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Seasonal increase of nest height of the Silver-throated Tit (*Aegithalos glaucogularis*): can it reduce predation risk?

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Abstract

Background: Nest predation is usually the main cause of bird nest failure. 'Predation avoidance hypothesis' of nest-site selection predicts that birds should prefer nest-sites with higher nesting success. We investigated the relationship between nest height and nest fate in Silver-throated Tits (*Aegithalos glaucogularis*) and asked whether the seasonal change of nest height was adaptive by simultaneously analyzing the seasonal variation of predation rates of the nests.

Methods: We monitored nests of the Silver-throated Tit across seven breeding seasons in the Dongzhai National Nature Reserve in Henan Province of China. We compared the difference of nesting success among nests of different heights and analyzed the effect of nesting date on nest height and nest predation rates.

Results: The overall nesting success rate was 24.1% ($n = 623$). Among the failed nests ($n = 472$), 59.75% were predated by birds and mammals, followed by snakes (9.11%). The average height of successful nests was significantly lower than that of predated nests. As the season progresses, the height of the nests increased significantly, companied by the decrease in nesting success. Daily survival rate of the nests also decreased with the progression of the season, regardless of breeding stages.

Conclusions: Our findings suggest that nest height is an important factor influencing the nesting success of Silver-throated Tits. However, the seasonal increase of nest height appears inconsistent to the 'predation avoidance hypothesis', because it is associated with higher predation rates. The reason for this maladaptive behavior remains to be explored in future studies.

Keywords: Nesting success, Nest height, Daily survival rate, Seasonal variation, *Aegithalos glaucogularis*

Background

Reproduction is an important stage determining an individual's fitness. For most bird species, reproductive success is directly associated with nesting success (Robertson 1995; Sieving and Willson 1998) and the nesting success of birds is influenced by various factors, such as predation (Martin 1993; Sherry et al. 2015; Fu et al. 2016), climate (Olsen and Olsen 1989; Heltzel and Earnst 2006; Sherry et al. 2015), human disturbance (Naguib et al. 2013), and the experience of the bird itself (Caudill

et al. 2016). Among these factors, predation is thought to be a major reason accounting for the nest failure in many birds (Martin et al. 2000; Fontaine and Martin 2006; Colombelli-Négrel and Kleindorfer 2009; Fu et al. 2016).

On the other hand, birds may actively take some strategies to avoid or reduce nest predation. For example, some species, like Black-billed Magpie (*Pica pica*) and Red-winged Blackbird (*Agelaius phoeniceu*), have developed certain nest-defense behaviors (Knight and Temple 1988; Redondo and Carranza 1989). Also, parents of some species are found to provision nestlings synchronously, the function of which was assumed to reduce nest conspicuousness to predators (Raihani et al. 2010; Bebbington and Hatchwell 2015). Besides, a probably more noticeable strategy is nest-site selection, which often determines

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the safety of a nest (Cody 1985; Natusch et al. 2017; Guil-herme et al. 2018). Usually, the increase of coverage and complexity of vegetation surrounding the nest can reduce nest predation rates (Holway 1991; Martin 1993; Arriero et al. 2006; Hollander et al. 2015; Buehler et al. 2017; Bellamy et al. 2018), and birds are expected to place their nests with good concealment (Lima 2009). This 'predation avoidance hypothesis' of nest-site selection therefore predicts that birds should adjust their nest-site preference according to varied predation risks. In accordance with this hypothesis, parent birds were found to prefer safer nest sites when predation risk was high in both Dusk Warbler (*Phylloscopus fuscatus*) (Forstmeier and Weiss 2004) and Siberian Jay (*Perisoreus infaustus*) (Eggers et al. 2006).

