

# Parental attendance of Chestnut Thrush reduces nest predation during the incubation period: compensation for low nest concealment?

Yun-Biao Hu<sup>1</sup> · Qing-Shan Zhao<sup>1,2</sup> · Ying-Qiang Lou<sup>1,2</sup> · Li-Jun Chen<sup>1,2</sup> · Manuel Antonio González<sup>3</sup> · Yue-Hua Sun<sup>1</sup>

Received: 29 March 2016/Revised: 11 June 2017/Accepted: 5 July 2017/Published online: 19 July 2017  
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**Abstract** A well-concealed nest site is supposed to reduce nest predation risk; however, the expected positive relationship between nest concealment and nest survival does not exist in some passerine species, especially in thrushes. Previous studies have suggested thrushes might be capable of defending their nest against predators and do provide compensation for their low nest concealment, but this mechanism is controversial. We conducted a field experiment on the Chestnut Thrush (*Turdus rubrocanus*) to test whether parental attendance reduced nest predation risk, and to explore the possible mechanism behind this. In this study, we found that natural nests (with parental attendance) suffered lower nest predation rate than paired re-used nests (without parental attendance). With infrared-triggered cameras, we observed that Chestnut Thrush successfully defended their nests against mice. We identified mice as the main predator in re-used nests, while nest concealment had no significant impact on mice predation. Overall, parental attendance of the Chestnut Thrushes reduced the nest predation risk by deterring opportunistic

predators, but not enough to offset the low nest concealment.

**Keywords** Chestnut Thrush · Nest predation · Parental attendance · Nest concealment · Incubation period · *Turdus rubrocanus*

## Zusammenfassung

**Die Anwesenheit der Elternvögel am Nest (“Parental attendance”) verringert bei der Kastaniendrossel (*Turdus rubrocanus*) Nesträuberei während der Brutzeit: ein Ausgleich dafür, dass die Nester weniger versteckt sind?**

Ein gut verborgenes Nest ist eine Maßnahme, Nesträuberei zu verringern. Aber es gibt Vogelarten, vor allem Drosseln, für die der zu erwartende Zusammenhang zwischen Verstecktheit des Nestes und Überleben der Brut nicht gegeben ist. Frühere Untersuchungen legten nahe, dass Drosseln möglicherweise in der Lage sind, ihre Nester gegen Räuber zu verteidigen und damit das Risiko der schlechter versteckten Nester zu kompensieren, wobei diese Art von Kompensation allerdings kontrovers diskutiert wird. Wir führten mit Kastaniendrosseln (*Turdus rubrocanus*) einen Feldversuch durch, um zu testen, ob die “parental attendance” tatsächlich das Risiko von Nesträuberei verringert und um die gegebenenfalls zugrunde liegenden Mechanismen zu untersuchen. In unserer Untersuchung fanden wir, dass neu angelegte Nester (mit “parental attendance”) weniger Nesträuberei erfuhren als wieder verwendete Nester (ohne “parental attendance”). Mithilfe von Infrarot-Kameras konnten wir in einem Fall beobachten, wie eine Kastaniendrossel ihr Nest erfolgreich gegen eine Maus verteidigte. Wir stellten Mäuse

Communicated by F. Lei.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10336-017-1476-1) contains supplementary material, which is available to authorized users.

✉ Yue-Hua Sun  
sunyh@ioz.ac.cn

- <sup>1</sup> Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China
- <sup>2</sup> University of Chinese Academy of Sciences, Beijing 100049, China
- <sup>3</sup> Department Biodiversity and Wildlife Management, University of León, 24071 León, Spain

als die hauptsächlichlichen Räuber in wieder verwendeten Nestern fest, wobei es keinen großen Einfluss auf ihre Nesträuberei hatte, ob die Nester gut oder weniger gut versteckt waren. Generell verringerte bei Kastaniendrosseln die Anwesenheit der Eltern am Nest das Nesträuber-Risiko, weil sie opportunistische Räuber abschreckten; dies schien jedoch kein Kompensationsmechanismus dafür zu sein, dass die Nester wegen der Anwesenheit der Elterntiere weniger verborgen waren.

