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Egg recognition and chick discrimination in colonial breeding birds

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ABSTRACT

Theory predicts that parents will not raise unrelated offsprings. For colonial breeding birds, evolving an ability to recognize their own eggs and chicks can prevent misdirecting parental behaviour. To verify this hypothesis, egg recognition experiments were performed on colonial breeding Chinese pond herons (*Ardeola bacchus*) and cattle egrets (*Bubulcus ibis*) in Chengmai and Lingao, tropical Hainan Island, China. Furthermore, a chick discrimination experiment was conducted on Chinese pond herons. In our study area, we did not record conspecific or interspecific brood parasitism in the two heron species. The results showed that Chinese pond herons had similar recognition rates for the four types of experimental eggs and lacked recognition ability. Cattle egrets had variable abilities to recognize different types of foreign eggs and have low egg recognition ability. Chinese pond herons cannot discriminate foreign chicks. Therefore, we suggest that the two species of colonial breeding herons may lack or have low egg recognition ability, and Chinese pond herons show no nestling recognition ability.

1. Introduction

Previous studies showed that many birds have evolved in their ability to recognize their own eggs (Rothstein, 1975; Bertram, 1979; Peer, 2006; Pike, 2011; Yang et al., 2014a, Yang et al., 2014b; Ruiz-Raya et al., 2016; Golüke et al., 2016; Liang et al., 2016; Luro et al., 2018). So far, four conditions have been known to select for rejection of foreign eggs by birds: (1) nesting in dense colonies in which individuals risk confusing their eggs with those of nearby breeding birds (Tschanz, 1959); (2) conspecific brood parasitism (hereafter CBP, Rothstein, 1990); (3) nest usurpation (Peer and Bollinger, 1998); and (4) interspecific brood parasitism (thereafter IBP, Rothstein, 1975, 1990). IBP by birds such as cuckoos is the main driving force for many passerine birds to evolve egg recognition and chick discrimination abilities (Davies and Brooke, 1989; Stoddard and Stevens, 2011; Ruiz-Raya et al., 2016). Rejection of foreign parasitic eggs is the most common and effective mechanism for defending against IBP when compared with chick discrimination (Davies, 2000; Soler and Soler, 2000; Yang et al., 2010). To date, only a few birds are known to possess chick discrimination abilities (Grim et al., 2003; Langmore et al., 2003, 2009; Grim, 2006, 2011; Sato et al., 2010; Tokue and Ueda, 2010; Yang et al., 2015b; Huo et al., 2018; Noh et al., 2018).

In addition to IBP, other situations may also cause birds to evolve in their ability to recognize foreign eggs and chicks. For example, the song thrush (*Turdus philomelos*) (Samaš et al., 2014) and the house sparrow (*Passer domesticus*) in the Passeriformes order (López-de-Hierro and Ryan, 2008; López-de-Hierro and Moreno-Rueda, 2010; Soler et al., 2011; but see Yang et al., 2015a), the American coot (*Fulica americana*) in the Rallidae family (Lyon, 2003, 2007; Jamieson et al., 2000) and the Ploceidae family (Jackson, 1998; Lahti and Lahti, 2002; Lahti, 2006) have evolved egg recognition to protect against CBP. Birds such as the mourning dove (*Zenaida macroura*) usurp nests of other birds (nest usurpation) and reject non-self-eggs from the nest (Harris et al., 1963; Weeks, 1980; Peer and Bollinger, 1998). Birds that breed in high-density colonies (colonial breeding) on the ground or cliffs have evolved egg recognition capabilities to avoid misdirecting parental care (Tschanz, 1959; Frederickson and Weller 1972; Schaffner, 1990).