In this study, we investigated the relationship between nest site and nest fate in Silver-throated Tits (*Aegithalos glaucogularis*) and asked whether the seasonal change of nest height was adaptive by simultaneously analyzing the seasonal variation of predation rates of the nests. For most non-ground nesting birds, nest height is also of importance in determining nesting success (Ludvig 1995). For example, in both Blue Tit (*Cyanistes caeruleus*) and Marsh Tit (*Parus palustris*), predation rates decrease as the nest height increases because of inaccessibility of higher nests by snakes and some mammals (Nilsson 1984; Li and Martin 1991; Hunter et al. 2016; Sosa and de Casenave 2017). Nest height of the Silver-throated Tit ranges from lower than 0.5 m to above 10 m, and nests suffer a high predation rate throughout their nesting period (Li et al. 2012), providing an opportunity to investigate the relationship between nest height and nest failure. In this species, it is also possible to discuss whether the change of nest height is likely a response to nest predation, because although they produce one successful brood annually, repeated nesting attempts are usually made when they fail in the initial nesting attempts.

Methods

Study species and field work

The Silver-throated Tit is a small passerine species in the family of Aegithalidae and a former subspecies of the Long-tailed Tit (*Aegithalos caudatus*) (Harrap 2008). The species distributes throughout central and eastern China and south towards Yunnan (Zheng 2017). They nest on various species of plants, like Chinese Fir (*Cunninghamia lanceolata*), Masson Pine (*Pinus massoniana*), Horny Holly (*Ilex cornuta*) and Tea (*Camellia sinensis*) at our study site in the Dongzhai National Nature Reserve (31.95°N, 114.25°E, 100–840 m a.s.l.) of Henan Province, China. The reserve is at the transitional area of subtropical and temperate zone and is thus characterized by its richness in bird diversity (see Li et al. 2012 for more

information of the study site). The breeding of Silver-throated Tits in the reserve usually starts in late January or early February, and ends in late April or early May, and has low nesting success (i.e. around 30%) (Li et al. 2012).

Data for this study were collected at a 4.5 km^2 area located in the experimental zone of the reserve between 2011 and 2017. The Silver-throated Tits were caught with mist-nets and banded with unique combination of color rings and a numbered metal ring either in winter (December and January) or during the breeding season (from February to May). During breeding seasons, we searched for nests by following adults carrying nest materials or foods, or by systematically checking potential nesting habitats. For most nests that we found, we recorded their heights and checked them every 1–3 days to determine breeding stages (e.g. egg-laying, incubating and nestling) and nest fate (i.e. successful or failed). Successful nests were those that produced at least one fledgling. Nest failure was mainly due to nest predation and nest abandonment. Similar to our earlier work (Li et al. 2012), a nest was classified as abandoned if there was no sign of nest damage, no loss of eggs or nestlings, but the adults disappeared from the nest area. Nests of Silver-throated Tits were dome-shaped, with a small entrance on the side, and were lined with feathers inside. We assumed a nest predated by birds (e.g. Corvidae) and mammals (e.g. weasel and domestic cat) if there was partial or complete damage of a nest, accompanied by feathers outside the nest. If eggs or nestlings disappeared before the assumed fledging date in the absence of damage to the nest, predation by snakes was assumed. In addition, we also recorded nest losses caused by human activity (e.g. local farmers cut a nest tree or burned the nesting shrubs) and adverse weathers (e.g. snow and rain).

Data analyses

We calculated nesting success as the 'apparent nesting success', i.e. the number of successful nests divided by the total number of nests. The change of mean nesting success was analyzed in a generalized linear mixed model (GLMM) and the change of mean nest height was analyzed in a linear mixed model (LMM) within seven years. In these analyses, year as an explanatory variable and male parents ID were treated as random factors to account for non-independence of multiple nest records. Here, the reason that we used male identity instead of female or pair identity as the random factor was that the nest-site in this species was likely selected by males (Jianqiang Li, unpublished data).

We investigated the relationship of nest height with nest predation rate in two ways. First, we compared the difference in the proportion of nests that succeeded

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between nests with height lower and higher than the population average (Chi square test). Second, difference in nest height between successful and predated nests was compared with a Mann–Whitney *U*-test, because data do not conform to normality.

