

*Yellow wing-patch of a nestling Horsfield's hawk cuckoo *Cuculus fugax* induces miscognition by hosts: mimicking a gape?*

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A chick of the Horsfield's hawk cuckoo *Cuculus fugax* has a vivid yellow skin patch on each wing-bend, which is very similar in colour to its own gape. Almost every time a host parent delivers food, the chick explicitly displays the wing-patch by raising and shaking the wing. We observed that host parents tried to place food onto the wing-patch of the nestling instead of into its mouth. The wing-patch would be perceived as a gape by host parents, possibly resulting in an overestimation of brood size. Signals induced by the wing-patch may vary with the luminosity of environments.

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Parasitism that crucially damages fitness or survival of hosts invokes a strong coevolutionary arms race (Dawkins and Krebs 1979, Davies and Brooke 1998). As a consequence, most social parasites, including birds, manipulate their hosts by using and amplifying the signals for hosts' social communication (Davies et al. 1989, Grim and Honza 2001, Hølen et al. 2001, Tanaka and Ueda 2005a). Thus the manipulative tactics by parasites vary with the mechanisms for parental care of hosts they exploit (Redondo 1993, Soler et al. 1995, Kilner et al. 1999, Davies 2000, Payne et al. 2001).

Here we show a series of unique characteristics in a parasite nestling of the Horsfield's hawk cuckoo *Cuculus fugax*. A hawk cuckoo chick has a naked skin patch of vivid yellow on each wing-bend, which is very similar in colour to its own gape (Fig. 1, see Tanaka and Ueda 2005b). It raises and shakes the wing when host parents deliver food to the nest, obviously displaying the wing-patch (Yamaguchi 1994, Tanaka and Ueda 2005b). Display of the wing-patch by the hawk cuckoo chick apparently manipulates its host visually. Because of the

conformity in the colour, we assumed that host parents mistake the wing-patch for a gape, which may cause an overestimation of brood size. We conducted field investigations to confirm whether the misperception by the host parents actually occurs.

Materials and methods

Study areas

We conducted the study in a sub-alpine coniferous forest at Subashiri, Oyama, in Shizuoka prefecture, Japan (35°21'N, 138°52'E; 2001–2003), and in deciduous forests at Karuizawa, Nagano prefecture, Japan (36°19'N, 138°38'E; 2002). Subashiri is located on the slope of Mt. Fuji, at about 2000 m a.s.l. Karuizawa is at 1000 to 1500 m a.s.l. We searched for the nests of host species throughout their breeding seasons in these areas.

Materials

The Horsfield's hawk cuckoo, which occurs in southern and eastern Asia, is an obligate brood parasite. It is a summer resident in Japan, and breeds from early May to late July (OSJ 2000). It mainly lays eggs in the nests of the Siberian blue robin *Luscinia cyane*, the red-flanked bushrobin *Tarsiger cyanurus* and the blue-and-white flycatcher *Cyanoptila cyanomelana* (Higuchi 1998), all of which usually nest on the ground. The Siberian blue robin and the blue-and-white flycatcher are also summer residents in Japan, and breed in valleys and on hillsides of mountainous regions from 300 to 1800 m a.s.l. The red-flanked bushrobin breeds in subalpine regions in summer, and winters in lowland. A nestling of the red-



Fig. 1. A chick of the Horsfield's hawk cuckoo, photographed just after fledging, raises its right wing and displays the wing-patch to the host father as he delivers food.

flanked bushrobin has a dull yellow gape with a yellow flange and nestlings of the Siberian blue robin and the blue-and-white flycatcher have a dull orange gape with a yellow flange, while the gape and wing-patch of hawk cuckoos are a vivid yellow overall.

On the day of hatching, the hawk cuckoo chick is totally naked and has a flesh-coloured skin, whereas host hatchlings are partly plumed on the head and back. In the next couple of days, with the development of feather buds, the skin acquires a black pigmentation on the backside, and a yellow pigmentation on the abdominal side of the body, including the tarsus and the wing. The whole of the skin is not fully covered with feathers, as it is in many altricial species, the wing-bend remains naked, and persists even after the hawk cuckoo chick becomes fledged. Adult hawk cuckoos, including juvenile breeders, have no such patch on the wing.