At present, there is limited research on the recognition of eggs of colonial breeding birds (Davies and Carrick, 1962; Buckley and Buckley, 1972; Victoria, 1972; Schaffner, 1990; Gaston et al., 1993; Peer and Sealy, 2000, 2004; Caspers and Krause, 2011; Craik et al., 2018). But even so, different researchers came to different conclusions. For instance, Lanier (1982) reported that colonial passerine bird pinyon jays (*Gymnorhinus cyanocephalus*) and great-tailed grackles (*Quiscalus mexicanus*) had no egg recognition. On the contrary, Peer and Sealy (2000) found that great-tailed grackles had evolved the ability to recognize conspecific eggs. For colonial breeding waterbirds, Leclaire et al. (2017) proposed that blue petrels (*Halobaena caerulea*) can discriminate the odor of their own egg from the odor of a conspecific egg, but Hořák and Klvaňa (2009) found that a semi-colonial breeder,

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Fig. 1. Brood parasitism experiments conducted in the nests of the Chinese pond heron and the cattle egret.
A, Four Chinese pond heron eggs and one quail egg; B, Two cattle egret eggs and one quail egg; C, Four Chinese pond heron eggs and one chicken egg; D, One Chinese pond heron egg and two cattle egret eggs; E, Three Chinese pond heron eggs and one Chinese pond heron egg from a different nest; F, Four cattle egret eggs and one cattle egret egg from a different nest.

common pochard (*Aythya ferina*) cannot discriminate between conspecific and heterospecific eggs. In members of Ardeidae, Peer (2006) suggested least bitterns (*Ixobrychus exilis*) that parasitized by American coots had evolved egg recognition abilities. However, little bitterns (*Ixobrychus minutus*) that parasitized by common moorhens (*Gallinula chloropus*) did not have egg recognition abilities (Trnka, 2015). For many birds that breed in colonies, egg recognition deserves further study. As the nests of colonial birds are very close to each other, recognition of their eggs or chicks can help parental birds avoid confusion with neighboring nests and quickly locate their nests when they return (Tschanz, 1959; Buckley and Buckley, 1972). Furthermore, high-density colonies of birds provide opportunities for CBP (Rohwer and Freeman, 1989). Therefore, it is conceivable that birds that breed at high-density in a homogeneous habitat environment can identify their eggs or chicks.

The Chinese pond heron (*Ardeola bacchus*) and the cattle egret (*Bubulcus ibis*) belong to order Pelecaniformes and family Ardeidae (Zheng, 2017) and are typical waders. The Chinese pond heron often nests in tall treetops or bamboo forests near water, usually in colonies, or mixed with the little egret (*Egretta garzetta*) and the cattle egret (Zhao, 2001; Liang et al., 2006). Similar to other colonial breeding birds of the Ardeidae family, both the Chinese pond heron and the cattle egret have been reported to engage in CBP (Yom-Tov, 2001; Gong and Lu, 2003; Telfair and Bister, 2004; Lyon and Eadie, 2008; Moralez-Silva and Lama, 2017), but their abilities for egg recognition and chick discrimination have never been reported. In the present study, we conducted a series of field experiments to investigate the egg recognition abilities of the Chinese pond heron and the cattle egret. In addition, chick discrimination experiments were conducted on the Chinese pond heron, which typically chooses a lower nest position and exhibits a higher breeding density than the cattle egret. We predicted that the two species of herons would evolve the ability to recognize eggs due to brood parasitism, and that the rejection rate of the two herons against non-mimetic eggs (e.g. chicken eggs) would be significantly higher than those of mimetic eggs (e.g. conspecific eggs).

2. Methods

2.1. Study area and species

This study was conducted in Songmei Village, Nanbao Town, Lingao County, and Chongwei Village, Yongfa Town, Chengmai County, tropical Hainan Island, China. The nesting area in Songmei Village (19°142′31″ N, 109°35′48″ E) was mostly shrub, with nest heights of 1–4 m. The nesting area was approximately 3 ha and it was about 2 km away from the village. A total of 62 nests of the Chinese pond heron were discovered in the area in 2007, and 34 nests were discovered in 2008. The nests of Chinese pond herons were extremely simple, consisting of dead branches and some hay. Each nest contained 3 to 7 eggs, the majority contained 4 to 5 eggs, and the eggs had a blue-green color and an oval shape (Cheng et al., 2011). The nesting area in Chongwei Village (19°40′26″ N, 110°11′50″ E) was mainly the bamboo forest with a small number of non-native gum trees and pine forest. The nesting area was approximately 5 hm^2 and was about 150 m away from the village. The west side of the nesting area was a fish pond. A total of 83 nests of the Chinese pond heron and 59 nests of the cattle egret were discovered in the area in 2007, and 29 nests of the Chinese pond heron and 16 nests of the cattle egret were discovered in 2008. The nest of the cattle egret was similar to that of the Chinese pond heron and was also composed of dead branches. Each nest contained 3 to 7 eggs, and the majority contained 3 to 4 eggs. The eggs were light blue, smooth and spotless, and larger than the eggs of the Chinese pond heron (Cheng et al., 2011). Due to conscious protection by the villagers, this area has become the largest heron nesting habitat in Hainan (Liang et al., 2006).