The relationship between nest height and nest initiation date was analyzed in a LMM with nest height treated as the response variable, and the effect of nest initiation date on nest fate was analyzed in a GLMM with nest fate as a binary response variable. In the above two models, nest initiation date was treated as an explanatory variable. To facilitate analyses, nest initiation date was classified into eight categories. The first date category is for nests built before February 11. Starting from February 11, every 10 days were treated as a category until April 11, after which all the nests found were assigned to the last category 'After April 11'. In addition, year and the identity of male parents were treated as random factors to account for non-independence of multiple nest records from a same year and a same individual, respectively. The reason that year was included as the random factor was that both nest height and nesting success varied by years (see "Results" section). Nests used in the analyses were only those with known initiation dates which could be estimated according to the completeness of a nest.

To get a better understanding of the effect of nesting date on nest survival, we also calculated daily nest survival rate for each nest and investigated whether it varied with season in a GLMM with binomial errors and a logit link (following Aebischer 1999). Because parental activities can affect nest predation (e.g. Martin et al. 2000), daily survival rate of a nest may vary with breeding stages with different parental actives. Therefore, we distinguished daily survival rates of a nest for egg stage (egg-laying and incubation) and nestling stage. Here we did not consider nest-construction stage because: (1) it is hard to determine the length of this stage if a nest failed before laying eggs, and (2) without eggs or nestlings, it is hard to judge whether a nest has been visited by predators if the nest was not damaged. In the GLMM, we fitted the number of days that a nest survived at a given breeding stage as the response variable and the length of this breeding stage that the nest could be observed if not failed as the binomial denominator. Year, male parents ID and nest ID were treated as random factors to account for non-independence of multiple nest records from a same year, a same individual and a same nest. Similar classification of date categories was used as the explanatory variable, but the last category was May 2 to May 11, and there were a total of eight categories.

In the above analyses, failed nests due to human interference ($n = 17$) and extreme weather ($n = 2$) were excluded. The abandoned nests ($n = 82$) were also excluded, as there is no clear evidence showed that nest-site security is directly related to nest-abandonment behavior in Silver-throated Tits. All analyses were conducted in SPSS 22.0 (IBM, Chicago, IL, USA). Tests were two-tailed and reported as significant when $p < 0.05$. Sample sizes in different analyses varied because data of some nests were incomplete.

Results

From 2011 to 2017, a total of 646 Silver-throated Tit nests were found. For nests with known fate ($n = 623$), only 24.1% produced fledglings and nesting success varied by year (GLMM, $F_{6,615} = 2.7$, $p = 0.014$; Fig. 1a). Among the failed nests ($n = 472$), 59.75% were predated by birds and mammals, followed by snakes (9.11%). In addition, 24.15% of the failed nests were due to nest abandonment by parental birds, 4.45% due to human activities, 1.48% due to adverse weathers, and 1.06% of unknown reasons.

