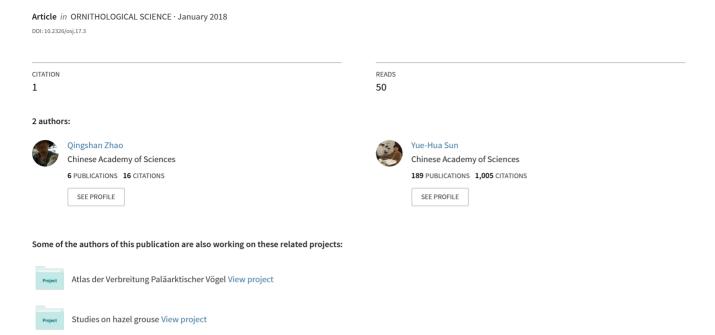
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ORIGINAL ARTICLE

Nest-site characteristics and nesting success of the Chestnut Thrush

Qingshan ZHAO1,2,3 and Yuehua SUN1,#

ORNITHOLOGICAL SCIENCE

© The Ornithological Society of Japan 2018 Abstract Nest-site characteristics may affect the daily survival rate of avian nests. We monitored the nests of Chestnut Thrush *Turdus rubrocanus* breeding in an agricultural landscape near the Lianhuashan Natural Reserve (central China) during the breeding seasons of 2013 and 2014. We describe the Chestnut Thrush's breeding ecology and used logistic-exposure methods and an information theoretic approach to assess the factors influencing daily survival rates of nests. Results from model averaging indicated that daily survival rates of nests consistently decreased from habitat edge to interior, contradicting the classic edge effect hypothesis describing predation of avian nests. Concealment of nests from below was positively correlated with nest daily survival rates, whereas concealment from the side and from above were not. These results suggest that determining the various effects of vertical and/or horizontal concealment on nest survival rates may help us assess the variation in the ability of local predators to detect nests.

Key words Breeding ecology, Chestnut Thrush, Daily survival rate, Nest site characteristic

Habitat selection, especially nest-site choice, is essential to an animal's fitness (Martin 1998; Clark & Shutler 1999; Chalfoun & Martin 2007). Selection pressures, such as maximizing embryo survival, modification of offspring phenotype, and offering suitable habitat for descendants, may drive non-random nest-site choice in birds (Refsnider & Janzen 2010). Nest-site specific nest success is a fitness proxy that has been studied extensively (Anich et al. 2013; Batáry et al. 2014; Vasseur & Leberg 2015), but general patterns are not emerging.

Predation on eggs and nestlings are major causes of nest failure in birds (Martin & Roper 1988). The edge effect on nest predation predicts that nest failure may generally be high in small, isolated fragments of habitat in a mosaic landscape (Andren & Angelstam 1988). However, a large aggregation of studies has revealed mixed results (Lahti 2001; Vetter et al. 2013). The positive relationship between dis-

tance from habitat edge and nest success has been revealed in many species, such as the Forest Batis Batis mixta (Newmark & Stanley 2011), the Brown Creeper Certhia americana (Poulin & Villard 2011), the Eurasian Nuthatch Sitta europaea (Deng & Liu 2015) and in artificial nest experiments (Suvorov et al. 2014; Malzer & Helm 2015). In contrast, in certain other species, this association has been found to be negative, such as in Cabanis's Greenbul Phyllastrephus cabanisi (Newmark & Stanley 2011; Spanhove et al. 2013). Furthermore, no discernible relationship has been shown in Sprague's Pipit Anthus spragueii (Jones & White 2012), Bobolink Dolichonyx oryzivorus (Keyel et al. 2013), and American Redstart Setophaga ruticilla (Falk et al. 2010). Moreover, temporal variation is also evident in the edge effect (Suvorov et al. 2014). Other than the edge effect, certain other nest-site characteristics, such as nest height, nest concealment, and timing of breeding, have also been shown to have inhomogeneous effects on nesting success and vary with breeding stage (Spanhove et al. 2013).