2.2. Egg recognition experiment

The fieldwork was performed in April and May of 2007–2008. The nests of Chinese pond herons and Cattle egrets that were discovered in the two study areas were GPS-located and numbered and the nests were regularly revisited. Different types of experimental eggs were used to examine egg recognition. The first group consisted of quail eggs, which are very different in size, background color and spots from the eggs of the two species of herons (Fig. 1A, B). The second group was chicken eggs. The chicken eggs and the eggs of the herons were similar in size but extremely different in color (Fig. 1C). The third group was comprised of the exchange of eggs between the two species of herons, which means adding one true egg from one species to the other species' nest. The eggs from the two species of herons are similar in size and appearance (Fig. 1D). The fourth group was the exchange of eggs within the two species of herons, which means adding one true egg from the other nest of the same species. They are highly simulated eggs used to test CBP (Fig. 1E, F). For egg recognition experiment all heron nests were used only once.

Previous studies on IBP have shown that replacing or directly adding an experimental egg does not affect the ability of the parental bird to recognize its eggs (Davies and Brooke, 1988; Liang et al., 2016). Therefore, one experimental egg was directly added before the hatching period to examine the ability of the two heron species to recognize eggs. The responses of the parental birds were observed for six days (Moksnes et al., 1991). If the parental bird did not reject the experimental egg within six days, the egg was recorded as accepted. If the experimental egg disappeared or the parental birds abandoned their nests within six days, it was considered as rejected. Experimental nests that were preyed upon or vandalized within six days were not included in the experimental results.

2.3. Chick replacement experiment

During the nestling period, the nests of the Chinese pond heron were treated as follows. In the first group, one Chinese pond heron chick (within 2–3 days old) was replaced by a chick of the same day-old age from another nest. In the second group, the entire nests of the Chinese pond heron chicks were replaced by a nest of chicks of a different age. The experimental nests were examined on days two and six. If the experimental chicks were still alive in the nest on the sixth day and the host did not abandon the nest, it was recorded as accepted; if the experimental chicks disappeared or the host abandoned the nest, it was recorded as rejected. Experimental nests that were preyed upon or vandalized within six days were not included in the experimental results.

2.4. Data analysis

Statistical analyses were performed using IBM SPSS 20.0 for Windows (IBM Inc. USA). Fisher's exact test was used to compare two or more sets of categorical variables with a significant level of $P < 0.05$.

3. Results

3.1. Comparison of egg rejection between the two species of herons

We did not find any conspecific or interspecific brood parasitism in these two heron species at our site. Chinese pond herons from the two locations showed no differences in their ability to recognize foreign eggs (Fisher's exact test, All $P > 0.05$). Thus, these results were combined. In the first group, the quail egg rejection rates of the Chinese pond heron and the cattle egret were 2.04% (n = 49) and 26.3% (n = 19), respectively, and the rejection rates of the latter were significantly higher than the former (Fisher's exact test, $P = 0.003$, Table 1), the herons rejected the quail eggs by ejection and no nests deserted was recorded. The second group of experiments was only conducted in Chinese pond herons due to an insufficient sample size of cattle egrets. All the experimental nests of the Chinese pond herons accepted chicken eggs (n = 52). In the third group, the interspecific egg rejection rates of the Chinese pond herons and the cattle egrets were 4.3% (n = 23) and 13.6% (n = 22), respectively, and the rejection rates of the two species of herons were similar (Fisher's exact test, $P = 0.346$, Table 1). In the fourth group, the conspecific egg rejection rates were 2% (n = 50) and 3.13% (n = 32), respectively, and the rejection rates of the two species of herons were similar (Fisher's Exact Test, $P = 1.000$, Table 1).