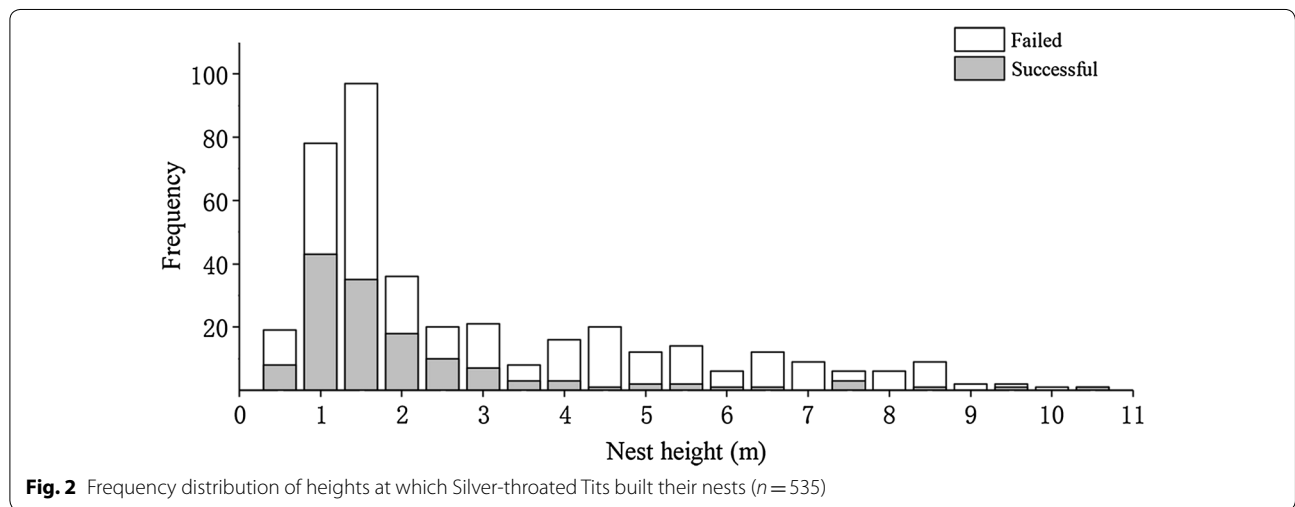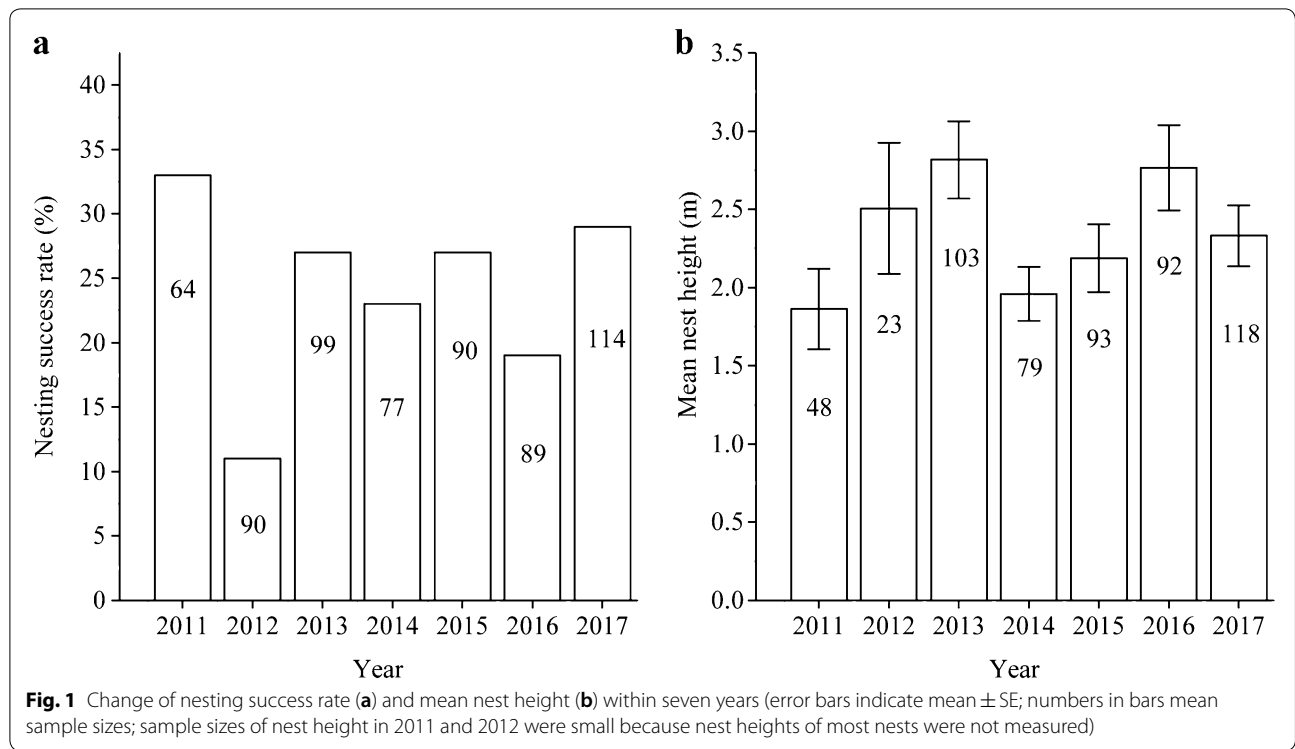### Effects of nest height on nesting success

The height of Silver-throated Tit nests ranged from 0.15 m to 10 m (Fig. 2), with an average of 2.32 m ($n = 535$). There was a significant variation in average nest height in different years (LMM, $F_{6,549} = 2.3$, $p = 0.037$; Fig. 1b). Excluding the nests which were abandoned, nests with height lower than the average (i.e. 2.32 m) had significantly higher nesting success than those higher than the average (39.7 vs. 17.7%; Chi square test, $\chi^2 = 21.6$, $p < 0.001$). Moreover, the successful nests were significantly lower than those failed (successful nests, $\bar{x} \pm SD = 1.75 \pm 1.73$ m, $n = 140$; failed nest, $\bar{x} \pm SD = 2.69 \pm 2.30$ m, $n = 294$; *U*-test, $z = -3.99$, $p < 0.001$).

