**ORIGINAL ARTICLE**

# Rejection of parasitic eggs by Yellow-bellied Prinias: importance of egg spot location

Longwu Wang[1,2] · Yu-Cheng Hsu[3] · Wei Liang[2]

## Abstract
Characteristics of egg surfaces serve as recognition cues that allow avian hosts to detect and reject foreign eggs in brood parasitism. The blunt egg pole hypothesis suggests that the blunt egg pole is an essential signal in parasitic egg recognition. In the present study, eggs of Yellow-bellied Prinia (*Prinia flaviventris*) were painted with black spots at either the blunt or sharp egg pole to determine and compare the responses of different populations exposed to brood parasitism (parasitized population) or not (non-parasitized population). These results supported the above hypothesis and showed that the parasitized population displayed a higher rate of rejection of eggs with blunt pole-painted spots than with sharp pole-painted spots. In contrast, the non-parasitized population accepted all experimental eggs, which may be related to decreased egg recognition resulting from low exposure to brood parasitism.

**Keywords** Brood parasitism · Egg discrimination · Recognition cues · Blunt pole · *Prinia flaviventris*

## Zusammenfassung
**Entfernen der Eier von Brutparasiten durch Gelbbauchprinien: Die Bedeutung der Position von Pigmentflecken**
Merkmale von Eioberflächen dienen als Erkennungssignale, die es Wirtsvögeln ermöglichen, im Fall von Brutparasitismus fremde Eier zu erkennen und zu entfernen. Die „stumpfer Eipol" Hypothese schlägt vor, dass der stumpfe Eipol ein entscheidendes Signal für das Erkennen der Eier von Brutparasiten darstellt. In der vorliegenden Studie haben wir die Eier von Gelbbauchprinien (*Prinia flaviventris*) mit schwarzen Punkten bemalt, entweder am stumpfen oder am spitzen Eipol, um die Antworten der Vögel in parasitierten und nicht parasitierten Populationen zu ermitteln und vergleichen. Unsere Ergebnisse stützten die obengenannte Hypothese und zeigten, dass Gelbbauchprinien in der parasitierte Population Eier, bei denen die Flecken auf den stumpfen Eipol gemalt wurden, mit höherer Wahrscheinlichkeit entfernten als Eier mit am spitzen Eipol aufgemalten Flecken. Im Gegensatz dazu wurden in der nicht parasitierten Population alle experimentellen Eier akzeptiert, was mit verminderter Eierkennung infolge geringer Brutparasitismusgefahr zusammenhängen könnte.

✉ Wei Liang
liangwei@hainnu.edu.cn

1 State Forestry Administration of China Key Laboratory for Biodiversity Conservation in Mountainous Areas of Southwest Karst, School of Life Sciences, Guizhou Normal University, Guiyang 550001, China

2 Ministry of Education Key Laboratory for Ecology of Tropical Islands, College of Life Sciences, Hainan Normal University, Haikou 571158, China

3 Department of Natural Resources and Environmental Studies, National Dong Hwa University, Hualien 97401, Taiwan

## Introduction

The evolutionary arms race between hosts and avian brood parasites is a classic example of co-evolution (Dawkins and Krebs 1979; Davies 2000). Parasitism can have severe and negative impacts on host fitness, forcing hosts to evolve corresponding counter-adaptations against parasites (Davies 2000, 2011; Soler 2014; Feeney et al. 2014). Among the various anti-parasite strategies, one such adaptation is the ability to recognize and reject foreign eggs (Davies and deL Brooke 1989a, b; Sealy and Underwood 2012).

