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Word count: 4571

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Running headline: Hissing calls in tit species

Abstract

Nest predation often leads to breeding failure, and is an important selective pressure of natural selection that affects nest defense behavior in birds. Many tit species give a hissing call for nest defense, but there are few studies on interspecific variation in hissing calls and whether these are related to nest predation and nesting success. In this study, we compared the hissing calls of five tit species including cinereous tit (*Parus cinereus*), marsh tit (*Poecile palustris*), varied tit (*Sittiparus varius*), willow tit (*Poecile montanus*), and coal tit (*Periparus ater*) in Saihanba National Forest Park in Hebei and Xianrendong National Nature Reserve in Liaoning. In Saihanba of Hebei, the proportion of individuals giving a hissing call and nest predation were similar among three tit species (cinereous, varied, and marsh tits). In Xianrendong of Liaoning, the proportion of cinereous, varied, and marsh tit individuals giving a hissing call differed significantly but nest predation did not. Cinereous and varied tits showed no differences in clutch size, date of the first egg, nest predation and nesting success between individuals that gave and those that did not give a hissing call. These results indicated that for tit species that breed in nest boxes distributed within the same area, there is interspecific variation in hissing calls, but these are not significantly correlated with nest predation risk.

Keywords: hissing call, nest defense, nest predation, repeatability, Paridae.

Introduction

Nest predation often leads to failed reproduction and is a major selective pressure that affects nest defense behavior in birds (Ricklefs 1969; Martin 1995; Forstmeier and Weiss 2004; Fontaine and Martin 2006; Lima 2009; Tilgar and Moks 2015; Fu et al. 2016; Guppy et al. 2017). Birds have evolved complex anti-predation strategies to protect their nests and demonstrate specific behaviors when facing predators of different types and risk levels (Lima et al. 2005; Yorzinski and Vehrencamp 2009; Krams et al. 2010; Yorzinski and Platt 2012; Suzuki 2011, 2015; Daniela et al. 2018; Maziarz et al. 2018). For example, when blue peacock (*Pavo cristatus*) encounters a raccoon during the day, it calls loudly, stretches its neck, opens its wings, and strikes a flying pose as it approaches the predator. However, at night it will instead remain silent and give a soft hissing call (Yorzinski and Platt 2012).

In animals sound is often used to transmit predator information (Zuberbühler 2009; Fasanella and Fernández 2009; Suzuki 2011, 2014, 2015; Fuong et al. 2014; Townsend et al. 2014). Individuals of the same or different species use this acoustic information to evade predation (Sherman 1977; Pipia et al. 2009; Kitchen et al. 2010; Suzuki 2011, 2015; Gill and Bierema 2013; Townsend and Manser 2013). For example, Japanese tits (*Parus minor*) give different warning sounds to indicate the predator type: the “jar” sound is used to indicate a Japanese rat snake (*Elaphe climacophora*) whereas the “chicka” sound indicates a jungle crow (*Corvus macrorhynchos*) (Suzuki 2014). When

chicks hear the “jar” sound coming from the female they jump out of the nest to evade predation by the snake, but upon hearing the “chicka” sound they instead huddle in the nest to avoid being preyed upon (Suzuki 2011).

Some birds have also developed acoustic Bayesian mimicry that simulates the sound of a toxic, inedible, or more dangerous species so as to gain security benefits (Gaul 1952; Sibley 1955; Klump and Shalter 1984; Apel and Weise 1986; Rowe et al. 1986; Owings et al. 2002; Kelly et al. 2008; Zub et al 2017). When it senses invasion by a predator, the bird stretches its wings forward and down rapidly in a curve, raises and extends its tail, and gives a spontaneous hissing call (Perrins 1979; Cramp and Perrins 1994) that leads to its misidentification as a snake by the predator, which is then discouraged from approaching (Cox 1930; Sibley 1955; Rowe et al. 1986; Perrins 1979; Krams et al. 2014). For example, the hissing call of burrowing owl (*Athene cunicularia*) simulates the crackling sound of alerted Prairie rattlesnakes (*Crotalus viridis*) and is used to scare off its predator, the California ground squirrel (*Spermophilus beecheyi*) (Rowe et al. 1986).