Seasonal variation of nest height

Nest initiation date had a significant effect on nest height (LMM, $F_{7,306} = 15.6$, $p < 0.001$). There was an overall trend that nest height grew as the season progressed and the increase became significant in mid- and late March (Fig. 3a). Although nesting success was not affected by nesting initiation date overall (GLMM, $F_{7,306} = 1.7$, $p = 0.121$) (Fig. 3b), nesting attempts before March 13 were significantly more successful than those after March 13 (GLMM, $F_{1,312} = 9.0$, $p < 0.001$).

Nest height variation of a same individual within a season

Within a breeding season, a Silver-throated Tit could make up to four nesting attempts if it failed to produce a successful brood (Fig. 4). Data from the repeated nesting records of same individuals within a reason showed that the nests of the first attempts were significantly lower than those of the second attempts on average (Paired *t* test, $t_{47} = -4.7$, $p < 0.001$).
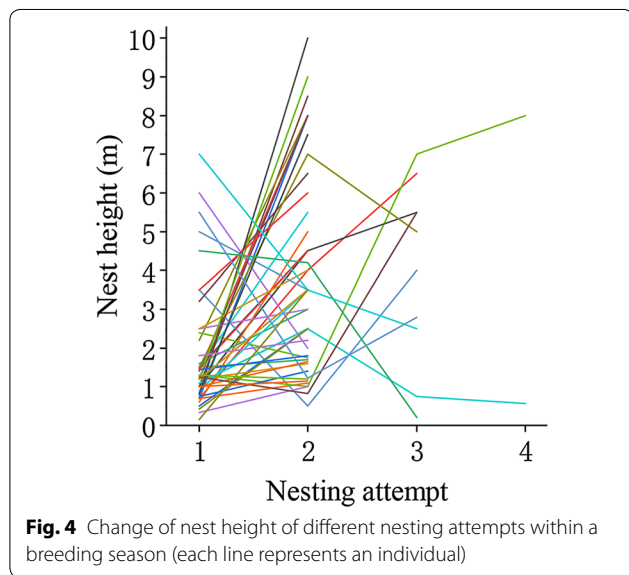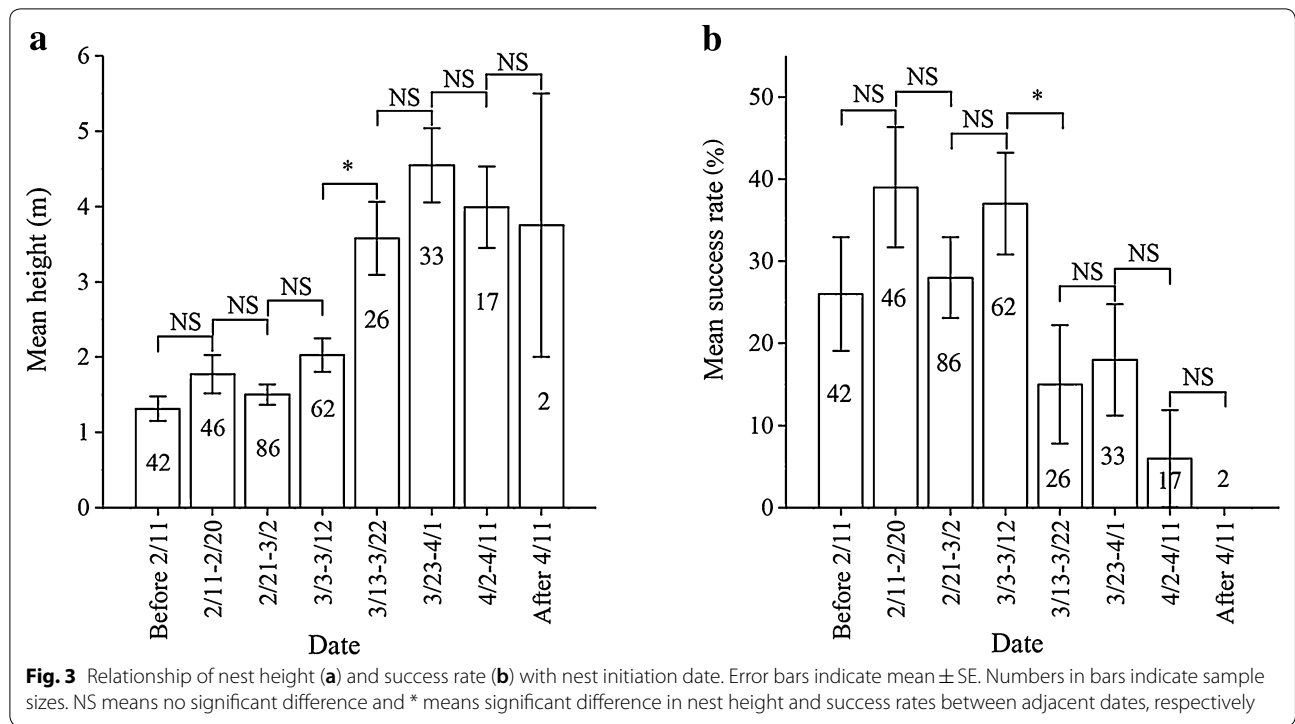
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Fig. 1 Change of nesting success rate (**a**) and mean nest height (**b**) within seven years (error bars indicate mean ± SE; numbers in bars mean sample sizes; sample sizes of nest height in 2011 and 2012 were small because nest heights of most nests were not measured)