Visual modeling has revealed that avian hosts recognize foreign eggs using multiple signals as recognition cues, with this selective pressure facilitating the extent of egg mimicry by parasites (Spottiswoode and Stevens 2010). Therefore, variations in the characteristics of eggs across species can serve as signals for recognition and rejection of foreign eggs by hosts in avian brood parasitism (Kilner 2006). These variations are smaller within intra-clutches, but larger across different inter-clutches (Øien et al. 1995; Soler and Møller 1996; Stokke et al. 2002; Yang et al. 2015a). The host may discriminate and reject foreign eggs based on various egg traits, such as size (Rothstein 1982; Marchetti 2000), shape (Rothstein 1982; Underwood and Sealy 2006), background color (Stokke et al. 1999; Cherry et al. 2007; Honza et al. 2007; Moskát et al. 2008a; Yang et al. 2010), and the presence or absence of spots or stripes (Stokke et al. 2007; Moskát et al. 2008b; López-de-Hierro and Moreno-Rueda 2010; Liu et al. 2019). A recent study showed that Magpies (*Pica pica*) use olfactory cues to identify and reject foreign eggs (Soler et al. 2014). Furthermore, in addition to visible light, birds can detect ultraviolet (UV) light using a fourth cone cell type in the retina (Bennett et al. 1996; Bowmaker et al. 1997; Cuthill et al. 2000). Spectral analyses of brood parasitism have indicated that UV light plays an important role in avian egg recognition cues (Cherry and Bennett 2001; Avilés and Møller 2004; Avilés et al. 2006; Honza and Polaciková 2008; Yang et al. 2013).

Among the numerous recognition signals, egg shape does not appear to affect egg recognition by hosts commonly (Underwood and Sealy 2006), whereas background color and spots on eggs may play more important roles in host egg recognition (Moskát et al. 2008a, 2010). For example, López-de-Hierro and Moreno-Rueda (2010) conducted a study on House Sparrows (*Passer domesticus*) and showed that egg spots are a key factor influencing egg recognition (also see Yang et al. 2015b).

Generally, avian eggs can be divided into two parts: the blunt pole (BP) and sharp pole (SP) (Polačiková et al. 2010; Polačiková and Grim 2010). Spots on eggshells are usually equally distributed or concentrated at the BP, but seldom at the SP (Lack 1968; Kilner 2006). Regarding the importance of specific egg parts in egg recognition, the blunt egg pole hypothesis suggests that spots at the BP play a key role in both intraspecific and interspecific egg recognition (Polačiková et al. 2007, 2010; Polačiková and Grim 2010). This hypothesis has been tested in several species of birds subjected to interspecific parasitism (e.g., Great-Reed Warblers *Acrocephalus arundinaceus* and Reed Warblers *A. scirpaceus*) or intraspecific parasitism (e.g., Song Thrushes *Turdus philomelos* and Blackbirds *T. merula*), which indicated that egg recognition cues are concentrated at the BP (Polačiková et al. 2010; Polačiková and Grim 2010). The eggs of the above host species contain spots that are mainly concentrated at the BP. To date, however, no study has investigated egg recognition ability in host species that have no spots on their eggs, as the effect of background color on egg spots cannot be excluded (Polačiková et al. 2010; Polačiková and Grim 2010).

Populations of the same species differ in rates of parasitism, which may lead to differential selection of egg recognition/rejection skills (Polačiková et al. 2009; Yang et al. 2014). The Yellow-bellied Prinia (*Prinia flaviventris*) is a small passerine bird species widely distributed in southern mainland China and Taiwan. Their eggs are red, with no markings on the surface (Yang et al. 2014; Figs. 1, 2); thus, the background color is suitable for adding experimental spots on the egg surface. In Taiwan, the Yellow-bellied Prinia has been geographically separated from the Chinese mainland for 2–3 million years (Chen et al. 2000; Yeung et al. 2011). This species is the main host of the Oriental Cuckoo (*Cuculus optatus*), which is the only obligate brood parasite of the Taiwanese prinia population (Yang et al. 2012, 2014). In contrast, no cases of cuckoo parasitism have been reported for Yellow-bellied Prinia in mainland China (Yang et al. 2012, 2013, 2014). Taiwanese populations also show significantly higher rates of rejection toward non-mimetic eggs than mainland populations (Yang et al. 2013, 2014; Wang et al., 2016). Thus, the Yellow-bellied Prinia is an ideal species for investigating and comparing egg recognition ability in host-parasitized (Taiwan) and non-parasitized systems (mainland). Yellow-bellied Prinias can recognize foreign eggs using egg color and UV light perception (Yang et al. 2013, 2014), but other recognition cues need to be further tested.

