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Egg recognition abilities of tit species in the Paridae family: do Indomalayan tits exhibit higher recognition than Palearctic tits?

DEAR EDITOR,

Recent studies have shown that the closely related cinereous tit (*Parus cinereus*) and green-backed tit (*P. monticolus*) in China display strong egg recognition ability in contrast to tit species in Europe, which lack such ability. However, egg recognition in other populations of cinereous and green-backed tits and additional Paridae species still requires further research. Here, we compared the egg recognition abilities of cinereous tits across China, green-backed tits (*P. m. insperatus*) in Taiwan, China, and five other species from the Paridae family, including the marsh tit (*Poecile palustris*), varied tit (*Sittiparus varius*), willow tit (*Poecile montanus*), coal tit (*Periparus ater*), and ground tit (*Pseudopodoces humilis*). Results showed that the Hebei (58.8% egg rejection, $n=17$) and Liaoning populations (53.3%, $n=15$) of cinereous tits, and the Guizhou (100%, $n=12$) and Taiwan populations (75%, $n=12$) of green-backed tits all exhibited high egg recognition ability. The egg recognition ability of these tits was significantly greater than that of the other five species in the Paridae family. The varied tit (5.4%, $n=37$), marsh tit (8.3%, $n=12$), willow tit (Hebei: 25%, $n=20$; Beijing: 9.5%, $n=21$), coal tit (16.7%, $n=18$), and ground tit (0, $n=5$) species all showed low egg recognition abilities, with no significant differences found among them. Egg recognition was not associated with a single phylogenetic group but occurred in several groups of tits. In particular, those species widely distributed in the Indomalayan realm, thus overlapping with small cuckoo species, displayed strong egg recognition ability, whereas tit species in the Palearctic realm exhibited low or no egg recognition ability.

Brood parasites, such as cuckoos (*Cuculus* spp.), do not build nest themselves but lay eggs in the nest of host birds, who will hatch and raise their chicks. Therefore, the costs of parental care are transferred to these hosts (Davies, 2000),

who not only experience reduced reproductive output but also expend considerable time and energy raising unrelated chicks, thereby greatly decreasing their reproductive success (Soler, 2014). Selective pressure causes hosts to evolve defensive measures to resist cuckoo parasitism, including nest defense (Davies & Welbergen, 2009; Feeney et al., 2014) and egg recognition (Davies, 2000; Soler, 2014). The recognition and rejection of parasitic eggs is one of the most widespread and effective methods for resisting brood parasites by the host (Antonov et al., 2011; Soler & Soler, 2000; Stokke et al., 2005; Wang et al., 2015; Yang et al., 2014). Studies on egg recognition in hosts or potential hosts of cuckoos can deepen our understanding of the interactions between these species, as well as the evolution and mechanisms of maintenance of egg rejection behavior in hosts (De L. Brooke & Davies, 1988; Spottiswoode & Stevens, 2010, 2011; Soler et al., 2011, 2012). For example, previous work has shown that nest sanitation behavior in birds is a pre-adaptive response of hosts to reject foreign eggs, which ultimately evolved as a way in which to decrease the cost of brood parasitism for hosts (Moskát et al., 2003; Rothstein, 1975; Yang et al., 2015a, 2015b). For some host species, once egg recognition ability has evolved, it can persist for a long time, even in the absence of brood parasitism (Medina & Langmore, 2015; Martín-Vivaldi et al., 2013; Peer et al., 2007; Rothstein, 2001; Underwood et al., 2004; Yang et al., 2014, 2015c).

Traditionally, suitable hosts are thought to possess two characteristics simultaneously: namely, approachable nests and suitable diets (Davies, 2000; Grim et al., 2014). In general, the entrances of cavity nests are considered too small for cuckoos to enter and lay eggs (Lambrechts et al., 2010; Moksnes & Røskoft, 1987; Maziarz et al., 2015). In addition, the nest space is smaller, which is not conducive for the growth and fledging of cuckoo chicks (Avilés et al., 2006). Therefore, cavity-nesting birds are not regarded as suitable