## Introduction

Nest predation is the major cause of nest failure in birds, especially in passerines. A well-concealed nest is supposed to reduce nest predation risk by reducing auditory, visual and olfactory cues for potential predators (Martin 1992, 1993). However, previous studies have found conflicting results for the expected positive relationship between nest concealment and nest survival (positive, e.g. reviewed in Martin 1992; neutral, e.g. reviewed in Götmark et al. 1995; Holway 1991; Howlett and Stutchbury 1996). Three likely explanations were proposed by Remeš (2005a): (1) different predators may use different cues to find nests (Remeš 2005b); (2) the majority of studies have simply used a correlational approach; and (3) parental behaviour may cause complex relationships between nest concealment and nest predation risk (Weidinger 2002). Besides these three explanations, Montgomerie and Weatherhead (1988) proposed that the armament variation between parents and potential nest predators might also influence the fate of nests. If parents could defend against most potential nest predators, there is no need to spend more energy in looking for a more concealed nest site. If not, a well-concealed nest site would help to improve nest survival rate.

Compared to the positive relationship found in most small body-sized passerines (reviewed in Martin 1992), we noticed that, in nest predation studies of thrushes (*Turdus* spp.), nest concealment had little effect on nest predation, for example in Song Thrush (*Turdus philomelos*; Götmark et al. 1995; Weidinger 2002), Common Blackbird (*Turdus merula*; Cresswell 1997; Weidinger 2002), American Robin (*Turdus migratorius*; Heltzel and Earnst 2006), Pale-eyed Thrush (*Turdus leucops*; Halupka and Greeney 2009), but see Lindell et al. (2011) on two Neotropical Thrushes. Both Cresswell (1997) and Halupka and Greeney (2009) suggested that parents were capable of efficient nest defence and could exclude a group of opportunistic predators, and thus compensated for the relatively poorer nest concealment. However, the experiment conducted on thrushes by Weidinger (2002) did not support the view proposed by Cresswell (1997).

During the breeding seasons of 2011 and 2012, within the same study area, we detected that the Chestnut Thrush (*Turdus rubrocanus*) suffered a lower nest predation rate than other shrub- or tree-passerines, although Chestnut Thrush nests showed the poorest concealment (own unpublished data). We hypothesized that: (1) poor concealment of Chestnut Thrush nests would incur a higher nest predation rate if without parents; and (2) Chestnut Thrushes may defend against most potential nest predators resulting in a low nest predation risk. Since the nestlings' behaviour (i.e. begging calls) may influence the nest predation risk during the nestling period (Briskie et al. 1999; Haskell 1994; McDonald et al. 2009), we conducted a field experiment to test the above two predictions only during the incubation period.

## Methods

### Study area and study species

We conducted the fieldwork at Lianhuashan Nature Reserve, Gansu Province, China (34°57'49"N, 103°45'26"E, 2000–2400 m above sea level), from May to July in 2013, 2014 and 2015. The study site is located on the edge of northern temperate forest and is mainly covered by agricultural land, with small woodland patches (mostly smaller than 1 ha) and bush clusters separated by the agricultural terrace system. Woodland in the study plots were dominated by *Picea asperata*, *Quercus wutaishanica*, *Populus* spp. and *Salix* spp., while shrub cover was mainly constituted by *Berberis* spp., *Lonicera* spp. and plants of the family Rosaceae (Sun et al. 2008).

The Chestnut Thrush is a relatively large body-sized passerine (~80 g) which is widespread and locally common in southwest China (Zheng 2011). This species builds open-cup nest in trees and shrubs. Only females take part in incubation while males provide incubation feeding (personal observation). The nests are usually 1–3 m above the ground with relatively low concealment, and most nests can be visually detected by experienced observers from a distance of 5 m.

### Nest monitoring

Nests were located by detecting parental behaviour and by systematically searching all potential habitats. When a nest was detected, we checked it every 1–3 days until the nest was depredated or the offspring fledged. A total of 38 infrared-triggered remote cameras (LTL ACORN 5210A, c.14 × 8 × 6 cm) were installed to identify nest predators at nests that were found during the egg-laying or early-incubation periods. Cameras were set ~1 m from

the nest with good camouflage (as the colour of camera was similar to the surroundings), attached to nearby branches or vegetation by nylon belts of a similar colour to leaves. The camera was set on “camera + video” mode, which means that, upon being triggered, the camera would take a photo and then a 20-s video, with the minimum interval between two consecutive recordings set at 1 min. When we checked the nests, we also checked the cameras to replace the batteries and the SD cards, and they were removed once the nesting period finished (fledged, depredated or abandoned). In total, we monitored 38 natural nests with the cameras.