In this study, the blunt egg pole hypothesis was investigated by painting black spots at either the BP or SP in two populations of Yellow-bellied Prinia that differed in parasitism pressure. It was predicted that (1) eggs painted at the BP would have higher rates of rejection than those painted at the SP, and (2) the population in Taiwan would show higher rates of rejection toward both BP- and SP-painted eggs than observed for the Chinese mainland population.

**Fig. 1** Photographs of experimental Yellow-bellied Prinia eggs in nest. **a** Painted blunt pole and **b** painted sharp pole, with remaining eggs unpainted. Photo by Longwu Wang

**Fig. 2** Mean reflectance of original eggshell surface ($n = 30$) and painted spots ($n = 5$) on Yellow-bellied Prinia eggs. Original eggs are brownish-red in color, and painted spots are black (color figure online)
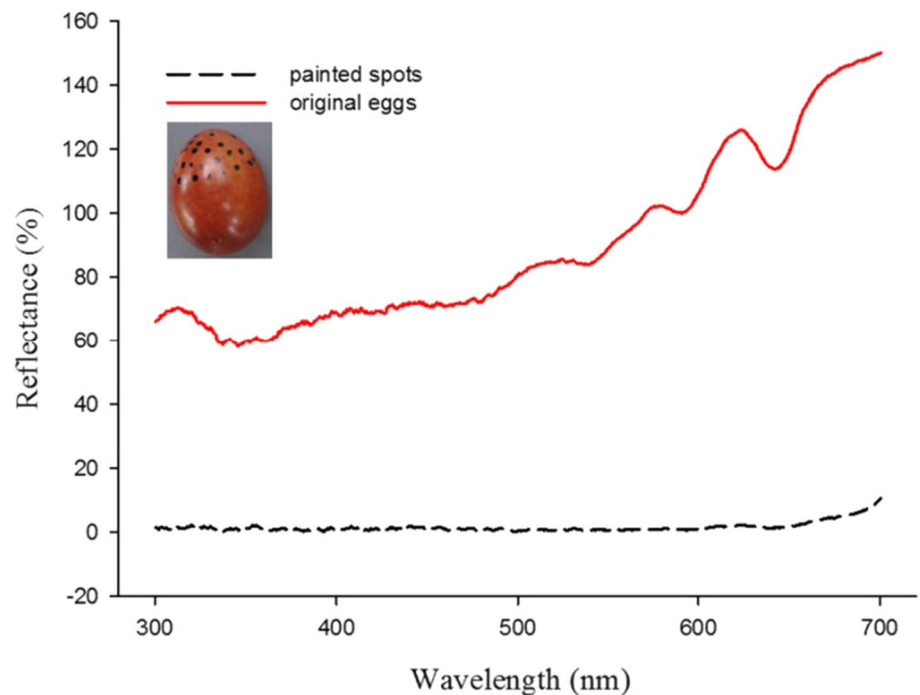


## Materials and methods

### Study areas and species

The study site in mainland China was located at the Nonggang National Nature Reserve, Guangxi, Southwest China (23°39′ N, 107°04′ E). The study period was from April to July 2012–2014. The Taiwan study site was located at Shoufong, Hualien County (23°51′ N, 121°31′ E). The study period was from April to July 2010–2011 (for study site details, see Yang et al. 2013, 2014). During the breeding season, both male and female Yellow-bellied Prinias participate in nesting in low bushes or small shrubs. Nests are built 1 m high above the ground and have an irregular

spherical shape with a side opening in the upper part of the nest (Ding et al. 2008). In this study, Yellow-bellied Prinia hosts exploited by oriental cuckoos were noted only in Taiwan, with a parasitism rate of 0.91% ($n = 110$). No cases of parasitism were found in mainland China ($n = 232$) (Yang et al. 2014), although several species of prinias have been listed as potential hosts for several other cuckoo species in mainland China (Yang et al. 2012, 2014). Furthermore, the Taiwanese Yellow-bellied Prinia populations show a stronger response to foreign egg rejection and defense against dummy cuckoos than populations in mainland China (Yang et al. 2013, 2014).