Hissing calls are common in cavity breeding birds including tits (Odum 1942; Hinde 1952; Sibley 1955; Apel and Weise 1986; Broughton 2005, 2012). In many tit species, females incubate the eggs while males scarcely engage in alerting behavior or assist with nest defense (Perrins 1979). A recent study showed that hissing females of great tits (*Parus major*) survive better than silent females (Krams et al. 2014). Playing recordings of the hissing calls of the great

tit, Eurasian blue tit (*Cyanistes caeruleus*), and marsh tit (*Poecile palustris*) affected nest exploration by their predators, the yellow-necked mouse (*Apodemus flavicollis*) (Zub et al. 2017). Among different tit species breeding in the same area, rates of nest predation are lower for those that exhibit hissing behavior than for those that do not (Walankiewicz 2002; Wesołowski 2002; Czeszczewik 2004; Wesołowski and Rowiński 2012; Maziarz et al. 2016). However, hissing calls of many tit species have not yet been investigated. Moreover, there is little information on whether there are interspecific variation in hissing calls of tit species located in the same area, and whether the hissing call of a species is related to its life history traits.

To address these questions, in this study we compared the hissing calls of five tit species located in the same area. For sympatric breeding cinereous and varied tits, we also investigated whether there are differences in the breeding parameters of individuals with or without a hissing call, such as date of the first egg, clutch size, nest predation rate and nesting success in order to determine the relationship between hissing call and breeding performance.

Materials and methods

Study area and study species

The Saihanba National Forest Park (SHB) is located in Weichang, 240 km from Chengde City, Hebei Province (42°02'–42°36' N, 116°51'–117°39' E) at an altitude of 1,350–1,650 m. The park has a semi-arid/semi-humid cold-

111 temperature continental monsoon climate and is the main natural secondary
112 forest and plantation forest area in Hebei. Within the park there are plateaus,
113 mountains, forests, and grasslands (Fig. 1; Liu et al. 2017).

114 The Xianrendong National Nature Reserve (XRD) is located in Zhuanghe,
115 Liaoning Province (39°54'–40°03' N, 122°53'–123°03' E) at an altitude of 200–
116 600 m. It is adjacent to the Yellow Sea and is located in a warm, temperate,
117 humid monsoon climate zone (Fig. 1; Du et al. 2010).

118 Tits belong to the Paridae family, which comprises small passerine birds
119 that are mainly distributed in the Northern hemisphere and Africa. These small,
120 stocky, woodland species have short bills and a length of 10–22 cm (Gosler and
121 Peter, 2007). The great tit, which were originally distributed in Eurasia, are now
122 classified as three separate species: great tits from Europe to Northwestern Asia,
123 the cinereous tit (*Parus cinereus*) of South Asia, and the Japanese tit of East
124 Asia (Päckert et al. 2005).

125 In 2018, the birds attracted to artificial nest boxes hung in SHB were
126 mainly cinereous tits, willow tits (*Poecile montanus*), and coal tits (*Periparus*
127 *ater*) (Fig. 1, A-C). Between 2016 and 2018, the birds that were attracted to nest
128 boxes hung in XRD were mainly cinereous, marsh, and varied tits (*Sittiparus*
129 *varius*) (Fig. 1, D-F).

130

131 **Field data collection**

The nest boxes, particularly those used by tits, were routinely examined during the breeding season. Hatching status was determined according to clutch size and date of the first egg. The date on which the female laid the last egg was defined as day 0 of the incubation period. In this study, the incubation period of each of the five tit species was approximately 12 days. We divided the incubation period into three stages: early, mid and late incubation. The nest box was inspected once during each stage. When we opened the lid of the nest box during the inspection, some of the tits gave a hissing call instead of escaping from the nest. Depending on the response of the female upon opening the nest box, we divided the birds into those with or without hissing calls. During the field work, we found that the hissing call behavior of the five tit species was highly repeatable—i.e., individuals that did not give a hissing call at the start of the study did not give any hissing calls during the whole breeding period.

Nest predation rate was defined as the proportion of predated nests to the total nests monitored (Krams et al. 2014). Nesting success was defined as the proportion of successful nests (success to fledge at least one young), and it was a dichotomous variable for measuring predation intensity (Pribil 1998).

Statistical analysis

Statistical analysis was performed using SPSS v.16.0 for Windows (IBM, Armonk, NY, USA). The one-sample Kolmogorov-Smirnov test was used to analyze the normality of the data. When the data normality condition was met,

the t-test or one-way analysis of variance was used to compare mean values. Otherwise, non-parametric tests—i.e., the Mann-Whitney U test and Kruskal-Wallis test—were used. All tests were two-tailed, with a significance level of $P < 0.05$. Data are expressed as mean ± standard deviation (mean ± SD).