Fig. 2 Frequency distribution of heights at which Silver-throated Tits built their nests ($n = 535$)

Daily survival rates

Daily survival rate was related to neither the breeding stage of the nest (GLMM, $F_{1,679} = 0.0$, $p = 0.984$) nor its interaction with date (GLMM, $F_{4,679} = 1.25$, $p = 0.288$), but was significantly affected by nesting date (GLMM, $F_{9,1076} = 16.7$, $p < 0.001$). For either of the two breeding stages, daily nest survival rates decreased with dates (egg laying and incubation stage, GLMM, $F_{6,388} = 16.4$, $p < 0.001$; nestling stage, GLMM, $F_{5,291} = 23.9$, $p < 0.001$) (Fig. 5).
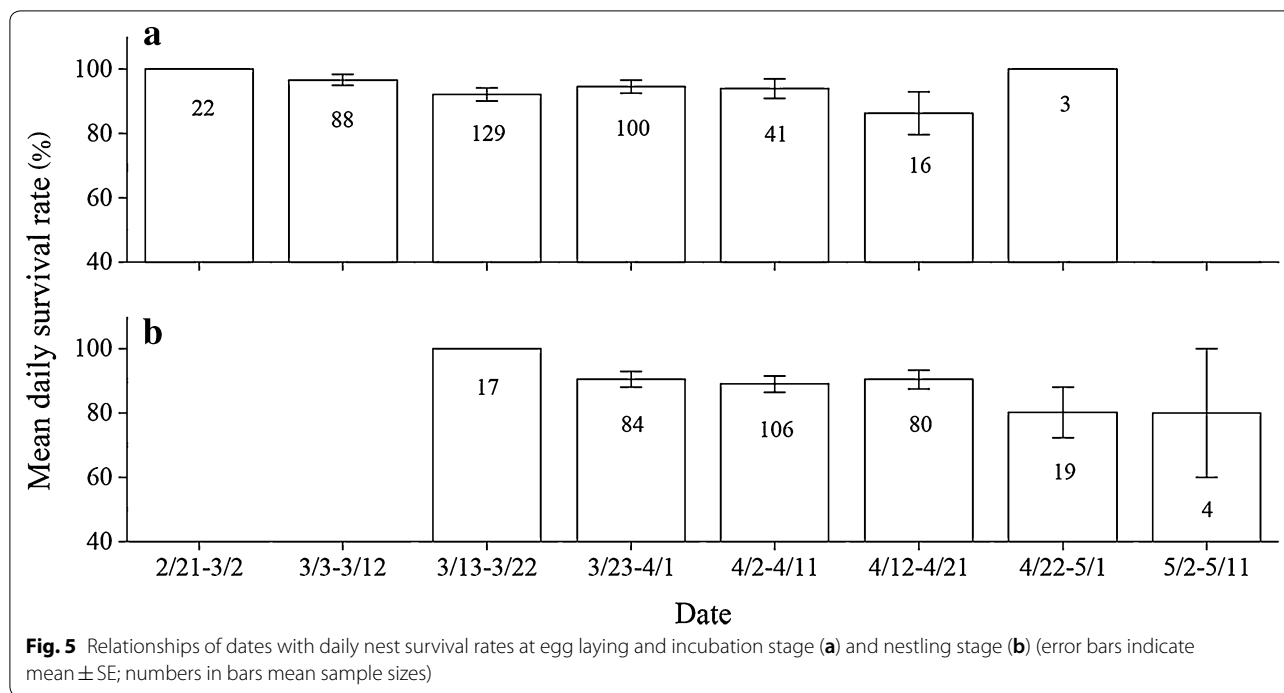
Discussion