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hosts for cuckoos and are not thought to possess egg recognition abilities (Davies & De L. Brooke, 1989; Davies, 2000; Grim et al., 2014; Moksnes & Røskaft, 1995; but see Yang et al., 2013). Although the diets of some insectivorous birds, such as tits (family Paridae), flycatchers (subfamily Muscicapinae), tree creepers (Certhiidae), and nuthatches (family Sittidae), are suitable for cuckoos, they are not regarded as suitable hosts as they are cavity nesters (Davies, 2000). However, recent studies have shown that semi-cavity-nesting birds are common hosts of cuckoos (Grim et al., 2014; Grim, 2016; Grim & Samaš, 2016; Samaš et al., 2016; Thomson et al., 2016; Yang et al., 2016). For example, the common redstart (*Phoenicurus phoenicurus*) and Daurian redstart (*Phoenicurus aureus*), which are common hosts of cuckoos (Rutila et al., 2002; Samaš et al., 2016; Thomson et al., 2016; Yang et al., 2016), have evolved polymorphic eggs and egg recognition ability to resist cuckoo parasitism (Samaš et al., 2016; Yang et al., 2016). This raises the question whether Paridae species are suitable hosts for cuckoos. Recent studies have indicated that the cinereous tit (*Parus cinereus*) and green-backed tit (*P. monticolus*) in China possess strong egg recognition abilities (Liang et al., 2016; Yang et al., 2019). Furthermore, as the cinereous tit was previously considered a subspecies of the great tit (*Parus major*) (Päckert et al., 2005), this suggests possible co-evolution between these birds and cuckoos. Grim et al. (2014) found that the great tit, crested tit (*Lophophanes cristatus*), and blue tit (*Cyanistes caeruleus*) were parasitized by and successfully reared the chicks of the common cuckoo (*Cuculus canorus*). In addition, Grim & Samaš (2016) also suggested that great tits and coal tits (*Parus ater*) are suitable cuckoo hosts as they rear such chicks well. These studies all challenge the traditional viewpoint that cavity-nesting birds from the Paridae family are unsuitable hosts for cuckoos (Davies, 2000).

Environmental heterogeneity causes hosts to experience heterogeneous parasitism and differences in the intensity of interactions with cuckoos (Langmore et al., 2012; Liang et al., 2013, 2016; Yang et al., 2014, 2015c). Therefore, geographical variation in anti-brood parasitism behavior in hosts is common (Hale & Briskie, 2007; Lindholm & Thomas, 2000; Langmore et al., 2012; Liang et al., 2013, 2016; Stokke et al., 2007; Yang et al., 2014, 2015c). Studies have shown geographical differences in egg rejection behavior in different host populations (Liang et al., 2013, 2016; Yang et al., 2014, 2015c). For example, Yang et al. (2014) reported that mainland Chinese populations of yellow-bellied prinia (*Prinia flaviventris*) reject 50% of non-mimetic eggs and accept 100% of conspecific eggs, whereas Taiwanese populations of the same species reject 100% of non-mimetic eggs and 16% of conspecific eggs. Liang et al. (2016) and Yang et al. (2019) found that, in contrast to great tits in Europe, Chinese populations of the closely related cinereous and green-backed tits exhibit strong egg recognition abilities. However, Liang et al. (2016) only studied egg recognition in five cinereous tit populations in China and Yang et al. (2019) only studied egg recognition ability in one green-backed tit population. Thus, it

is still unclear whether co-evolutionary relationships exist among other Paridae species and cuckoos and whether egg recognition ability has evolved in such species.

We hypothesized that tit species distributed in the Indomalayan realm, which overlaps with small cuckoo species in South China, e.g., Asian emerald cuckoos (*Chrysococcyx maculatus*), violet cuckoos (*C. xanthorhynchus*), and plaintive cuckoos (*Cacomantis merulinus*), will possess egg recognition ability, whereas tit species in the Palearctic realm will display limited or no egg recognition ability.

In this study, the egg recognition abilities of seven tit species from the Paridae family, i.e., cinereous tit, green-backed tit, coal tit, marsh tit (*Poecile palustris*), varied tit (*Parus varius*), willow tit (*P. montanus*), and ground tit (*Pseudopodoces humilis*), were compared. In addition, the phylogenetic distribution of egg recognition ability in tit species was determined to examine the relationship between the evolution of egg recognition ability and the phylogeny of the Paridae family.