The number of tits with hissing calls in the two study areas were as follows: in SHB, 32 nests of cinereous tits, 17 nests of coal tits, and eight nests of willow tits were found to give hissing calls in 2018. In XRD, 48 nests of varied tits and 45 nests of cinereous tits in 2016; and 39 nests of varied tits, 40 nests cinereous tits, and 17 nests of marsh tits in 2018 were found to give hissing calls. Since no breeding of marsh tits was recorded in XRD in 2016, and the proportion of varied tits giving hissing calls differed significantly between the 2 years, only the 2018 data were included when analyzing interspecies differences of hissing calls of tits located in the same area of Liaoning. However, both the 2016 and the 2018 data were used when analyzing differences in the reproductive parameters of birds with and without hissing calls.

Results

During 2018 in SHB, 19 out of 32 (59.4%) cinereous tits, 14 out of 17 (82.3%) coal tits, and 3 out of 8 (37.5%) willow tits gave hissing calls. There were no significant differences among hissing calls of the three tit species located in the same area (Fig. 2; $P = 0.076$, Fisher's exact test).

During 2018 in XRD, 16 out of 39 (41.0%) varied tits, 24 out of 40 (60.0%) cinereous tits, and 3 out of 17 (17.6%) marsh tits gave hissing calls. Significant differences were observed among hissing calls of the three tit species located in the same area (Fig. 2; $P = 0.011$, Fisher's exact test).

In SHB, none of the 66 cinereous tits and 45 coal tits and only one of the 31 willow tit nests were depredated. There were no significant differences in predation rates among the three tit species ($P > 0.05$, Fisher's exact test).

In XRD, 18 out of 39 (46.2%) varied tits, 14 out of 40 (35.0%) cinereous tits, and 8 out of 19 (42.1%) marsh tits were targeted by predators. There were no significant differences in predation rates among the three tit species ($P = 0.597$, Fisher's exact test). For a total of 51 depredated nests, 30 nests were confirmed to be depredated by mice (10%; 3 out of 30 nests) or snakes (90%; including Korean rat-snakes *Elaphe anomala* and steppe rat-snakes *E. dione*).

For cinereous tits, 62 tits gave hissing calls whereas 23 tits did not. The date of the first egg and clutch size did not differ significantly between the two groups of tits [9.75 ± 1.31 (n = 60) vs. 9.77 ± 1.23 (n = 22)] ($P = 0.880$, Mann-Whitney U test). Similar rates of nest predation (19.4% vs. 30.4%) and nesting success (64.5% vs. 52.2%) were also observed between the two groups (Fig. 3; $P > 0.05$, Fisher's exact test).

For varied tits, 52 tits gave hissing calls whereas 37 tits did not. The two groups were similar in terms of date of the first egg and clutch size (7.31 ± 1.08 vs. 7.10 ± 1.12) ($P = 0.264$, Mann-Whitney U test) as well as nest predation

(21.6% vs. 30.8%) and nesting success (56.8% vs. 44.2%) (Fig. 3; $P > 0.05$, Fisher's exact test).

Discussion

Nest predation is one of the major causes of death in birds, and it has led to the evolution of morphological, physiological, and behavioral strategies to avoid predation (Lima 2009; Parejo et al. 2013; Fu et al. 2016). Previous work showed that cavity breeding tits give hissing calls to frighten approaching predators (Rowe et al. 1986; Zub et al. 2017) and thereby increase the survival rate of female birds and fledglings (Krams et al. 2014). Our study indicated that in SHB, there were no significant differences in the proportion of cinereous, willow, or marsh tit giving hissing calls. In contrast, in XRD, differences were observed in the proportions of cinereous, varied, and marsh tits. However, in both SHB of Hebei and XRD of Liaoning, nest predation rates of tits breeding in nest boxes located in the same area were similar. Cinereous and varied tits showed no differences in clutch size, date of the first egg, nest predation rate and nesting success between birds with and those without hissing calls.