Our results showed that the nesting success of Silver-throated Tits was only 24.1%, which was similar to that of the Long-tailed Tits (Gaston 1973; Glen and Perrins 1988; Hatchwell et al. 1996; Akazuka 2005; Hernández 2010). Moreover, nest height was found to significantly affect nesting success, with higher nests being more likely to be predated. This is also similar to the results found in the Long-tailed Tit populations (Gaston 1973; Hatchwell et al. 1999; MacColl and Hatchwell 2003).

Fig. 3 Relationship of nest height (**a**) and success rate (**b**) with nest initiation date. Error bars indicate mean ± SE. Numbers in bars indicate sample sizes. NS means no significant difference and * means significant difference in nest height and success rates between adjacent dates, respectively

Fig. 4 Change of nest height of different nesting attempts within a breeding season (each line represents an individual)

Given the fact that higher nests are more likely to fail, Silver-throated Tits are expected to place their nests at lower sites based on the prediction of 'predation avoidance hypothesis' of nest-site selection. However, it was found that there was a seasonal increase in the height of the Silver-throated Tit nests, which was most apparent in mid-March. Meanwhile, the increase of nest height was accompanied by a significant dropping in nesting success in mid-March. This is contrary to the 'predation avoidance hypothesis'. One may argue that the seasonal increase of nest height in Silver-throated Tits may be a response to the disturbance of research activities (e.g. frequent nest check). Change of nest preference as a strategy to avoid the impact of human activities has been reported in some species, such as Black Redstart (*Phoenicurus ochruros*) (Chen et al. 2011) and Blue-crowned Laughingthrush (*Garrulax courtoisi*) (Zhang et al. 2017). However, we believe that this is not the case in Silver-throated Tits, because for some individuals whose nests of their first nesting attempts were not found in the early season, the heights of their repeated nests after failing in earlier nesting attempts were also high. We think that the seemingly maladaptive behavior may be due to the following reasons.

First, it could be due to the change of structures of lower plants or microclimate. Change of nest-site preference due to growing vegetation has been found in other birds (Takagi and Abe 1996). As temperature gradually increases with the season, bushes begin to grow at our study site. The vegetation structure of lower plants may thus become inappropriate for nesting, forcing Silver-throated Tits to place their nest at higher sites. However, we do not think this is the case, because many nesting plants (e.g. Teas) do not have obvious change of their structure during the breeding season of Silver-throated Tits.