Data were collected at six study sites. The Saihanba National Forest Park, which is located in the northernmost part of Hebei Province, China (N42°02'–42°36', E116°51'–117°39'), has an altitudinal range of 1 350–1 650 m a.s.l. and a cold-temperate continental monsoon climate. The park contains major natural secondary forest and plantation forest (Liu et al., 2017). The Xiaolongmen National Forest Park (N42°00'–42°02', E115°26'–115°30'), which is located in the western mountains of Beijing, China, has a mean altitude of 1 330 m a.s.l. and a temperate monsoon climate. The park consists mainly of deciduous broad-leaf forest (Liang et al., 2016). The Xianrendong National Nature Reserve, which is located in Zhuanghe, Liaoning Province, China (N39°54'–40°03', E122°53'–123°03'), has an altitudinal range of 200–600 m a.s.l. and a temperate-humid monsoon climate (Du et al., 2010). The Gahai Nature Reserve is located in Luqv, Gansu Province, China (N33°58'–34°32', E102°05'–102°47'), with an altitude reaching 3 470 m a.s.l. (Mu et al., 2008). The Kuankuoshui National Nature Reserve, which is located in Zunyi, Guizhou Province, southwestern China (N28°10', E107°10'), as an altitude of up to 1 500 m a.s.l. and contains subtropical moist broad-leaf-mixed forest (Yang et al., 2019). The Aowanda National Forest Recreation Area is located at central Taiwan, China (N23°56'–23°95', E121°10'–121°51'), with an area of 2 787 ha and an altitudinal range of 1 100–2 600 m a.s.l. (Tzeng et al., 2018).

At each study site, artificial nest boxes were established to attract various tit species for breeding (except for Gahai Nature Reserve, where natural ground tit nests were searched in 2010). In 2009–2010, nest boxes were hung at Xiaolongmen National Forest Park to attract willow tits. In 2011, nest boxes were hung at Aowanda National Forest Recreation Area to attract green-backed tits. In 2016–2018, nest boxes were hung at Xianrendong National Nature Reserve to attract cinereous tits, marsh tits, and varied tits. In 2017–2018, artificial nest boxes were hung at Saihanba National Forest Park to attract cinereous tits, coal tits, and willow tits. The experiments reported here complied with the

current laws of China. Experimental procedures were in accordance with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (Permit No.: HNECEE-2011-001).

During the birds' breeding season (April to August), the nest boxes were examined daily to determine breeding status. One blue model egg was added to the nests of the seven tit species one or two days after the clutch was completed to simulate parasitism. The model eggs used in this experiment were identical to the blue model eggs used by Liang et al. (2016) and Yang et al. (2019). The experimental nests were monitored for five consecutive days. The blue model eggs were made of clay to a size and mass similar to the eggs of the Asian emerald cuckoo. If the experimental egg was still present in the nest on day 6 and the host did not abandon the nest, the experimental egg was considered as accepted. If the experimental egg disappeared or was pecked, the experimental egg was considered as rejected. Nests that were preyed upon or destroyed within the six days were excluded from analysis. All individuals were ringed to ensure nests of the same individual were not sampled several times in several years.

To examine the relationship between the evolution of egg recognition ability and tit phylogeny, we built a phylogenetic tree for all 23 tit species in China following Jetz et al. (2012). We first pruned the global phylogenetic tree of birds from BirdTree (<http://birdtree.org>) under the option of "Hackett All Species: a set of 10 000 trees with 9 993 OTUs each" to include the 23 tit species in China (Jetz et al., 2012). We

sampled 5 000 pseudo-posterior distributions and constructed a Maximum Clade Credibility tree using mean node heights with TreeAnnotator (BEAST v1.8.2; Drummond & Rambaut, 2007).

Statistical analyses were performed using IBM SPSS 25.0 for Windows (IBM Inc., USA). A generalized linear mixed model (GLMM) with a binomial error distribution and logit link function was used to compare responses to blue model eggs by different tit species. Host species and region (Palearctic, Indomalayan) were used as response variables, while clutch size, study site, and sample year were included as random effects. Fisher's exact test was used to compare the rejection rate of blue model eggs between different sites. All tests were two-tailed, with statistical significance at $P < 0.05$. Data were expressed as mean \pm standard deviation (Mean \pm SD).