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A range of behaviors, including nest-site selection, nest success, egg size, clutch size, hatching asynchrony, singing behavior, and post fledging, has been studied for many species of thrushes, including Grey-backed Thrush Turdus hortulorum (Yang & Tain 1987; Zhou et al. 2011), Song Thrush T. philomelos (Kelleher & O'Halloran 2007; Congdon & Briskie 2010), Creamy-bellied Thrush T. amaurochalinus (Astié et al. 2006; Astié & Luchesi 2012), American Robin T. migratorius (Quinn et al. 2013), White-throated Robin T. assimilis (Cohen & Lindell 2004), Common Blackbird T. merula (Hatchwell et al. 1996), Fieldfare T. pilaris (Slagsvold 1982), Forest Thrush T. lherminieri (Parashuram et al. 2015), Japanese Thrush T. cardis (Ishizuka 2009), Pale-eyed Thrush T. leucops (Halupka & Greeney 2009), and Rufous-bellied Thrush T. rufiventris (Lomáscolo et al. 2010). Data obtained from such studies is essential for the development of avian life-history theory and the implementation of reasonable management and conservation actions for these species and their habitats. The Chestnut Thrush *Turdus rubrocanus*, of which there are two subspecies, has so far received little attention. Nominate T. r. rubrocanus occurs in the Himalayas, whereas subspecies T. r. gouldi occurs from the northeastern Tibetan Plateau east to central China and winters in Myanmar and southwestern Thailand (Zhang et al. 1986; Clement 2000).

Little detailed information is available on the life history traits of this species such as egg size, clutch size, nest-site characteristics, and the relationship between nest-site characteristics and potential predators. Therefore, we examined the breeding ecology of the Chestnut Thrush during two consecutive breeding seasons in agriculture fragments in central China. Moreover, we modeled nest success in terms of nest-specific explanatory variables. As discussed above, the direction and strength of the relationships between nest-site characteristics and nest success vary significantly between species. Given that we do not have a priori knowledge for the relationship between nest site characteristic and nest success, we used an information-theoretic approach to rank a set of models as a priori, without making a priori predictions on single factor effects.

MATERIALS AND METHODS

1) Study area and subjects

We conducted this study in the breeding seasons of 2013 and 2014 in the highly fragmented agricultural

landscape at Badu station (an area of 1.39 km²) of the Lianhuashan Nature Reserve, Gansu Province, in central China (34°40'N, 103°30'E, 2100 m above sea level). For a more detailed description of the nature reserve, see Sun et al. (2003). In our study area, the Chestnut Thrush begins building open-cup nests (primarily in hedgerows surrounding crop fields) in late-April, and clutches are initiated from early May to late June. We conducted daily nest searches from April until early July in both years, and found a total of 86 nests. Six of these nests were excluded from daily survival rate analysis, because they had been abandoned (no eggs nor nestlings were found when four nests were revisited (three in 2013 and one in 2014)), or had been destroyed by strong winds (one nest per year). Laying, hatching, and fledging dates were recorded for each nest. We measured all eggs and estimated egg volume based on egg length (L) and breadth (B), using the formula 0.51 LB² (Hoyt 1979). We recorded the body weight of all nestlings when they were 10 days old, in order to prevent premature fledging. We used the incubation period and the nestling period as the exposure days when calculating daily survival. We considered a nest to have been successful if at least one young survived to fledge. Potential nest predators of the Chestnut Thrush in our study area included: Siberian Weasel Mustela sibirica, Siberian Chipmunk Tamias sibiricus, Common Cuckoo Cuculus canorus, Himalayan Cuckoo C. saturatus, Large Hawk Cuckoo C. sparverioides, and Dione Ratsnake Elaphe dione.

2) Nest-site characteristics

As soon as the fate of each nest had been determined, we collected vegetation data at each of the nest sites. A modified version of the Breeding Biology Research and Monitoring Database (BBIRD) field protocol developed by Martin et al (1997) was used. Nest-site characteristics within 5 m radius circles were surveyed including nest height (Nest height), nest lateral concealment (Lateral concealment), concealment above (Above concealment) and below the nest (Below concealment), distance to habitat edge (Dis edge), shrub cover (Shrub cover), and woody cover (Woody cover). Other nest characteristics were measured including distance to human residences (Dis residence), road (Dis road), and water (Dis water). Nest height was determined by measuring the distance from the rim of the nest cup to the ground. Nest lateral concealment was the mean of the percentage of the nest hidden from view by vegetation three meters from the nest in the four cardinal horizontal directions. Nest concealment from above and below the nest is the percentage of the nest that was obscured by vegetation from one meter above and one meter below the nest. We estimated the percentage of woody cover and shrub cover. We recorded nest-site coordinates using a Global Positioning System (GPS) receiver, and nest site coordinates were entered into ArcGIS 10.2. and we digitized the research area from Google Earth (2015) satellite imagery. In order to determine distances to residences, roads, water (perennial streams) we used the measuring tool in ArcGIS 10.2. All heights were measured to the nearest 10 cm, whereas distances to other habitats and habitat edges were measured to the nearest meter.