The availability of our cameras meant that we were not able to monitor every nest. For nests without camera monitoring, we considered a nest successful when at least one young fledged (without predation cues, e.g. no eggs or nestlings missing between two consecutive nest surveys) or when the nest was empty 12 days after hatching. Nests in which eggs or nestlings disappeared prior to their expected fledging date were considered as depredated. When egg remains occurred in or around the nest, it was considered as depredated (i.e. egg predation event). When no parental activity was detected and eggs remained in the nest on least two consecutive surveys, the nest was considered to be abandoned.

According to our own unpublished data the average incubation period of the Chestnut Thrush was  $15.1 \pm 0.3$  days ( $n = 8$ , data from 2011 and 2012), and a nest was considered to be successful during the incubation period when they survived more than 15 days or all eggs found hatched. Predators were identified through images and videos, but not mice or snakes. As we could not identify the exact species of mouse (most probably Confucian Niviventer *Niviventer confucianus* and Korean field mouse *Apodemus peninsulae*, judging from body size according to potential locally distributed rodent species) and snakes (mostly *Gloydius strauchii* and *Elaphe dione*, the most two local common snake species, according to our own observations in the field) through the image and video, we categorized them as ‘mice’ or ‘snakes’.

These parameters were measured in the last nest survey: height above ground (m), height of supporting plant (m), percentage of canopy within a 5-m radius from the nest, nest concealment (calculated from three levels: lateral direction, 1 m above the nest and from the ground). The lateral nest concealment was calculated as 100% minus the exposed proportion of the nest cup to the nearest 5% (ranging from 0 to 100%) from the most obvious direction for each nest at a distance of 5 m after the observer checked from all directions. The nest concealment was always monitored by the same observer to control for observer errors.

## Experiment

To test the effect of parental attendance on nest predation during the incubation period, we designed a field experiment: natural nests were used at the same site (without parental activity) as artificial nests in order to avoid the effect of nest site on nest predation. Natural nests to be used in the experiment were selected if they met all the four following criteria: (1) successful or depredated nests; (2) nest concealment did not change from the day of being found to the day of termination (fledged or depredated); (3) the canopy cover of the nest-site (within a radius of 5 m) changed less (no trees or shrubs were cut or damaged); and (4) the nest was in good condition (not destroyed by predators or bad weather). In total, 41 nests were used for the experiment.

Previous studies have shown that some predators remembered former predation events and returned to a previously depredated nest (Pelech et al. 2010). To diminish this effect, we removed any remains of the nests previously depredated and waited at least 5 days to use them in the experiment, and we did the same with successful nests. We placed one Japanese uail (*Coturnix japonica*) egg (weights  $\sim 11$  g, and larger than the Chestnut Thrush’s egg  $\sim 7$  g) in each re-used nest. Quail eggs were used due to their availability; however, it is important to note that previous research (e.g. Marini and Melo 1998; Roper et al. 2010) and our field experiment demonstrated that quail eggs were too large to be depredated by small rodents, while these same rodents can readily depredate eggs of Chestnut Thrushes (personal observation). When a small rodent visiting the nest was captured on video, we considered this to be a nest predation event.

The re-used nests were monitored for 15 days (e.g. average incubation period) with the same methodology as for the real nests. The terminal date for depredated nests was identified as the day the first predation event happened, as all re-used nests were monitored by cameras.