Tit species in the wild are known to give hissing calls (Pickens 1928; Sibley 1995). However, there has been few studies investigating interspecific variation in hissing calls of tit species (Sibley 1995; Krams et al. 2014; Koosa and Tilgar 2016; Zub et al. 2017). An early report suggested that the hissing calls of tits was an acoustic form of Bayesian mimicry and provided a brief

219 description of the hissing calls of different species (Sibley 1995). In this study,
220 we recorded in detail the hissing calls of five tit species located in the same area
221 and investigated interspecific differences. In SHB of Hebei, we found that
222 between cinereous and willow tits, there was no difference in the proportion of
223 individuals giving a hissing call. However, in XRD of Liaoning, the proportions
224 differed among cinereous, varied, and marsh tits. We found that 60% of
225 individual cinereous tits gave a hissing call; this is comparable to the 70%
226 reported in a previous study in which hissing calls of great tits were found to
227 substantially reduce the predation rate of breeding females (Krams et al. 2014).
228 The hissing call of tits was also shown to discourage nest exploration behavior
229 of yellow-necked mouse (*Apodemus flavicollis*) (Zub et al. 2017). However, tit
230 species differing in the proportion of individuals giving a hissing call did not
231 have lower nest predation rate. In SHB, artificial nest boxes were mainly
232 distributed in plantations located in areas where there were few snakes and
233 Swinhoe's striped squirrels (*Tamiops swinhoei*)—two of the natural predators of
234 tits—due to the high altitude and low temperature. In contrast, in XRD, nest
235 predation rates of cinereous, varied, and marsh tits did not differ despite
236 variation in the proportion of individuals with hissing calls. This is because the
237 main nest predators in this area were Korean and steppe rat-snakes, which are
238 not affected by the hissing calls of tits. The nest predation rate is markedly
239 lower for great tits when compared to those without hissing calls (Krams et al.
240 2014). However, comparison of nest predation rates in cinereous and varied tits

241 was similar for individuals with and without hissing calls. A possible reason for
242 this discrepancy is our small sample size (85 cinereous and 89 varied tits vs.
243 477 samples in the study by Krams et al. 2014). Additionally, predators in their
244 study were mainly European pine marten (*Martes martes*), least weasel
245 (*Mustela nivalis*), and great spotted woodpecker (*Dendrocopos major*), which
246 are more likely scared off by the snake-like hissing calls of great tits than the
247 predators in our study area (mainly snakes).

248 Hissing calls are unrelated to the breeding performance of female birds
249 (Koosa and Tilgar 2016). For example, females with and without hissing calls
250 were found to lay a similar clutch size. Our results support this observation.
251 Furthermore, we also determined that the hissing calls of all five tit species are
252 unrelated to nest predation risk.

253 In conclusion, our results showed that hissing calls are common among
254 sympatrically breeding tit species such as cinereous, willow, coal, marsh, and
255 varied tits. In SHB of Hebei, the hissing calls of cinereous, willow, and coal tits
256 showed no interspecific variation. In XRD of Liaoning, although the proportion
257 of individuals giving hissing calls was higher in cinereous as compared to marsh
258 tits, the two species had similar predation risk. In addition, the hissing calls of
259 cinereous and varied tits were unrelated to nest predation risk or life history
260 traits such as date of the first egg, clutch size and nesting success. The present
261 study demonstrated the behavioral adaptations of different tit species to nest

predation, which can in turn provide insight into the life history traits of members of the Paridae family.

Ethics. The experiments reported here comply with the current laws of China. Fieldwork was carried out under the permission from Saihanba National Forest Park and Xianrendong National Nature Reserve, 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-2011-001).

Data accessibility. Data used in this study are available in Electronic Supplementary Materials.

Authors' contributions. The research idea was developed from discussion with APM. DW and WL designed the study; LZ, JL, ZG and LZ performed field experiments; LZ and JL carried out laboratory and statistical analyses. JL wrote the draft manuscript, and WL and APM revised and improved the manuscript. All authors approved the final submission.

Competing interests. The authors declare that they have no competing interests.

Funding. This work was funded by the National Natural Science Foundation of China (no. 31772453 to WL and no. 31872231 to DW).

Acknowledgments. We are grateful to the anonymous referees for their constructive comments that significantly improved this manuscript. We thank Saihanba National Forest Park and Xianrendong National Nature Reserve for their help and cooperation, Chunlei Jing and Congying Zhang for their assistance with field work.