In Saihanba, the rejection rates of blue model eggs by cinereous tits, coal tits, and willow tits were 58.8% ($n=17$), 16.7% ($n=18$), and 25% ($n=20$), respectively. In Xianrendong, the rejection rates by cinereous tits, varied tits, and marsh tits were 53.3% ($n=15$), 5.4% ($n=37$), and 8.3% ($n=12$), respectively. In Xiaolongmen, the rejection rate of willow tits was 9.5% ($n=21$). In Gahai, the rejection rate of ground tits was 0% ($n=5$). In Guizhou, the rejection rate of green-backed tits was 100% ($n=12$), including egg burial in three nests. In Taiwan, China, the egg rejection rate of green-backed tits was 75% ($n=12$) (Table 1; Figure 1A). The egg rejection rate differed significantly among different tits species ($F=5.871$, $P < 0.001$, GLMM), with the Hebei and Liaoning cinereous tit populations and Guizhou and Taiwan green-backed tit populations exhibiting higher egg recognition abilities. The egg

Table 1 Rejection frequencies of experimental blue model eggs by tit species

Locality	Study site	Species	No. nests tested (n)	Rejection rate (%)	References
China	Diaoluoshan	Cinereous tit	10	100	Liang et al., 2016
China	Qiandaohu	Cinereous tit	10	90	Liang et al., 2016
China	Dongzhai	Cinereous tit	9	66.7	Liang et al., 2016
China	Xiaolongmen	Cinereous tit	24	54.2	Liang et al., 2016
China	Xianrendong	Cinereous tit	15	53.3	This study
China	Saihanba	Cinereous tit	17	58.8	This study
China	Zuojia	Cinereous tit	37	78.4	Liang et al., 2016
Czech Republic	Velky Kosir	Great tit	15	0	Liang et al., 2016
Czech Republic	Sumperk	Great tit	20	5	Liang et al., 2016
Norway	Røros	Great tit	26	34.6	Liang et al., 2016
Norway	Stjørdal	Great tit	12	8.3	Liang et al., 2016
Norway	Vikhammer	Great tit	5	40	Liang et al., 2016
China	Aowanda, Taiwan	Green-backed tit	12	75	This study
China	Kuankuoshui	Green-backed tit	12	100	This study
China	Kuankuoshui	Green-backed tit	28	100	Yang et al., 2019
China	Gahai	Ground tit	5	0	This study
China	Xianrendong	Varied tit	37	5.4	This study
China	Xianrendong	Marsh tit	12	8.3	This study
China	Xiaolongmen	Willow tit	21	9.5	This study
China	Saihanba	Coal tit	18	16.7	This study
China	Saihanba	Willow tit	20	25	This study

recognition ability of these two species was significantly greater than that of the other five Paridae species tested. The egg rejection rate did not differ significantly between the two regions (Palearctic or Indomalayan) ($F=0.071$, $P=0.931$, GLMM).

The egg rejection rate of coal tits was 16.7%, which we classified as low egg recognition ability. There was no difference in the egg rejection rate of willow tits from Saihanba and Xiaolongmen (Fisher's exact test, $P>0.05$). Therefore, the

egg rejection rate of willow tits was combined, with the 17.1% rate ($n=41$) also classified as a low egg recognition ability. Phylogenetic distribution of egg recognition ability in tit species showed that the same evolutionary branches contained species with and without egg recognition ability (Figure 1B). Therefore, egg recognition ability in the Paridae family was not associated with a single phylogenetic clade.

Successful parasitism by cuckoos will cost the host time and effort and result in reduced reproductive output. Therefore,