3) Data analyses

To examine factors influencing the daily survival rate of nests, we used the logistic-exposure method (Shaffer 2004). In brief, we ran a generalized linear model (GLM) with binomial distribution and a customized logistic link function: $\ln[\theta^{1/t}/(1-\theta^{1/t})]$, where θ is the daily survival rate and t is the interval length

(in days) between two nest checks (implemented in R 3.1.1; R Core Team 2014). We also assessed temporal effects, including the following variables: nest age (Nest age), quadratic effect of nest age (Quadratic nest age), Julian date (Date), and year (Year). We did not find any variables strongly intercorrelated (r>0.6) using Spearman rank correlation. We selected a priori a set of 20 models (Table 1) that we believed could potentially explain variation in daily nest survival. Serious multicollinearity (variance inflation factor, VIF>10) was not detected in our analyses. Information theoretic approaches and model averaging were used (Grueber et al. 2011). We used the effective sample size (N) to compute Akaike Information Criterion (AIC_c) (i.e. N=total number of days that nests were known to survive+total number of intervals in which a failure occurred) (Rotella et al. 2004). The small-sample version of the AIC_c was used to rank models. For all variables included in models receiving support (ΔAIC_c<2), model-averaged parameter estimates were reported with their 95% confidence intervals in order to incorporate model-selection uncertainty (Burnham & Anderson 2002). Our inferences were based on the model-averaged estimates.

Table 1. Candidate models for assessing the influence of spatial and temporal variation on daily survival rates of Chestnut Thrush nests. Models are compared based on the number of parameters (k), an information criterion corrected for sample size (AIC_c), difference in AIC_c from the most parsimonious model (Δ AIC_c), and model weight (W_i) indicating the relative support for each model.

| Model | k | AIC_{c} | ΔAIC_{c} | \mathbf{W}_{j} |
|--|----|-----------|------------------|------------------|
| Below_concealment+dis_edge | 3 | 277.54 | 0 | 0.28 |
| Below_concealment | 2 | 279.21 | 1.67 | 0.10 |
| Below_concealment+dis_edge+nest_height | 4 | 279.34 | 1.80 | 0.08 |
| Below_concealment+dis_edge+woody_cover | 4 | 279.41 | 1.87 | 0.07 |
| Below_concealment+dis_edge+shrub_cover | 4 | 279.52 | 1.98 | 0.07 |
| Below_concealment+dis_edge+nest_height+nest_age | 5 | 279.60 | 2.05 | 0.07 |
| Lateral_concealment | 2 | 279.62 | 2.07 | 0.07 |
| Below_concealment+dis_water | 2 | 279.78 | 2.24 | 0.06 |
| Below_concealment+dis_edge+nest_height+quadratic_nest_age | 4 | 280.06 | 2.52 | 0.05 |
| Null model | 1 | 280.14 | 2.59 | 0.05 |
| Below_concealment+dis_residence | 3 | 280.37 | 2.82 | 0.05 |
| Below_doncealment+dis_edge+nest_height+date | 5 | 280.76 | 3.22 | 0.04 |
| Below_concealment+dis_road | 3 | 281.21 | 3.67 | 0.03 |
| Below_doncealment+dis_edge+nest_height+year | 5 | 281.35 | 3.81 | 0.03 |
| Above_concealment | 2 | 281.62 | 4.09 | 0.02 |
| Above_concealment+horizontal_concealment+down_concealmen | 4 | 281.76 | 4.22 | 0.02 |
| Below_concealment+dis_edge+woody_cover+shrub_cover+nest_height | 6 | 282.97 | 5.43 | 0.01 |
| Below_concealment+dis_resident+dis_road+dis_water+dis_edge | 6 | 282.97 | 5.44 | 0.01 |
| Below_concealment+dis_edge+nest_height+nest_age+date+year | 8 | 284.46 | 6.93 | 0.00 |
| Full model | 15 | 295.18 | 17.64 | 0.00 |

We used the function model.avg of the 'MuMIn' package (Bartoń 2012) to conduct model averaging. Means are given±standard error (SE).

