs were accepted, four nests had two host eggs and one Large Hawk-Cuckoo egg, and three nests had three host eggs and one Large Hawk-Cuckoo egg. In the four cases in which Large Hawk-Cuckoo eggs were not accepted, three nests were deserted and the egg in the fourth was ejected. Desertions occurred at nests in which the Large Hawk-Cuckoo egg was the only egg in the nest ($n = 2$) or when there was only one host egg left ($n = 1$). Desertions from nests containing only a foreign egg or suffering heavy clutch reduction may not be a true response to the parasitic egg in co-evolutionary terms (Rothstein 1975, Hoover 2003, Kosciuch *et al.* 2006). The hatching success, fledging success and overall breeding success of the Large Hawk-Cuckoo was 50% (4/8), 50% (2/4) and 25% (2/8), respectively.

The incubation period of Large Hawk-Cuckoos was 13–14 days and the nestling period was 19.5 ± 0.7 days ($n = 2$). Large Hawk-Cuckoo nestlings at hatching (Fig. 3) were 4.94 ± 0.50 g in weight and 10.26 ± 0.84 mm in tarsus-length ($n = 3$). The Large Hawk-Cuckoo nestlings at 18 days of age (shortly before fledging) weighed on average 95.65 ± 5.44 g with a mean tarsus-length of 28.32 ± 1.87 mm ($n = 2$) (Fig. 4). Large

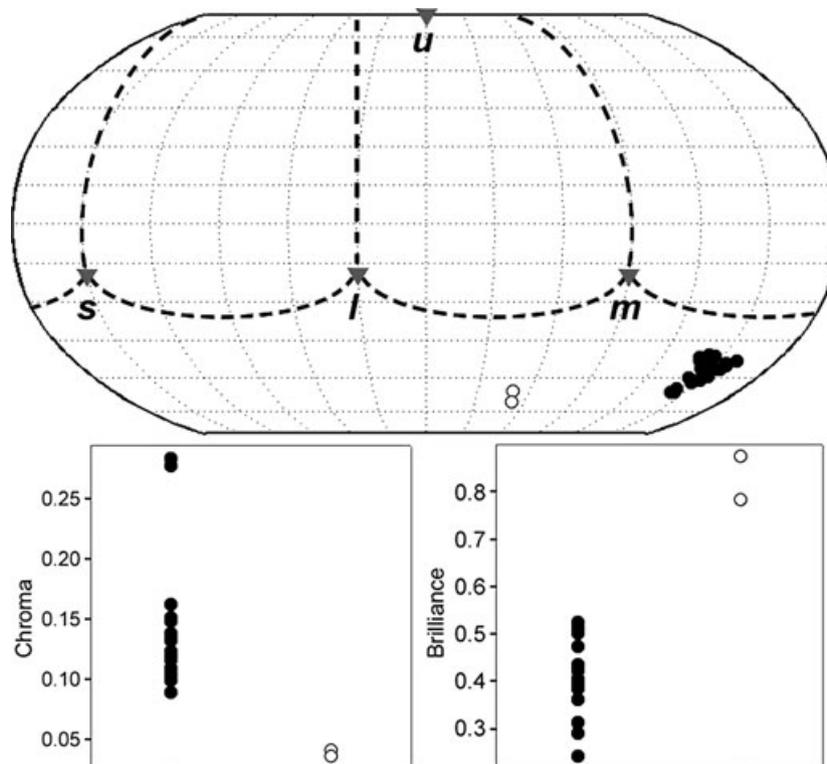


Figure 2. Robinson projection of egg colour hue, chroma and normalized brilliance as a measure of achromatic brightness of the Large Hawk-Cuckoo ($n = 2$) and Chinese Babax ($n = 27$). Grey triangles indicate projections of the short (s), medium (m) and long (l) wavelength vertices of the tetrahedron. Open and black circles refer to the Large Hawk-Cuckoo and Chinese Babax, respectively.



Figure 3. Nestling of a Large Hawk-Cuckoo at hatching. Photo by C.C. Yang.



Figure 4. Nestling of a Large Hawk-Cuckoo at 18 days of age, shortly before fledging. Photo by W. Liang.

Hawk-Cuckoo chicks ejected host eggs 1.67 ± 0.58 days ($n = 3$) after hatching, typical for other evicting cuckoo species.

Large Hawk-Cuckoo nestlings are naked at hatching with obvious raised nostrils and a slightly concave dorsum that facilitates egg ejection (Fig. 3). The skin of a Large Hawk-Cuckoo hatchling is salmon pink, becoming blackish after 2 days. The gape is light orange and gape flanges are lemon-yellow, both being lighter in colour than that of Common Cuckoo nestlings (Higuchi 1998, also see Payne 2005). The back plumage of Large Hawk-Cuckoo fledglings is dark brown with lighter brown margins and one or two conspicuous white spots on the nape. However, the plumage of the ventral side of the body was white with distinctive dark brown vertical bold streaks (Fig. 4), completely different from Common

Cuckoo fledglings. The tail plumage was dark brown with a clear broad white terminal bar, and both the tarsus and the foot were yellow. Young Hodgson's Hawk-Cuckoos *Hierococcyx nisicolor* are similarly white with black streaks on the underparts, but the crown is grey (Payne 2005).

DISCUSSION

We document for the first time Large Hawk-Cuckoo parasitism on the Chinese Babax. Parasitism rates were within the range of those reported for most of the major hosts of the Common Cuckoo (range: 0.09–21.1%) (Brooke & Davies 1987, Moksnes & Røskaft 1987, Schulze-Hagen *et al.* 1996, Antonov *et al.* 2006, Stokke *et al.* 2007, Yang *et al.* 2010). Similarly, fluctuations in parasitism rates among years are not unusual (e.g. Brooke *et al.* 1998, Alvarez 2003).

To our knowledge, the white egg colour type of the Large Hawk-Cuckoo found in the present study has not been described previously. Two egg morphs of the Large Hawk-Cuckoo have been reported in previous studies: (1) light brownish olive, in rare cases with darker specks, and (2) blue, unspotted (Baker 1906, 1942, Osmaston 1912, 1916, also see Payne 2005). The egg sizes reported by the latter two authors (27.0×19.0 mm and $27.9\text{--}30.0 \times 20.6\text{--}21.3$ mm) are similar to those of the present study. Despite the low sample sizes, Large Hawk-Cuckoo breeding success with Babax hosts is within the range of the Common Cuckoo with several of its major hosts (Kleven *et al.* 2004).

Large Hawk-Cuckoos laid highly non-mimetic eggs that were largely accepted by the Babax, consistent with a scenario that the Babax may be an evolutionarily recent host of this parasite. To better understand this host-brood parasite system, experiments involving introduction of foreign eggs in unparasitized Babax nests while controlling for egg stage are necessary.

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