## Data analysis

We calculated daily survival rate (DSR) during the incubation period using the RMark Package (Laake 2013) in R software (v.3.2.2; R Development Core Team 2007). The number of exposure days for natural nests without cameras was estimated by the ‘Early termination’ variant of the Mayfield method (Manolis et al. 2000; Weidinger 2002) with the exception that the exposure days of successful nests was truncated by the hatching day and not by the last visit. When comparing DSR between natural nests with cameras and those without, the exposure days for nests with cameras were calculated, since the camera was established but not on the day found. As several re-nests

were found to be depredated or hatched, we only included 35 of the 41 nests in comparing the DSR between re-used and natural nests. Monitoring equipment may influence nest predation rates (Pietz and Granfors 2000; Richardson et al. 2009), so we determined whether nest survival varied between real nests monitored with and without cameras (Carter et al. 2007). Otherwise, nest predation risk may vary throughout the breeding season and influence the result of experiments (Cox et al. 2012), so we also examined differences in the daily survival rate of each month (May, June and July, i.e. experimental period).

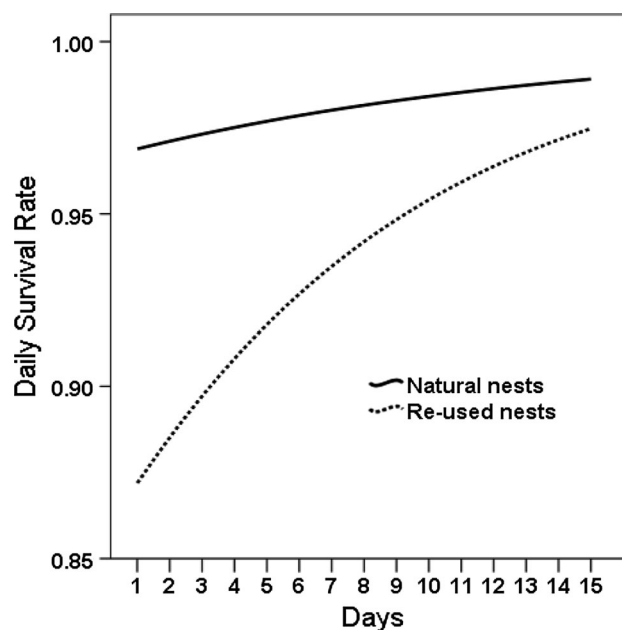
Differences in nest-site characteristics among nests depredated by different predators (visual predators vs. not visual, and mice vs. not mice) were calculated using two independent sample *t* tests. All tests were two-tailed and the results were presented as mean  $\pm$  SE. All analyses were conducted using R software (v.3.2.2; R Development Core Team 2007).

## Results

Natural nests with cameras had higher daily survival rates than those without during the incubation period ( $0.980 \pm 0.009$  vs.  $0.978 \pm 0.006$ ), but the difference was not significant ( $\chi^2_1 = 0.73$ ,  $P = 0.393$ ). And, we found no significant difference in the DSR during the 3 months of the incubation period (May:  $0.966 \pm 0.008$ ; June:  $0.968 \pm 0.010$ ; July:  $0.971 \pm 0.028$ ,  $\chi^2_2 = 0.20$ ;  $P = 0.903$ ).

Compared to paired natural nests, a larger proportion of re-used nests were depredated in the experimental period (63% vs. 27%,  $n = 41$ ). Re-used nests had a lower DSR than paired natural nests ( $0.923 \pm 0.016$  vs.  $0.979 \pm 0.007$ ,  $\chi^2_1 = 9.709$ ,  $P = 0.002$ ). The probability of a nest surviving during the 15-day period were 0.298 and 0.699 for re-used and natural nests, respectively. The DSR of re-used nests and paired natural nests increased with date during the 15-day period (Fig. 1).

In total, seven predator species or groups were recorded at natural and re-used nests, and more opportunistic predators were recorded in experimental period (Table 1). A total of 17.1% of re-used nests were depredated by visual predators (mostly birds and chipmunk), and these nests had poorer lateral ( $0.51 \pm 0.07$ ,  $n = 9$  vs.  $0.77 \pm 0.04$ ,  $n = 32$ ,  $t_{39} = 3.17$ ,  $P = 0.003$ ) and top ( $0.59 \pm 0.07$ ,  $n = 9$  vs.  $0.77 \pm 0.04$ ,  $n = 32$ ,  $t_{39} = 2.336$ ,  $P = 0.025$ ) concealment, but had better concealment from the ground ( $0.73 \pm 0.07$ ,  $n = 9$  vs.  $0.54 \pm 0.05$ ,  $n = 32$ ,  $t_{20.012} = -2.312$ ,  $P = 0.032$ ). Compared to nests not found by mice, nests depredated by mice (56.1%, 23/41) were located closer to the ground ( $1.70 \pm 0.08$  m,  $n = 23$