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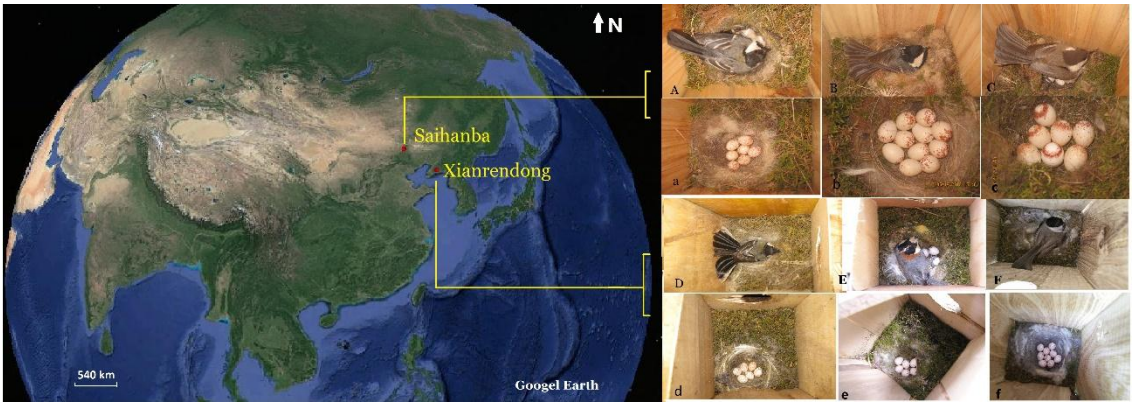
Legends to figures

Figure 1. Study areas and study species in this study. Capital letters (A-F) refer to bird species and lower case letters (a-f) refer to nest and eggs. A and D refer to cinereous tit; B refers to coal tit; C refers to willow tit; E refers to varied tit; and F refers to marsh tit.

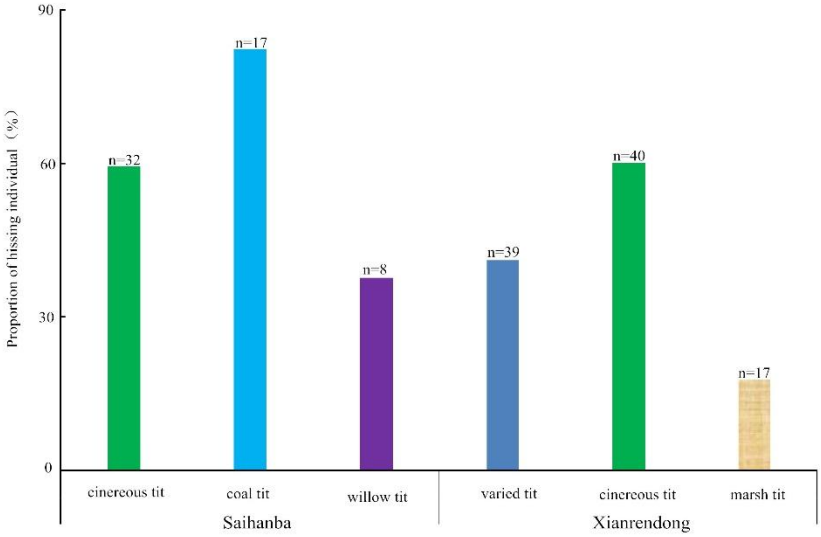
Figure 2. Proportion of hissing individuals in five tit species at two study sites.

Figure 3. Comparison of nesting success between individuals with hissing call and individuals without hissing call in cinereous and varied tits.

441 

442 **Fig. 1**

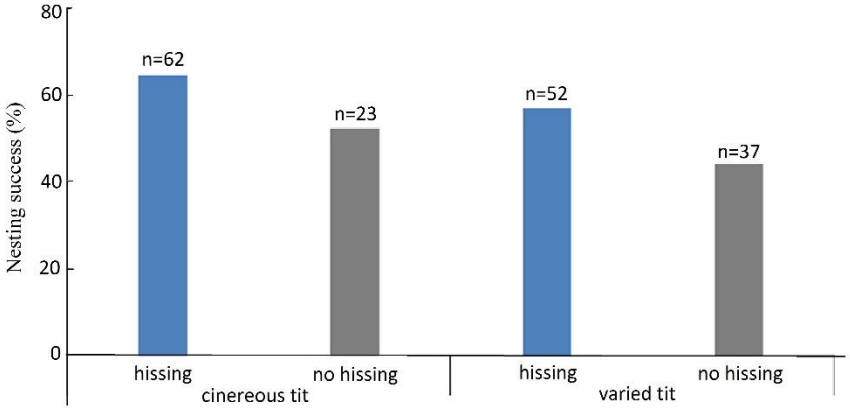
443



444

445 **Fig. 2**

446


80
60
40
20
0
Nesting success (%)
n=62
n=23
n=52
n=37
hissing
no hissing
hissing
no hissing
cinereous tit
varied tit

447

448 **Fig. 3**