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Fig. 5 Relationships of dates with daily nest survival rates at egg laying and incubation stage (**a**) and nestling stage (**b**) (error bars indicate mean ± SE; numbers in bars mean sample sizes)

Another possibility is the change of microclimate. Dense vegetation not only provides protection, but also protects the nests from wind and nighttime heat loss (Walsberg 1981; Marzluff 1988; Colwell 1992). Therefore, microclimate can also be an important factor associated with nest-site selection in birds. A typical example of this is that bird nests are not randomly distributed in dense vegetation (Gloutney and Clark 1997). Microclimate can influence the temperature in the nest (Paclík and Weidinger 2007; Maziarz and Wesołowski 2013), which can affect energy consumption of birds to maintain body temperature (Gabrielsen and Unander 1987; Novoa et al. 1990) and affect the hatching rate of eggs, as well as the investments of parental birds in incubation and brooding (O'Connor 1975; Haftorn and Reinertsen 1985). From this point of view, the possibility that the seasonal change of Silver-throated Tit nest height is a result of the change of microclimate cannot be excluded.

Second, the change of nest height could be a response to increased activity of snakes. Snakes often pose threats to bird eggs and nestlings of nests close to grounds. Because snakes are poikilotherms, they usually do not appear until the weather gets warm. At our study site, the earliest date when we have recorded a snake-predation event of Silver-throated Tit was on March 19 (in 2015). This is consistent to the time when Silver-throated Tits start to increase nest height. Therefore, although the 'predation avoidance hypothesis' of nest-site selection does not predict that Silver-throated Tits should place

their nests at higher sites, it is very likely that the raise of nest height later in the season is a sole response to the appearance of nest predation by snakes, despite that the increased height results in higher probability of predation by bird predators.

Finally, nest-site choice of Silver-throated Tits may be a process of trial and error. At the beginning of the breeding season, most individuals place their nest at lower sites (Fig. 4) for some reasons (e.g. microclimate and previous experience). When nest failure happens at these lower sites, they then try to move to higher sites for nesting. This process of trial and error was possible, because from Fig. 4 it can be found that as opposed to the individuals nesting lower in their first nesting attempts, the few individuals nesting higher in their first nesting attempts chose to nest lower in their second nesting attempts.

Consistent to the seasonal decrease of nesting success, our results also show that the daily nest survival rate of Silver-throated Tit decreased as the season progressed. However, it is somewhat surprising that nest daily survival rate was not different between incubation and nestling stages, because nests at nestling stage are expected to have lower daily survival rate than those at incubation stage as both the begging behavior of nestlings and feeding behavior of adults may attract predators. The effect of breeding stage on nest daily survival rate has been investigated in several species. Support for the effect of breeding stage on nest daily survival rate has been reported, for example, in Brown-and-yellow Marshbirds (*Pseudoleistes*

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virescens) (Mermoz 1996) and Yellowbellied Sapsuckers (*Sphyrapicus varius*) (Tozer et al. 2009). However, in Blackbirds (*Turdus merula*) (Cresswell 1997) and Redwinged Blackbirds (*Agelaius phoeniceus*) (Yasukawa 2016), little evidence is found that the sound of nestling begging is important to predation. Therefore, the relationship between breeding stages and nest predation rate seems to vary by species.

It is noteworthy that cooperative breeding behavior exists in our Silver-throated Tit population (Li et al. 2012). Based on our observation, more than half of the helpers are those failed in their own breeding attempts. It was once thought in the Long-tailed Tit that the switch from independent breeding to helping was due to reduced reproductive success later in the breeding season (MacColl and Hatchwell 2002). Our finding of the significant drop in nesting success in mid-March may thus help to explain why Silver-throated Tit helpers usually appear in late March and April (Jianqiang Li, unpublished data).

Conclusions

Our study showed that there was a seasonal increase of average nest height in our Silver-throated Tit population, and the increase of nest height did not lead to higher, but instead resulted in lower nesting success. This suggests that the nest-site selection of birds may be maladaptive. Future studies need to explore whether the seemingly maladaptive increase of nest height in Silver-throated Tits is due to factors like the change of vegetation and microclimate. In addition, a detailed examination of the role of snakes and other predators (especially birds) in affecting nesting success, i.e., for example, to quantify their abundance and activities, is also important.

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Competing interests
The authors declare that they have no conflict of interests.

Availability of data and materials
The data used in the study are available from the corresponding author on reasonable request.

Consent for publication
Not applicable.

Ethics approval
The study complies with the current laws of China in which they were performed.

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