**Fig. 1** Daily survival rate of paired natural nests and re-used nests ( $n = 35$ ) of the Chestnut Thrush (*Turdus rubrocanus*) during the incubation period; solid line paired natural nests and dotted line re-used nests

vs.  $2.05 \pm 0.15$  m,  $n = 18$ ,  $t_{39} = -2.18$ ,  $P = 0.035$ ), while no significant differences were found in the other recorded parameters (height of supporting plant:  $4.27 \pm 0.23$  vs.  $4.81 \pm 0.70$ ,  $P = 0.469$ ; percentage of canopy:  $0.39 \pm 0.05$  vs.  $0.39 \pm 0.05$ ,  $P = 0.996$ ; lateral concealment:  $0.25 \pm 0.05$  vs.  $0.33 \pm 0.06$ ,  $P = 0.325$ ; top concealment:  $0.28 \pm 0.05$  vs.  $0.25 \pm 0.05$ ,  $P = 0.675$ ; ground concealment:  $0.43 \pm 0.06$  vs.  $0.41 \pm 0.07$ ,  $P = 0.878$ ).

## Discussion

Chestnut Thrushes at the Lianhuashan Nature Reserve may reduce predation risk during the egg period by attending the nest. This finding does not support what was proposed by Skutch (1949), which was that parental activity around the nest may attract a nest predator's attention and thus increase the nest predation risk. This finding is also not consistent with the neutral effects reported in other studies (Cresswell 1997; Svagelj et al. 2009), but similar to findings in thrushes by Weidinger (2002).

Re-used nests (without parents) suffered a higher nest predation risk, but we cannot relate it to the low nest concealment. Re-used nests depredated by visual predators had poorer lateral and top concealment, but only accounted for 17.1% of all the re-used nests, which was lower than the nest predation ratio of natural nests (27%). The larger proportion of depredated re-used nests was mainly caused

**Table 1** Nest predators identified at natural and re-used nests of the Chestnut Thrush (*Turdus rubrocanus*)

All nest predators identified	Natural nests $n = 7^a$	Re-used nests $n = 26^a$
Mice <sup>b</sup>	4 (2) <sup>c</sup>	23
Siberian Chipmunk ( <i>Tamias sibiricus</i> )	1	6
Large Hawk Cuckoo ( <i>Cuculus sparverioides</i> )	1	1
Common Cuckoo ( <i>Cuculus canorus</i> )		1
Chest-winged Cuckoo ( <i>Clamator coromandus</i> )		1
Great Spotted Woodpecker ( <i>Dendrocopos major</i> )		1
Elliot's Laughingthrush ( <i>Garrulax elliotii</i> )		2
Unknown <sup>d</sup>	2 (2) <sup>c</sup>	

<sup>a</sup> One natural nest and five re-used nests were depredated by two different predators, two re-used Chestnut Thrush nests were depredated by three different predators

<sup>b</sup> Most probably Confucian Niviventer (*Niviventer confucianus*) and Korean Field Mouse (*Apodemus peninsulae*), judged by body size according to potential locally distributed rodent species

<sup>c</sup> Number in parentheses means it happened at the nestling stage and  $n$  is uculusnumber of nests depredated

<sup>d</sup> The two unknown nest predators occurred at dawn at two natural nests and incapable nestlings disappeared with uculusnest in good condition, while no photos and videos were captured by uclusstrapping cameras; these were the only two nests where the camera failed to detect a predation event

by olfactory mice, on which concealment had no significant impact. Re-used nests depredated by mice were located closer to the ground than those not predated, suggesting that mice might be restrained by their climbing ability to reach higher nests. However, this might just be a coincidence, as climbing up 0.35 m higher seems not very difficult for a mouse. According to videos captured at one natural nest, the female Chestnut Thrush successfully deterred a mouse from the nest (Video S1, see supplemental material). Combining the fact that the major nest predation events occurring at re-used nests were caused by mice, we supposed that a successful defence against mice decreased the nest predation risk of natural nests. Mice detect nests by smell and do not rely on nest concealment to locate nests, so these results support the theory that the lack of a within-species relationship between nest concealment and survival in thrushes do not result from parental behaviour compensating for predation risk associated with poor nest concealment, as suggested by Weidinger (2002).

