

Letter to the Editor

Absence of anti-parasitic defenses in an Asian population of the magpie, a regular host of the great spotted cuckoo in Europe

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Obligate brood parasitism, which refers to parasitic birds, fish, and insects that lay eggs in host nests, imposes strong selective pressure on hosts because the reproductive output of hosts is reduced considerably or eliminated completely while the foster parents provide extra-parental care to unrelated nestlings (Soler 2016). After parasites succeed in laying eggs, egg rejection by hosts plays an important role in avoiding parasitism by recognition and rejection of parasite eggs from host nests (Yang et al. 2014). Coevolution between brood parasites and hosts occurs in the great spotted cuckoo *Clamator glandarius* and the Eurasian magpie *Pica pica* is a classical parasite–host system. To counter cuckoo parasitism, Eurasian magpies were capable of attacking and expelling adult cuckoos from their nests, and recognizing and rejecting parasitic eggs by either visual or olfactory cues (Soler et al. 2014). However, these studies on Eurasian magpies all came from European populations, where parasitism is common in many populations. To understand coevolution between magpie hosts and cuckoo parasitism, it is necessary to investigate anti-parasitic defenses of magpies from other populations because behavior in 1 population may be totally different from that in other populations (Yang et al. 2015). Eurasian magpies have a wide distributional range across Europe and Asia, but great spotted cuckoos have a much narrower distribution of allopatry with the Asian population of magpies. It is necessary to study such Asian populations of magpies because anti-parasitism defenses would help us understand the coevolutionary interaction between magpies and cuckoos. For host populations that are allopatric with parasites and lack anti-parasite defenses, their absence of defenses can either be explained as (1) the loss of defenses after the release of parasitism pressure or (2) simply no evolution of defenses due to no contact with brood parasites. In contrast, some host populations that are allopatric with parasites or not exploited by parasites may retain

their anti-parasitism defenses. Black-billed magpies *Pica hudsonia* and yellow-billed magpies *P. nutalli* are closely related to Eurasian magpies, but only distributed in America. Both are allopatric with great spotted cuckoos and not used by any cuckoo species. Still, they possess 100% egg recognition capacity, which is higher than that of Eurasian magpies (Soler 2016).

Here we performed the first empirical study (see [Supplementary Materials](#) for the study materials and methods) on an Asian population of Eurasian magpies to examine whether it has evolved anti-parasitic defenses, including nest defense and egg rejection. This study population is allopatric with the great spotted cuckoo, but sympatric with other cuckoo species, including Northern hawk cuckoo *Hierococcyx hyperythrus*, Indian cuckoo *Cuculus micropterus*, common cuckoo *C. canorus*, Oriental cuckoo *C. optatus*, and lesser cuckoo *C. poliocephalus* (Yang et al. 2012). The anti-parasitic defenses of magpies in Asia have so far not previously been reported, and the aim of this study was to fill this gap and provide information for better understanding the coevolutionary interaction between magpies and cuckoos. We found no case of parasitism in magpie nests ($N = 79$), and no rejection or desertion in nests with either visual ($N = 15$) or olfactory treatment ($N = 10$) in parasite experiments. The control nests for these treatments ($N = 15$ and $N = 10$, respectively) provided similar results. For the nest defense experiments ($N = 16$), magpies exhibited 2 cases of mobbing, 12 cases of alarm and 2 cases of no response to the cuckoo dummy, and 7 cases of alarm and 9 cases of no response to the dove dummy, and 16 cases of alarm to the sparrowhawk dummy (Figure 1). The responses differed significantly among dummies ($F_{2,36} = 9.902$, $P < 0.001$, generalised linear mixed model (GLMM), although the interaction between dummy species and dummy order, and the interaction between dummy species and dummy replicates, were not

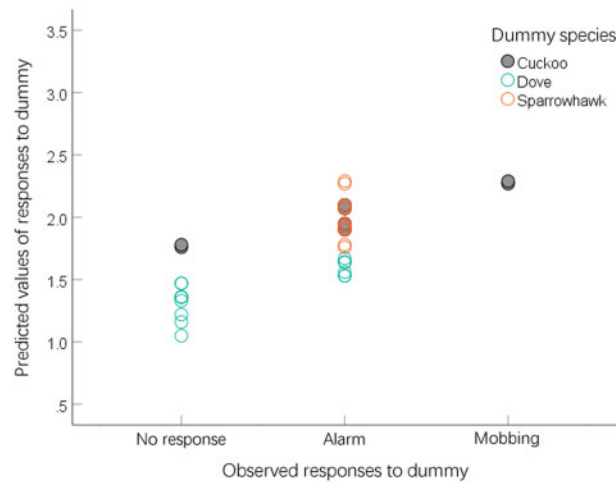


Figure 1. Observed and predicted responses toward dummies during nest defense experiments. Expected values were generated from generalized linear mixed models.

significantly different (dummy species \times dummy order: $F_{6,36} = 0.09$, $P = 0.997$, GLMM; dummy species \times dummy replicates: $F_{3,36} = 0.108$, $P = 0.955$, GLMM). *Post hoc* tests indicated significance ($P < 0.05$, Tukey HSD) between responses of cuckoo and dove, and sparrowhawk and dove, but not between responses of cuckoo and sparrowhawk.