Methods

We located micro CCD cameras (AVDech Pinhole CCD Camera, Tokiwa Shoko, Tokyo, Japan, or PBC IR LED Waterproof CCD Camera, Tsukamoto Musen, Co., Ltd., Mie, Japan) beside parasitized nests to record the behaviour of parasitic young and host parents. We recorded video data using Sony CCD TRV-66K Hi8 Video Camera (Sony Corp., Tokyo, Japan) or Canon

FV30 Digital Video Camera (Canon Inc., Tokyo, Japan), via the micro CCD cameras. Video data was recorded for a maximum of 8 hours a day. We also measured luminosity inside and outside the parasitized nests near noon on a day with clear weather after the nestlings had fledged, using SLX-1334 digital lux-meter (Shiro Industry Co., Osaka, Japan).

Using the video observations, we counted misfeedings when the host parents pecked exactly at the displayed wing-patch, mostly when they had prey in the bills for feeding. They sometimes pecked at the wing when it was down by the side of hawk cuckoo chicks' body, which looked like as if they stimulated lying nestlings, or at times they removed ectoparasites. Neither of them were counted.

Results

We located 200 host nests, 25 of which had been parasitized. We recorded the behaviour of the hawk cuckoo nestlings in seven parasitized nests. All recorded nests were of the red-flanked bushrobin. We were unable to standardize the age of chicks for video recordings because these nests were not always found before hatching (Table 1). We measured the luminosity in only three nests (Table 1). These three nests were all quite dark, so we are continued that the other nests were dark as well.

In three of the seven observed nests, we noticed that host parents tried to place food onto the wing-patch instead of into the mouth of the parasite nestlings (Fig. 2a). Such inappropriate delivery is clearly distinguishable from a correct feeding (Fig. 2b). These misfeedings occurred variably and infrequently (Table 1).

Discussion

In the present study, we confirmed that host parents mistook the wing-patch of the Horsfield's hawk cuckoo nestlings for a gape of a chick. This indicates that the hawk cuckoo chick exploits the hosts' cognitive ability in order to obtain sufficient food by mimicking a gape with

Table 1. Records of observed misfeedings in each nest.

No.	Nestling age at video recordings (days)	No. misfeedings/ feedings	No. observation h (days)	Luminosity inside the nests (lux)	Year
1	10–13*	8/340	23 (4)	–	2001
2	12–14	3/244	15 (3)	–	2002
3	7, 10, 12, 14*	0/476	24 (4)	–	2002
4	12–14*	1/141	13 (3)	–	2002
5	15, 16	0/347	16 (2)	110 (474)†	2003
6	16, 17*	0/184	8 (2)	53 (3520)†	2003
7	15, 17	0/410	15 (2)	3.05 (1065)†	2003

*The age is approximate because we could not confirm the hatching date. †Luminosity outside the nests is shown in parentheses.

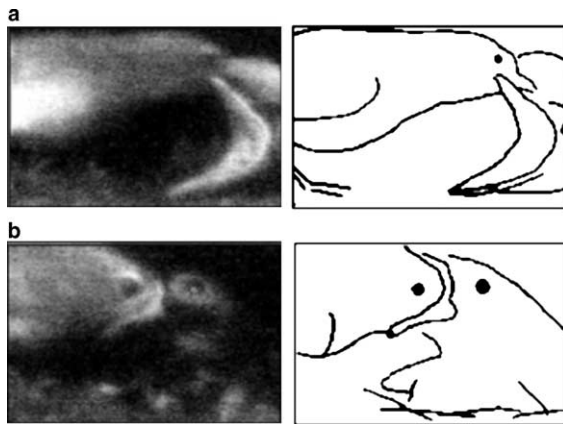


Fig. 2. A host parent misperceives the skin patch of a parasite chick as a gape in the dark nest. (a) A host parent attempting to feed the wing-patch of a parasite chick by mistake. (b) A host parent feeding the parasite chick correctly just after the misfeeding. Camera images on the left were traced to enhance visibility (right).