### Field procedures

The Yellow-bellied Prinia species shows considerably stronger egg recognition ability and refuses all foreign eggs, including conspecific eggs (Yang et al. 2014), as well as their own eggs treated with UV-blocking agent (to reduce UV spectral reflectance) (Yang et al. 2013). Therefore, prinia nests were artificially parasitized by painting one egg within a clutch (Fig. 1) rather than replacement with conspecific eggs from other prinia nests (e.g., Polačiková et al. 2010; Polačiková and Grim 2010), thus eliminating interference caused by conspecific eggs. Nests were searched and the BP or SP of one egg in each nest was painted using a waterproof black pen (pen point size: 1.0 mm) after hosts laid their last egg or during early incubation. Before painting, each experimental egg was divided into two parts of equal area across their diagonal axis (see Polačiková and Grim 2010). Spots were then applied in one-third region of two poles (BP or SP) of these eggs, but in the mid-region, all the spots of approximately 1 mm diameter at a distance of about 2 mm from each other were painted by the same manipulator to eliminate manipulation deviation (see Fig. 1). Nests with unpainted conspecific clutches were used as the control ($n = 12$ in each population). For all treatments, prinia nests were monitored daily for six consecutive days (following Moksnes et al. 1991). Responses of the Yellow-bellied Prinias were classified into rejection or acceptance. Rejection referred to the disappearance of the experimental egg or abandonment of the clutch within the experimental period. Acceptance referred to a situation when the experimental egg remained unharmed in the nest and the clutch was incubated (Yang et al. 2013). The latency to rejection (i.e., time interval from brood parasitism to rejection) was calculated daily (considering days as units).

### Egg spectrophotometric measurements

Conspecific eggs collected from deserted nests were used to replace the whole clutch and sent them back when measurement of egg reflectance was over. All eggs were measured and then one-eggpainted spots were selected on blunt or sharp pole to measure the spots. Because the painted color was from the same pen and had no color variation, only five eggs were selected and the spots were measured as representative reflectance spectra of this species (Polačiková and Grim 2010). Similarly, only 30 eggs from all samples were selected for mean egg reflectance. These treatments were used to show differences in painting spots and original surface egg color. Egg spectrophotometric measurements were performed using an Avantes-2048 spectrometer with a 10 W tungsten halogen light source (Avalight-Hal-S; Avantes, Apeldoorn, the Netherlands). Six spectral reflectance measurements were obtained per egg after the egg surface was divided into the three regions (i.e., blunt, middle, and sharp poles). Measurements covered a spot size of approximately 1 mm in diameter on the egg surface, so was the painting spots, and the reflection of the surface was measured at an angle of 45°, with the co-axial reflectance probe held 5 mm from the surface (FCR-7UV200-2-ME). The spectral data were analyzed using Ava-Soft 7.0 software (Avantes, Apeldoorn, the Netherlands) and interpolated at 1 nm steps in the 300–700 nm range.

### Statistical analysis

The responses of Yellow-bellied Prinia to experimental eggs were compared using the generalized linear model (GLM) with binomial distribution and logit link function used to assess host responses to parasitic eggs (acceptance or rejection) according to (1) populations in Taiwan and mainland China (two groups), (2) painted spots (three experimental groups, i.e., control, blunt pole, sharp pole), and (3) interactions between populations and groups. One-way ANOVA was used to test egg rejection latency between painted BP and SP. Statistical analyses were performed using IBM SPSS 25.0 (IBM Inc., Armonk, NY, USA). Values are presented as mean ± standard deviation (SD) unless stated otherwise.