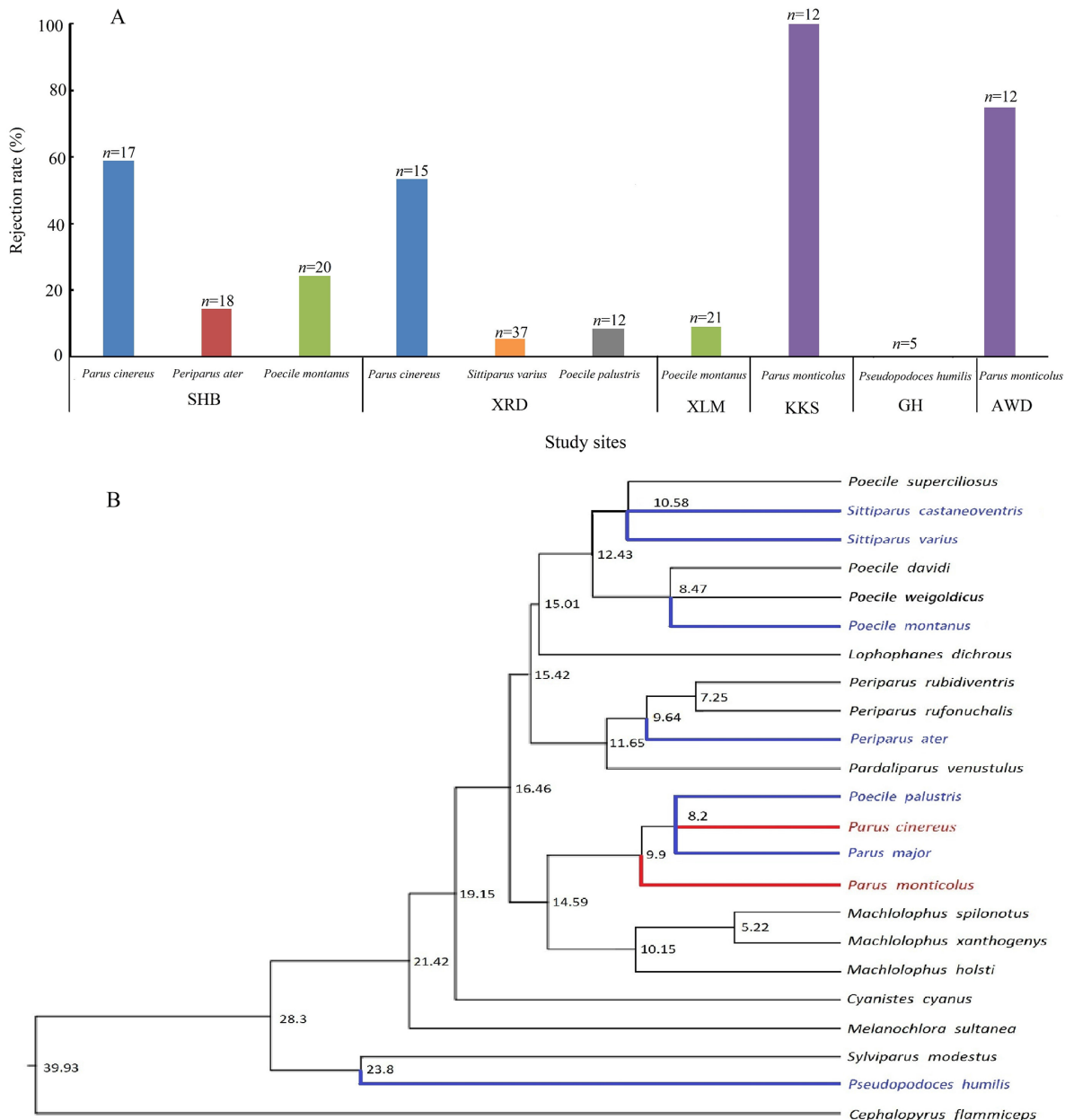


Figure 1 Egg rejection of tits in the Paridae family and their phylogenetic tree

A: Frequencies of egg rejection by seven tit species in Paridae family. B: Phylogenetic tree of 23 tit species in China used for comparative analysis. Phylogeny was built following tree construction method of Jetz et al. (2012). Blue font represents species with low or no egg recognition ability, red font represents species with egg recognition ability, black font represents species with unknown egg recognition ability.

selection will cause the host to evolve egg recognition to resist cuckoo parasitism. Our results showed that the egg rejection rate differed significantly among the different tit species across China. Namely, the cinereous tits in Saihanba (Hebei) and Xianrendong (Liaoning) and the green-backed tits in Guizhou and Taiwan showed significantly higher egg recognition abilities than those of the other five species (varied tits, marsh tits, willow tits, marsh tits, and ground tits). Except for ground tits, which showed no egg recognition ability, the remaining four tit species evolved low egg recognition abilities. Although analysis showed that the egg rejection rate did not differ significantly among the two regions (Palearctic, Indomalayan), we still considered that the distribution regions have had an important influence on the ability of tit species to evolve egg recognition ability, that is, tit species whose distributional ranges overlap with small parasitic cuckoo species will have higher egg rejection abilities. Due to the limited tit species studied, our analysis did not include all tit species and populations from southern China. For example, the cinereous tit is a widespread species in China, but our analysis only included cinereous tits from Hebei and Liaoning populations. In addition, our study showed that egg recognition ability in tits was not related to a single clade only in the phylogenetic tree of the Paridae family.