the wing-patch (cf. Lyon 2003). However, the frequency of misfeedings is very low (Table 1). It may be because the hawk cuckoo chick moves its head towards wherever the host parent is attempting to feed, thus successfully obtaining most of the food and lowering the rate of misfeedings. Hawk cuckoo chicks may try to avoid the misfeedings since the wing-patches of some chicks occasionally showed signs of scraping, suggesting the possibility that misfeedings may impose physical damage to nestlings, as a cost of begging (e.g. Kilner and Johnstone 1997).

The host parents clearly mistook the wing-patch of the Horsfield's hawk cuckoo chick for a gape. How does this behaviour operate in this host-parasite system? One apparent function is to elicit food provisioning (Tanaka and Ueda 2005b). By deceiving host parents into believing that they have a larger brood, the hawk cuckoo nestling may stimulate them to gather more food, because parents tend to feed the larger broods more (Trivers 1972, Brooke and Davies 1989, Kilner and Johnstone 1997). This is a kind of mimicry, which may depend on the darkness of a nest since the shapes of the wing-patch and a gape do not resemble each other. Decreased visibility in the dark nests may prevent the host parents from noticing this difference (e.g. Fraga 1998). The yellow pigmentation of the gape and wing-patches of the hawk cuckoo chick indicates that the wing-patch manipulation has evolved to exploit hosts that nest in dark places (e.g. Kilner and Davies 1998). The yellow gape of a nestling could enhance detectability in the dark nest, and thus induce parental feeding (Heeb et al. 2003).

On the other hand, expanding the total area of gape-coloured skin may increase parental care given by hosts without each wing-patch being perceived as a particular

gape, as Kilner et al. (1999) shows in the host-parasite system in the common cuckoo *Cuculus canorus*. Host parents of the reed warbler *Acrocephalus scirpaceus* adjusted food provisioning in relation to the total displayed area of nestling gapes, both for their own broods and for the cuckoo chicks (Kilner et al. 1999). The latter way may be particularly advantageous in high luminosity.

In the case of the common cuckoo, parasitic young beg for food with an extraordinarily loud and rapid call (Davies et al. 1998, Kilner et al. 1999), to compensate for its deficient visual stimulus as shown by the smaller gape area compared to the total gape area of a normal brood of hosts (Kilner et al. 1999). On the contrary, both hawk cuckoo chicks and their host nestlings rarely beg loudly before they fledge (pers. obs.), which may be an adaptation to avoid predation by mammals since the hosts typically nest on the ground (e.g. Haskell 1999). Further investigation is necessary to elucidate the host manipulation system of the Horsfield's hawk cuckoo chick.

Acknowledgements – We greatly appreciate the assistance provided by the following people. In the field: Mr. T. Ishizuka, Mr. N. Ohnishi, Ms. T. Makita, our laboratory members especially Mr. S. Sudo, Mr. T. Miyashita and Mr. Y. Harashima, Mr. H. Uchida, Mr. A. Bowman, Mr. S. Shirai, Ms. K. Yamaguchi, Mr. E. Uematsu, Mr. H. Takano, and people of lodges on Mt. Fuji. Producing the manuscript: Dr. N. Yamaguchi, Dr. R. M. Kilner, Mr. M. Ueta, Mr. S. Imanishi, Dr. S. Hamao, Mr. G. Fujita, Dr. K. Ishida, Dr. J. Pierre, Ms. C. Tanaka, Ms. J. Tamura, and Ms. A. Saito. This study was financed by the Japan Society for the Promotion of Science (No. 12640622). We conducted our fieldwork with the permission of the Forestry Agency and the Ministry of the Environment of Japan.

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(Received 9 April 2004, revised 8 September 2004, accepted 22 September 2004.)