### Results

The mean spectral reflectance of painted spots was close to zero in the investigated wavelength range of 300–700 nm (Fig. 2), with no differences in reflectance found between BP ($36.11 \pm 11.9$) and SP ($36.19 \pm 12.81$) ($t$ test, $t = -0.019$, $df = 58$, $P = 0.985$).
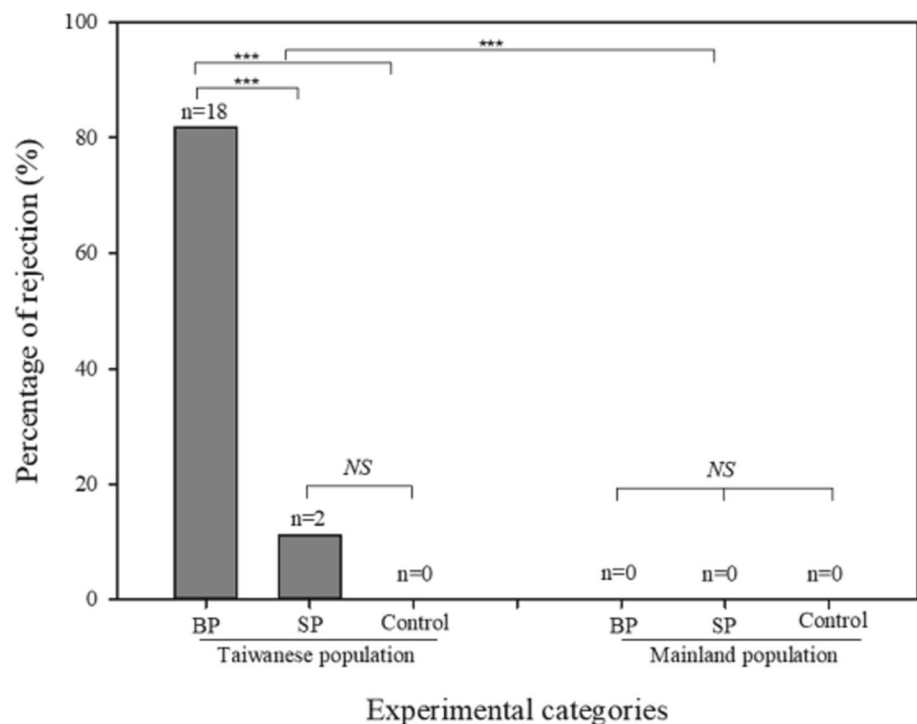
**Table 1** Results of GLM with a binomial distribution assessing rejection responses of two Yellow-bellied Prinia populations (Taiwan and mainland China) to parasitic eggs

| Source | $F$ | $df1$ | $df2$ | Sig. |
| --- | --- | --- | --- | --- |
| Corrected model | 6.874 | 5 | 92 | < 0.001 |
| Group | 7.575 | 2 | 92 | < 0.001 |
| Population | 1.402 | 1 | 92 | 0.239 |
| Group × population | 7.575 | 2 | 92 | < 0.001 |

"Group" means three types of experiments, including blunt pole-painted spots, sharp pole-painted spots, and unpainted eggs

The rejection of eggs was explained by interaction between populations and experimental groups (Table 1). This interaction showed that while no rejection was observed in the control groups in either population, the rejection rate of experimental eggs varied between populations (GLM, $F = 7.575$, $P < 0.001$). Specifically, no experimental eggs were rejected by the mainland population, whereas experimental eggs painted at the BP were rejected at a higher rate than experimental eggs painted at the SP by the Taiwan population (GLM, SP vs. BP, $P < 0.001$, SP vs. control, $P = 0.560$, BP vs. control, $P < 0.001$, Fig. 3). In the Taiwan population, the egg rejection latency showed no significant differences between painted BP and SP (ANOVA, $F = 1.507$, $P = 0.235$), with eggs painted at the BP rejected within 3 days ($n = 18$), and those painted at the SP rejected after 4–5 days.

## Discussion

These results confirmed the predictions that the island population of Yellow-bellied Prinia used the BP as a discrimination cue to recognize and reject foreign eggs. On the other hand, the mainland Chinese population, a non-parasitized system, accepted all experimental eggs, and the blunt pole hypothesis was not supported. Generally, hosts under high parasitic pressure show higher egg rejection rates than those under low parasitic pressure (Davies and deL Brooke 1989a; Moksnes et al. 1991; Lindholm and Thomas 2000; Stokke et al. 2008; Yang et al. 2013, 2014). The Taiwanese prinia population parasitized by cuckoos exhibits stronger foreign egg rejection ability and stronger defenses against invaders (Yang et al. 2014), suggesting that the Taiwanese population is under high parasitic pressure, unlike mainland populations. In this study, it was found that the Taiwanese population rejected eggs painted at the BP within 3 days, whereas those painted at the SP were rejected after 4 to 5 days. This suggests that the latency to rejection was smaller for BP-painted eggs than for SP-painted eggs. Thus, these findings are consistent with those of previous studies showing that the Taiwanese prinia populations have higher rejection rates than those in mainland China (Yang et al. 2014).