Our second prediction was that Chestnut Thrush was capable of defending against most nest predators (Montgomerie and Weatherhead 1988). Of the seven predator species recorded (Table 1), Chestnut Thrush (~25 cm and ~80 g) was larger than or outweighed most of them (e.g. mice less than 50 g), Elliot's Laughingthrush (~26 cm and ~50 g) and Great Spotted Woodpecker (~24 cm and ~70 g), only slightly smaller than Chipmunks (~29 cm and ~100 g) and the two cuckoos (>30 cm and >100 g). None of these predators can prey on or cause severe damage to adult Chestnut Thrushes, which can chase these predators away when attending the nest or in the nest surroundings. In temperate forests of the northern hemisphere, where potential nest predators are mainly corvids,

squirrels and small rodents, with few raptors and larger mammals (Weidinger 2009), *Turdus* nests were found to suffer a lower nest predation risk than other songbirds (Cresswell 1997; Falk et al. 2011; Heltzel and Earnst 2006; Weidinger 2002). Otherwise, in Neotropical forests, where diverse nest predators exist (raptors, snakes), with a similar body size of their temperate relatives, thrushes suffered higher nest predation (Lindell et al. 2011). This evidence supports the importance of the birds' capability of defending against different predators in determining the fate of nest.

Moreover, different nest predators use different cues to locate nests, which may cause the irregular effect of concealment on nest predation (Remeš 2005b). Mice were responsible 88% of all the depredated nests in this study. Therefore, based only on the artificial nest experiment, we would overestimate the importance of mice in nest predation of the Chestnut Thrush. However, we did not agree with the conclusion that the importance of mice was overestimated in artificial nest studies suggested by Weidinger (2009), as no predation caused by mice was recorded in his study, nor for the inter-species variation in nest location and defence capability, nor the variation in mice species and behaviour. Due to the disadvantages of infra-triggered cameras in monitoring parental activities (i.e. intermittently recording, not continuously), we got no detailed data to compare parental behaviours among different nest predation events. We considered both male and female defence behaviour together with comparing active nests (with parents) to re-used nests (without parents), we cannot differentiate between female and male behaviour in decreasing nest predation risk. However, a radio-tracking study on the Wood Thrush (*Hylocichla mustelina*) showed that males spent more time near the nest when the females

were off the nest (Evans and Stutchbury 2012). Although more evidence is needed, the same pattern is likely to exist in the Chestnut Thrush, since we also recorded several nests where the males were standing on the nests when the females were away.

In this study, we did not record any nest predation event caused by raptors, but four cases were caused by cuckoos at natural and re-used nests, while none of the three cuckoo species parasitise Chestnut Thrushes. Common Cuckoo parasitise the nests of White-bellied Redstart (*Luscinia phaenicuroides*) (Hu et al. 2013a) and the Large Hawk Cuckoo parasitises the nests of Elliot's Laughingthrush (Hu et al. 2013b) and Plain Laughingthrush (*Garrulax davidi*) (unpublished data) in our study area, Chest-winged Cuckoo parasitises laughingthrushes as reported by Yang et al. (2012), but no nest parasitism event was recorded in our study area. This is not evidence for the 'avian mafia' reported by Soler et al. (1995), but probably just occasional destruction as the Chestnut Thrush was not the host of these three cuckoo species.

Finally, this work supports the theory Chestnut Thrush parents reduce nest predation risk by deterring most opportunistic predators, but this is not simply compensation for low concealment. To better understand inter- and intra-species variation in nest predation risk, we strongly suggest combining knowledge of parental activities, nest site characteristics and predators in future studies.

**Acknowledgements** We thank De-Jun Wang, Ya-Xi Chang and other workers of Lianhuashan Nature Reserve for their help in the field. We also thank local people for allowing us to access to their farmland. This work was funded by the National Natural Science Foundation of China (No. 31270468).

#### Compliance with ethical standard

**Conflict of interest** We declare that all authors have no conflict of interest.

**Ethical standards** The study comply with the current laws of China in which they were performed.

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