The recognition rates of the Chinese pond herons for different types of experimental eggs were similar (Fisher's exact test, $P = 0.380$), and thus lacked egg recognition ability; the cattle egrets had a different ability to recognize different types of foreign eggs (Fisher's exact test, $P = 0.036$). The rejection rate was the highest for the quail eggs having different sizes and colors, followed by the Chinese pond heron eggs that had different sizes but similar colors. The rejection rate was the lowest for conspecific eggs that had both similar sizes and colors. In general, the ability of cattle egrets to recognize eggs was somewhat stronger than that of Chinese pond herons.

3.2. Chick discrimination of the Chinese pond heron

In both experimental groups, Chinese pond herons accepted all foreign chicks (N = 12 nests for the first group, N = 4 nests for the second group), indicating that the Chinese pond heron could not recognize individual chicks of the conspecific species.

4. Discussion

Contrary to predictions, our results indicated that the two species of herons that breed in high-density colonies lack strong egg recognition abilities. Chinese pond herons accepted all types of foreign eggs, while cattle egrets rejected a few extremely dissimilar experimental eggs, but their recognition ability is limited, as the rejection rate of non-conspecific eggs was not significantly higher than that of conspecific eggs. Furthermore, we did not find any conspecific or interspecific brood parasitism in these two heron species at our site. Moreover, Chinese pond herons fed the same-species foreign chicks which had the same or different ages in a normal manner, indicating that they cannot recognize individual chicks of the same species. Therefore, our study suggests that the two species of colonial breeding herons may lack or have low egg recognition ability, and Chinese pond herons have no nestling recognition ability.

Numerous nests available in a nesting area provide opportunities for CBP in birds that breed in high-density colonies (Rohwer and Freeman, 1989), which is also the reason why colonial breeding can facilitate CBP events (Hamilton and Orians, 1965). Previous studies have found that CBP exists in about 250 species of birds (Rohwer and Freeman, 1989; Davies, 2000; Yom Tov, 2001; Gong and Lu, 2003; Moralez-Silva and Lama, 2017), of which more than 57% are colonial breeding species (Yom Tov, 2001). Both Chinese pond herons and cattle egrets are high-density colonial birds, and both have been reported to exhibit CBP. The rate of multiple CBP in the cattle egret is as high as 21% (Moralez-Silva and Lama, 2017). This relatively high rate may also be the reason why

Table 1
Comparison of egg recognition abilities between the Chinese pond heron and the cattle egret (*N* was the number of nests tested).

Species	Egg rejection rate (%)							
	Quail egg	*N*	Chicken egg	*N*	Interspecific egg	*N*	Conspecific egg	*N*
Chinese pond heron	1 (2.0)	**49**	0 (0)	**52**	1 (4.3)	**23**	1 (2)	**50**
Cattle egret	5 (26.3)	**19**	—	**—**	3 (13.6)	**22**	1 (3.1)	**32**

cattle egrets have slightly stronger recognition ability than Chinese pond herons. However, despite the existence of CBP, Chinese pond herons and cattle egrets have not evolved egg recognition ability like other colonial breeding birds such as zebra finches (*Taeniopygia guttata*) (Golüke et al., 2016), and great-tailed grackles (Peer and Sealy, 2000, 2004), least bitterns (Peer, 2006), the genus *Ploceus* (Bertram, 1992; Jackson, 1998), or the common ostrich (*Struthio camelus*) to have the ability to recognize parasitic eggs. Although Samaš et al. (2014) concluded that egg recognition of the song thrush and the common blackbird (*Turdus merula*) were due to CBP but not IBP, Soler (2014) posited that the conclusions of Samaš et al. (2014) were not consistent with traditional perspectives that IBP promotes the evolution of egg recognition in birds. In the first objection, Soler (2014) posited that CBP and IBP did not produce the same levels of counter-parasitism strategies in the host. Because the eggs from conspecific parasitism were more similar to those of the hosts when compared to interspecific parasite eggs, identification is more difficult (Reeve, 1989). At the same time, the cost of CBP is smaller when compared with IBP. Therefore, selection pressure to develop defense strategies is relatively weak for birds with CBP (Davies, 2000; Lyon and Eadie, 2008; Petrie and Moller, 1991). As a second objection, although song thrushes are not consistently parasitized by cuckoos, their egg recognition ability may be maintained for many years without pressure from parasitic cuckoos (Peer et al., 2011). A third consideration is that when song thrushes and common blackbirds attacked cuckoo specimens and showed an unwillingness to feed cuckoo chicks suggests that they have been parasitized previously. Lastly, the parasitic rate of the two thrush species was too low to cause them to evolve egg recognition abilities to resist CBP.