RESULTS

In our study area the Chestnut Thrush built nests in 15 plant species (N=86). The species used most commonly for nesting were: willow Salix sp. (N=17, 20%), littleleaf buckthorn Rhamnus parvifolia (N=14, 16%), dragon spruce Picea asperata (N=12, 14%), Liaotung oak Ouercus liaotungensis (N=12, 14%), and white poplar *Populus alba* (N=11, 12%). Other tree species used for nests included: Siberian apricot Prunus sibirica (N=5), Japanese plum P. salicina (N=4), Siberian crabapple Malus baccata (N=4), Gansu hawthorn Crataegus kansuensis (N=2), Japanese honeysuckle Lonicera japonica (N=2), Father David's rose Rosa davidii (N=2), Père David's maple Acer davidii (N=1), Chinese Angelica-tree Aralia chinensis (N=1), sea buckthorn Hippophae rhamnoides (N=1), and Daurian larch Larix gmelinii (N=1).

Nests were cup-shaped, with a weight of 249.31 ± 15.99 g (93.79–451.00 g; N=25), an inner diameter of 99.60 ± 2.10 mm (87.12–145.04 mm; N=25), an exterior diameter of 140.51 ± 3.32 mm (70.42-152.55 mm; N=25), a depth of 62.22 ± 1.38 mm (48.54-75.09 mm; N=25), and a cup height of 93.81 ± 2.58 mm (65.79–127.46 mm; N=25). The density calculated for the study area was 33.09 pairs/ km² in 2013 and 28.78 pairs/km² in 2014. Nest heights above the ground ranged between 0.90 and 4.50 m (mean= 2.10 ± 0.10 m; N=86). The clutch size of the Chestnut Thrush was typically three (53%, N=46) or four (38%, N=33) eggs, with a mean of 3.37 ± 0.06 (range 2-5, N=86). The average length of eggs was 31.18 ± 0.08 mm (range 27.07-35.57 mm; N=288) and the average breadth was 21.70±0.01 mm (range 19.26–23.55 mm). The mean volume of eggs was 7.50 ± 0.04 cm³ (range 5.93-9.17 cm³; N=288). Ten days after hatching, the mean number of nestlings was 2.39 ± 0.15 (range 1-4, N=41). Mean nestling mass was 60.76 ± 1.03 g (range 42.21-77.21 g; N=105). Incubation lasted 13.61 ± 0.27 days (range 12-15 days, N=18) and the nestling stage lasted 15.12 ± 0.20 days (range 14–17 days, N=16).

We successfully monitored the fates of 80 Chestnut Thrush nests, 42 in 2013 and 38 in 2014, leading to effective sample sizes of 1310. Most nests were discovered at an early stage of nest development (24 in the nest building stage, 49 in the egg stage, and seven in the nestling stage). The main causes of nest failure were nest predation (47 %, N=38). All nestlings in one nest died without evident wounds, and had perhaps been abandoned. At least one fledgling was produced in 41 nests. The overall daily survival rate was estimated from logistic-exposure models and averaged 0.96.

The model receiving the most support by far included the main effects of concealment below the nest and distance to habitat edge (Table 1). The concealment only model (Below concealment), the model including nest height (Below concealment+dis edge+nest height), woody cover (Below concealment+dis edge+woody cover), and shrub cover (Below concealment+dis edge+shrub cover) also received support (Table 1). Nest lateral concealment, nest concealment above, distance to the residence, distance to road, distance to water, nest age, quadratic effect of nest age, Julian date, and year were not present in the final model, indicating that those factors were not useful predictors of daily nest survival for the Chestnut Thrush (Table 2). Confidence intervals for nest height, shrub cover, and woody cover included zero, so there was little evidence that any of those predictor variables affected the daily nest survival rate. In addition, the only model-averaged parameter estimates for which the 95 % CI did not include zero were for concealment below the nest and distance to habitat edge (Table 2). Nests with greater concealment below the nest and near the habitat edge had higher daily nest survival rates.

DISCUSSION

Although the Chestnut Thrush is a common species, little has previously been published on its breeding ecology. T. r. gouldi was previously known to nest in trees or bushes, included the purple cone spruce Picea purpurea, Farges' fir Abies fargesii, and the willow Salix hypoleuca in Wanglang Nature Reserve in Sichuan Province at an altitude of 2700 m (Zhang et al. 1986). In our study area, the average nest height was similar to that in Wanglang (1.5-3.0 m, N=3; Zhang et al. 1986);however, nest dimensions were smaller (mean exterior diameter × inner diameter × depth × height at Wanglang= $16.65 \times 9.80 \times 7.8 \times 12.5$ cm, N=3, Zhang et al. 1986). Clutch size in our study was slightly larger than in Wanglang (mean=3, N=3), however egg size was slightly smaller than in Wanglang