Parasitism was not detected in our study population of magpies, and magpies were not found to possess any capacity of egg recognition, neither based on visual nor olfactory cues. Although their responses to the cuckoo and sparrowhawk dummies were more aggressive than toward the dove dummy, no significant difference was found between responses to cuckoo and sparrowhawk models. One possible explanation for this may be that common cuckoos were not a brood parasite of magpies, and thus magpies fail to distinguish between cuckoos and sparrowhawks. Unlike non-evicting great spotted cuckoo chicks that are reared together with cuckoo chicks, and compete with host chicks such as those of the cuckoo for food (Soler et al. 1999), all sympatric cuckoo species recorded in our study area evicted parasite eggs (Yang et al. 2012). Therefore, an alternate explanation may be that significantly smaller cuckoo eggs (for the detail of egg size information see Yang et al. 2012) do not succeed in parasitism of magpie nests because cuckoo chicks are too small to evict magpie eggs/chicks. If reared together with host chicks, evictor parasites such as common cuckoos are not as superior as non-evictor parasites because shared parental care with host chicks is costly for evicting cuckoo chicks (Hauber and Moskát 2008). However, common cuckoos succeeded in parasitizing common redstarts *Phoenicurus phoenicurus* even though their nestlings frequently failed to evict host eggs (Rutilla et al. 2006). Therefore, body size should not be the major or single reason explaining the absence of parasitism in Asian magpies. Another explanation may be that this type of brood parasite (i.e., evictor or killer vs. non-evictor) because each of these types of brood parasites has been adapted to parasitize hosts with a different breeding strategy (Soler 2001). Clutch size adjusters tend to distribute food evenly among nestlings in the nest, preferentially feeding offspring that are in poor condition. In contrast, brood reducers tend to feed larger offspring independently of begging intensity (Soler 2001). When cuckoos parasitized clutch size adjusters, it is costly for their nestlings to compete with nestmates because host parents tend to feed nestlings evenly. In contrast, the

cuckoo chicks need a quantity of food equivalent to that of a whole brood of the hosts. However, it is less costly for cuckoos to parasitize a clutch reducer when they are non-evictors because host parents tend to feed larger nestlings. Cuckoo chicks would benefit from this breeding strategy by their earlier hatching and larger size compared with that of host nestlings (Soler 2001). All cuckoo species found in our study area were evictors with smaller size than that of magpies. None of these cuckoo species could successfully utilize magpies because the cuckoos were too small for evicting magpie offspring, and, more importantly, they also failed to compete with magpie nestlings because magpies are brood reducers that tend to feed larger nestlings (in this case magpie nestlings). In summary, the absence of large-sized non-evictor cuckoos may together contribute to explain the absence of parasitism in this Asian population of magpies. Therefore, these features may further explain the absence of egg rejection in this magpie population. Although magpies were not parasitized by cuckoos, the absence of parasitism may not exclusively lead to the absence of anti-parasitic defenses. The absence of defenses in this Asian population of magpies may be due to magpies either (1) never having been parasitized by any brood parasite, and thus no specific defenses have evolved. Alternatively, (2) magpies may have been in contact with great spotted cuckoos previously, but lost their defenses after diverging from its common Eurasian ancestor. Most previous studies suggested that non-parasitized populations of hosts maintained their defenses after long time of release from parasitism (up to 3 million years) (e.g., Peer et al. 2011). Eurasian and Asian populations of magpies were separated ca. 2.3 million years ago, although the divergence time of great spotted cuckoos was earlier at ca. 17.7 million years ago (Jetz et al. 2012). This implies that if Asian magpies have acquired egg recognition before divergence, they have lost this recognition capacity in 2.3 million years. Therefore, the more likely explanation for the absence of anti-parasitic defenses in this Asian population of magpies is that they have not acquired egg recognition capacity because they never previously were exploited successfully by any brood parasite.

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Ethical note

The experiments reported here comply with the current laws of China. Fieldwork was carried out under the permission from Xianghai National Nature Reserve, Jilin, China. Experimental procedures were in agreement with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (permit no. HNECEE-2014-005).

Competing interests

The authors declare that they have no competing interests.

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