Our experimental results showed that Chinese pond herons and cattle egrets could not recognize conspecific eggs. It is likely, as Soler (2014) mentioned, that conspecific eggs are too similar in appearance, making them more difficult for the host to recognize as foreign (Reeve, 1989). In fact, it is very rare for birds to identify and reject conspecific parasitic eggs (Davies, 2000), and only a few species can recognize and reject conspecific eggs that appear in the nest before their egg-laying period (Brown and Brown, 1989; Jackson, 1993; Stouffer et al., 1987). However, there are some colonial breeding birds that do not suffer CBP that have evolved the ability to recognize eggs or chicks, including the Charadriiformes order, Laridae family (Buckley and Buckley, 1972; Schaffner, 1990) and the Alcidae family (Gaston et al., 1993); the Sphenisciformes order, Spheniscidae family (Fredrickson and Weller, 1972); the Procellariiformes order, Procellariidae family (Leclaire et al., 2017); and birds of the Passeriformes order (Peer and Sealy, 2000; Caspers and Krause, 2011). These observations suggest that there should be a selection pressure in the colonial breeding birds that forces them to evolve the ability to identify nests, eggs, or chicks. Our results indicate that the two species of herons that breed in high-density colonies lack strong egg recognition abilities. Only cattle egrets can recognize a few extremely dissimilar experimental eggs, but their recognition ability is limited. Therefore, we speculate that the limited egg recognition ability of the two species of herons may have evolved not to cope with conspecific brood parasitism, but to locate the nests in colonial breeding and avoid confusing the parents. Nevertheless, the two species of herons may not use single egg characteristics to locate their nests, because their egg recognition ability was too low to locate their nests. Moreover, Chinese pond herons cannot recognize chicks of their conspecific species. Our results are similar to the results from some other birds that breed in colonies. For example, the females of the red-winged blackbird (*Agelaius phoeniceus*) cannot recognize their nests, eggs, and nestlings younger than the age of 7 days old but can find their nests based on the nest site (Peek et al., 1972). To avoid misdirecting parental care, sooty terns (*Onychoprion fuscatus*) respond so strongly that they accept any nests that are placed on their nest sites (Lashley, 1915). The caspian tern (*Hydroprogne caspia*) may use landmarks, location, and characteristics of neighbor's nests to locate their nests instead of using the nest characteristics of their own (Baerends and Hogan-Warburg, 1982). Some colonial cavity breeding birds can quickly locate their nests among thousands by smell (Thibault and Holyoak, 1978; Warham, 1996; Bonadonna et al., 2003). These studies, however, which used whole clutch replacement, were different from our study. All of these results indicate that for colonial breeding birds, egg and chick recognition is not the only way to avoid misdirecting parental care.

In conclusion, our results indicate that the colonial breeding Chinese pond heron and the cattle egret have almost no egg recognition ability, and Chinese pond herons cannot distinguish individual chicks of conspecific species. We suggest that the two species of herons may not use single egg characteristics to locate their nests, and chick characteristics may also be not useful for Chinese pond heron parents to locate their nests. Whether the whole clutch characteristics were useful or there be some other cues for herons to locate their nests to avoid misdirecting parental care should require further investigation.

Ethics

The experiments reported here comply with the current laws of China. Fieldwork was carried out under the permission from the two villages. 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-2007-001).

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Declaration of Competing Interest

The authors declare that they have no competing interests.

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