The conventional viewpoint states that cavity-nesting birds are not suitable hosts for cuckoos (Davies, 2000; Moksnes et al., 1991; Moksnes & Røskaft, 1995) because these birds prefer to nest in cavities with small entrances. This nest characteristic effectively prevents cuckoos from entering to lay eggs and is also difficult for cuckoo nestlings to fledge (Carlson et al., 1998; Grim, 2016; van Balen et al., 1982). However, under natural conditions, the lack of tree holes will cause some secondary cavity-nesting birds to breed in nests with larger holes (Maziarz et al., 2015; van Balen et al., 1982; Wesolowski, 1989). These holes can allow cuckoos to enter and lay eggs and cuckoo nestlings to fledge (Carlson et al., 1998; van Balen et al., 1982). Therefore, nest type alone cannot be used to determine whether a nest is suitable for cuckoo parasitism (Medina & Langmore, 2015). Great tit populations in Europe do not possess egg recognition and hence are not considered to have co-evolved with cuckoos. However, Liang et al. (2016) found that closely related cinereous tit populations in China possess strong egg recognition ability, suggesting that a co-evolutionary relationship exists between Chinese cinereous tit populations and cuckoo parasitism. Our study found that cinereous tit populations in Saihanba (Hebei) and Xianrendong (Liaoning) possessed strong egg recognition abilities, and the egg rejection rates also gradually decrease from south to north, as described by Liang et al. (2016). Interestingly, although there is only one breeding cuckoo species in Taiwan, i.e., the Oriental cuckoo (*Cuculus optatus*) (Xia et al., 2016), green-backed tits in Taiwan also showed strong egg recognition ability. It may be that the egg recognition abilities of green-backed tits have been retained despite the absence of brood parasitism (Martín-Vivaldi et al., 2013; Medina & Langmore,

2015; Peer et al., 2007; Yang et al., 2014, 2015c). In addition, varied tits, marsh tits, willow tits, and coal tits all possessed egg recognition abilities, albeit low, showing that a co-evolutionary relationship may exist between these tit species and cuckoos.

There are several possible explanations for the differences in egg recognition abilities in birds from the Paridae family: i.e., phylogeny, general learning skills, and intensity of interaction with cuckoos. Here, however, the egg recognition abilities of the seven species from the Paridae family were not related to phylogeny. Given that cinereous tits have evolved specific egg recognition ability (Liang et al., 2016), it is possible that the other four tit species may have learned about parasitic eggs based on general cognitive skills. Living in a region with high cuckoo density means there will be many opportunities to learn which eggs belong to their own. The third possible explanation is differences in the intensity of interactions between these birds and cuckoos. For example, Liang et al. (2016) found that the egg recognition ability of southern cinereous tit populations is greater than that of northern populations. They considered that the higher diversity and quantity of southern small cuckoos compared with northern cuckoos has resulted in significantly stronger interactions between southern cinereous tit and cuckoo populations than between northern populations, and therefore greater egg rejection rates. In contrast, varied tits, marsh tits, willow tits, coal tits, and ground tits, which are mainly distributed in northern China, possess little or no egg recognition ability. In addition, although these tits have not evolved strong egg recognition ability, whether they have evolved corresponding nest defense and nestling recognition ability to cope with cuckoo parasitism remains to be studied. As the numbers and abundance of small cuckoo species in southern China are greater than that in northern parts, we suggest that tit species that are widely distributed in the Indomalayan realm, and which overlap with small cuckoo species, possess egg recognition ability, while tits located in the Palearctic realm have limited or no egg recognition ability.

Our results support the hypothesis that egg rejection of tit species varies with species diversity of parasitic cuckoos, suggesting that the strength of egg recognition ability in birds from the Paridae family may be associated with their distributional range, i.e., the strength of their interactions with cuckoos. We showed that tits distributed widely in the Indomalayan realm, thus overlapping with the distribution of small cuckoo species in South China, possess strong egg recognition ability, whereas tits located in the Palearctic realm display limited or no egg recognition ability. To confirm our conclusions, however, further research on egg recognition abilities of other species within the Paridae family and other populations is required.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Permissions for field surveys were granted by the Xiaolongmen and Saihanba National Forest Parks and

Xianrendong and Kuankuoshui National Nature Reserves.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

W.L. and D.M.W. designed the study. J.P.L. carried out field experiments in Saihanba, L.Z. and L.Z. in Xianrendong, W.L. in Xiaolongmen, C.C.Y. in Kuankuoshui, X.L. in Gahai, and C.T.Y. in Aowanda. J.P.L. performed statistical analyses and wrote the draft manuscript, and W.L. and A.P.M. discussed, revised, and improved the manuscript. All authors read and approved the final version of the manuscript.

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