The mainland Chinese population accepted all experimental eggs, which was likely due to decreased recognition of foreign eggs by hosts. In previous study, the hosts in this population showed only a 50% rejection rate to non-mimetic

**Fig. 3** Percentages of rejection for experimental categories in mainland and Taiwanese populations, i.e., BP, SP, and control, respectively, (*NS* refers to no significance and *** refers to $P < 0.001$)

**Table 2** Comparison of egg rejection behavior toward eggs painted black at blunt (BP) or sharp (SP) poles and summary of rejection rates against model and conspecific eggs between mainland China and Taiwan populations of Yellow-bellied Prinia

| Study site | Rejection (%) | Acceptance (%) | Nest tested | Rejection lag (day) | Source |
|---|---|---|---|---|---|
| Taiwan | | | | | |
| BP | 81.8 | 18.2 | 22 | $< 2.4 \pm 0.5$ ($n = 18$) | This study |
| SP | 11.1 | 88.9 | 18 | $< 4.5 \pm 0.7$ ($n = 2$) | This study |
| Model egg | 100 | 0 | 13 | $< 1 \pm 0$ ($n = 13$) | Yang et al. (2014) |
| Conspecific egg | 16.7 | 83.3 | 18 | – | Yang et al. (2014) |
| Guangxi | | | | | |
| BP | 0 | 100 | 19 | – | This study |
| SP | 0 | 100 | 15 | – | This study |
| Model egg | 50 | 50 | 18 | $< 1.6 \pm 0.7$ ($n = 9$) | Yang et al. (2014) |
| Conspecific egg | 0 | 100 | 15 | – | Yang et al. (2014) |

eggs but accepted all conspecific eggs. On the other hand, the Taiwan population showed 100% rejection toward non-mimetic eggs and even partial rejection toward conspecific eggs (16.7%) (Yang et al. 2014; Table 2). Retreat of parasites may be one of the reasons for the reduced recognition ability in the mainland population. In addition, the surfaces of eggs within a clutch are highly uniform in the Taiwanese population, unlike that in the mainland population (Yang et al. 2014), which may help explain why the latter showed reduced recognition ability and further supports the hypothesis that parasitic interaction may be the agent promoting the co-evolution of egg appearance (Swynnerton 1916; Takasu 2003; Davies 2011).

Recognition cues such as egg color and markings affect host decisions against foreign eggs. Markings on eggs are considered as fingerprints by female individuals and, hence, play a decisive role in egg recognition (Davies and deL Brooke 1989a; Lahti and Lahti 2002; López-de-Hierro and Moreno-Rueda 2010). However, some studies indicate that egg color is a more important recognition cue (Moskát et al. 2008a, 2010). Both prinia populations showed higher rejection of non-mimetic model eggs (Yang et al. 2014) than of experimental eggs painted with spots (this study) (Table 2). In particular, for the mainland population, spots on eggs did not provoke detection and recognition by the parental birds for rejection, whereas half of the model eggs were rejected. These findings imply that, in contrast, eggshell color is a potentially more important recognition cue than egg spots in the Yellow-bellied Prinia.

In conclusion, this study provides further support for the blunt egg pole hypothesis, showing that the parasitized population displayed a higher rate of rejection of BP-painted eggs than of SP-painted eggs.

## Compliance with ethical standards

**Ethical standards** The studies reported in this paper conformed to the laws in the countries in which they were performed. Experimental procedures were conducted in agreement with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (No. HNECEE-2011-005).

**Conflict of interest** There are no competing conflicts to declare.

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