Table 2. Model-averaged parameter estimates, unconditional standard errors (SE), 95% confidence (95% CI) and relative importance for factors from supported models predicting nest-specific daily survival rates of Chestnut Thrush. The relative importance indicated the total sum of the AICc-weights of all the models in the model selection in which the given predictor variable occurs.

| Variables in averaged model | Estimate | SE | 95%CI | Relative importance |
|-----------------------------|----------|------|--------------|---------------------|
| Intercept | 2.95 | 0.45 | 2.23,3.69 | |
| Below_concealment | 0.83 | 0.47 | 0.03,1.72 | 1 |
| Dis_edge | -0.02 | 0.01 | -0.04, -0.01 | 0.83 |
| Nest_height | -0.24 | 0.48 | -0.48, 0.29 | 0.16 |
| Woody_cover | 0.20 | 0.50 | -1.35, 2.03 | 0.15 |
| Shrub_cover | -0.23 | 0.49 | -1.71, 1.32 | 0.14 |

(length×breadth=31.9×22.1 mm, N=6) (Zhang et al. 1986). Such differences may be attributed to the difference in altitude between the two study locations. Similar variation (in clutch size and egg size) along an elevational gradient has been described previously for the Common Blackbird (Lu 2004).

The Chestnut Thrush lays a medium-sized clutch compared with other congeneric species. The mean clutch size of the Chestnut Thrushes (3.37, 34°40′N, 103°30′E) is quite similar to that of the Common Blackbird (2.96, 36°46'N, 7°28'E) (Zeraoula et al. 2016), Creamy-Bellied Thrush (3.10, 32°51'S, 68°42'W) (Astié et al. 2006) and American Robin (3.60, 45°35′N, 73°40′W) (Morneau et al. 1995), but higher than that of the White-throated Thrush (1.93, 8°47′N, 82°57′W) (Sekercioglu et al. 2007), Pale-eyed Thrush (1.93, 0°35'S, 77°53'W) (Halupka & Greeney 2009) and Rufous-bellied Thrush (2.74, 34°16′S, 58°56′W) (Sackmann & Reboreda 2003), and lower than that of the Japanese Thrush (3.9, 35°86'N, 137°94'E) (Miyazawa 1971), Grey-backed Thrush (4, 42°42′N, 123°29′E) (Yang & Tain 1987), Song Thrush (4.10, 52°00'N, 10°00'W) (Kelleher & O'Halloran 2006) and Fieldfare (5.41, 63°00'N, 10°00′E) (Slagsvold 1982). It seems that in the genus Turdus clutch size increases along a latitudinal gradient, which is a common pattern among passerines (Jetz et al. 2008).

Nest concealment by vegetation might be the most important factor affecting nest survival in all of the nest-site characteristics (Weidinger 2002). Nest concealment is often measured as an average of coverage in vertical and horizontal directions. It might be meaningful to determine whether vertical and/or horizontal concealment are important for nest success. Discerning this relationship may help assess the variation in the ability of local predators to detect nest sites. Concealment of the nest from above it

known to have a positive effect on nesting survival possibly indicating that the majority of local predators might be aerial predators (Robertson & Olsen 2014). However, concealment of the nest from below had a positive effect on nesting survival for the Chestnut Thrush, perhaps implying that the majority of its local predators are terrestrial. Our results suggest that the daily nest survival rate of the Chestnut Thrush increases near habitat edges. This finding contradicts the predictions of the edge effect on nest predation hypothesis (Lahti 2001). Such an inverse edge effect has also been observed in Cabanis's Greenbul P. cabanisi (Spanhove et al. 2013). And these inverse edge effects may be due to a preference for interior habitat by nest predators (Spanhove et al. 2013). Given that avian predators tend to be more abundant near habitat edges (Chalfoun et al. 2002), and combined with the result that concealment of the nest from below had a positive correlation on Chestnut Thrush nest survival, we assume that the majority of local predators may not be birds, but rather terrestrial mammals with greater abundance and activity within the interior of habitats.

Our study of the reproductive biology of the Chestnut Thrush in central China, taken together with other studies of species in the genus *Turdus*, provide evidence for the well-recognized pattern of clutch size variation across latitudinal gradients. Our study also added to the growing evidence that nest-site characteristics may affect avian nesting success. We showed that Chestnut Thrush nests that were better concealed and placed near habitat edges appeared to have higher daily survival rates.

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