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Personality-dependent nest site selection and nest success during incubation in wild chestnut thrushes

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Highlights

We measured two personality traits in a wild population of female chestnut thrushes

More active females chose nest sites with great nest lateral concealment

Females with higher breathing rate laid small clutch sizes

Nests of females with lower breathing rate had higher nest success during incubation

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Personality-dependent nest site selection and nest success during incubation in wild chestnut thrushes

Yingqiang Lou,[1] Qingshan Zhao,[2] Yunbiao Hu,[1] Lijun Chen,[1] Pengfei Liu,[3] Yun Fang,[1] Huw Lloyd,[4] and Yuehua Sun[1,5,*]

SUMMARY

In birds, little is known about how individuals choose nest sites based on their personality traits. Here, we investigate whether a female's personality (activity and breathing rate) can affect patterns of nest site selection at different spatial scales in a wild population of chestnut thrush (*Turdus rubrocanus*) and determine whether nest site characteristics and female personality traits affect clutch size and nest success during incubation. We found that neither activity nor breathing rate were associated with large-scale nesting habitat variables. At the fine-scale level, more active females chose nest sites with greater nest lateral concealment. Females with higher breathing rates laid smaller clutch sizes than individuals with lower breathing rates. Nests of females with lower breathing rate had higher nest success during incubation. This work highlights the relationships between personality and nest site selection in birds, and the important role of female personality traits in reproductive success.

INTRODUCTION

Animal personality is defined as individual behavioral differences that are consistent over time and/or across contexts.[1–3] Having been studied across many animal taxa,[4] animal personality is now known to play important roles in sexual selection,[5–7] parental care,[8,9] and other life history traits.[10,11] For example, female zebra finches (*Taeniopygia guttata*) choose mates with similar personality traits,[12] and parents with similar personality traits have higher reproductive success.[13–15] Recently, quantifying spatial distribution patterns of individuals within a population based on animal personality has attracted increasing interest.[16–18] Personality could reflect individual ability to cope with environmental conditions, which may in turn lead to personality-dependent distribution,[19,20] which forms the premise of the personality-matching habitat choice hypothesis.[17,19,21]

Nest site selection at different spatial scales (i.e., large- and fine-scale) is an important process for successful breeding,[22] and is affected by many factors such as food resources and predator abundance.[23,24] Recent studies have found that individual differences in personality traits are known to be related to large-scale nest site selection.[17,25,26] For example, bold female common eider (*Somateria mollissima*) select nest sites with greater concealment and which are located further from landscape features.[27] To our knowledge, less is known about how personality traits affect patterns of fine-scale nest site selection in birds. Therefore, to gain an understanding of personality-dependent nest site selection requires a comprehensive examination of animal personality differences at different spatial scales.

Fine-scale nest site selection also affects individual reproductive strategy.[28–30] Nests with better concealment can have larger clutch sizes,[23,31] which may covary with nest fate. Large clutch size could produce more nestlings which would require adults to make more foraging trips, and nesting in areas with greater concealment could reduce the risk of nest predation.[32] Furthermore, clutch size could also be affected by personality traits.[33] For example, Araya-Ajoy et al.[34] found that more explorative female great tit (*Parus major*) laid larger clutch sizes.

Personality traits may be a significant factor that affects avian reproductive success.[17,35,36] Nest defense is one kind of personality traits, and more intense nest defense is associated with lower risk of predation,[37,38]

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Table 1. Repeatability of activity and breathing rate in chestnut thrush

Trait	N_{ind}	Range	R	P
Activity	153	0–18.385	0.337	0.003
Breathing rate	165	55–180	0.477	<0.001

N_{ind} = total number of individuals, and R = repeatability (R), and range = range of traits.
Activity is represented as the square root of the number of movements in the simple cage test. Breathing rate is defined as the number of breast movements during 60 s while being handled. The LMMs of activity and breathing rate were used to calculate the repeatability and can be found in Table A1.

and different personality traits may cause different responses to nest predators[39]; for example, more proactive individuals are shown to respond more boldly toward human intruders or natural predators[37,40] during incubation and nestling periods. Furthermore, nest site characteristics are also associated with reproductive success, since individuals who choose to select nest sites with greater nest concealment could increase the difficulty for predators to find the nests.[30] A recent study found that nest success was positively associated with nest concealment across 21 species on the Tibetan Plateau.[30] To date, few studies have investigated how multi-scale nest site characteristics (fine- and large-scale) and personality traits affect nest success during incubation.[41]

In this study, we extend the previous research of Zhao et al.[25] of a wild breeding population of chestnut thrush to investigate whether nest site selection and nest success during incubation are related to females' personality traits. We use two measures of animal personality—breathing rate and activity—which are easily measurable and repeatable in our study population.[15,25] Although breathing rate is considered by some as a physiological trait-reflecting stress response,[42,43] many authors have argued a strong case for boldness to be measured (at least as a proxy) by breathing rate (lower breathing rate reflecting greater boldness), as the two appear to be very closely linked.[44–49] In chestnut thrushes, only females participate in nest site selection, incubation, and in brooding nestlings,[15] and both sexes participate in nest defense and provisioning to offspring. Furthermore, our previous study found that nest site characteristics, such as concealment of nests from below, were positively associated with nest daily survival rate.[50] Therefore, the wild chestnut thrush population is a suitable model species with which to explore the relationship between personality with nest site selection and nest success during incubation.

Our objectives of this study are 3-fold: (1) to examine whether large- and fine-scale nest site characteristics were associated with female personality traits. Based on the previous results of Seltmann et al.[27] and Holtmann et al.,[19] we predicted that females with lower breathing rate and activity select nest sites nearer from areas of human disturbance (e.g., human residence, roads, and farmland) and in more concealed areas (higher concealment of lateral, above and below around the nests). (2) To examine whether the nest site characteristics, and female personality traits were associated with clutch size. We predicted that nests with more concealment and females with lower breathing rate would lay larger clutches. (3) To examine whether the nest site characteristics, and female personality traits are related to nest success during incubation. Based on the results of Liu et al.[30] and Tamin et al.,[36] we predicted that nests with more concealment and nests of females with lower breathing rate would have higher nest survival rates during incubation.

RESULTS

Personality traits of females, clutch size and nest site characteristics

In 2013–2016, we measured the activity test 211 times in 153 female chestnut thrushes and breathing rate test 230 times in 165 females. Both activity and breathing rate were repeatable with individuals across time (Table 1). In total, we also collected the nest site characteristics of 125 female chestnut thrushes that were measured for activity and breathing rate from 2013 to 2016.

The results of pSEM showed that two hypothesized unidirectional relationships were statistically significant (Figure 1). Breathing rate was negatively associated with clutch size (Figure 1): females with higher breathing rate laid smaller clutch sizes. Neither activity nor PC1 scores of large- and fine-scale nest site characteristics were associated with clutch size (Figure 1). Activity was positively associated with PC1 score of fine-scale nest site characteristics (Figure 1): more active individuals chose nests with greater lateral concealment. We did not find any relationships between breathing rate and any nest site characteristics (Figure 1).

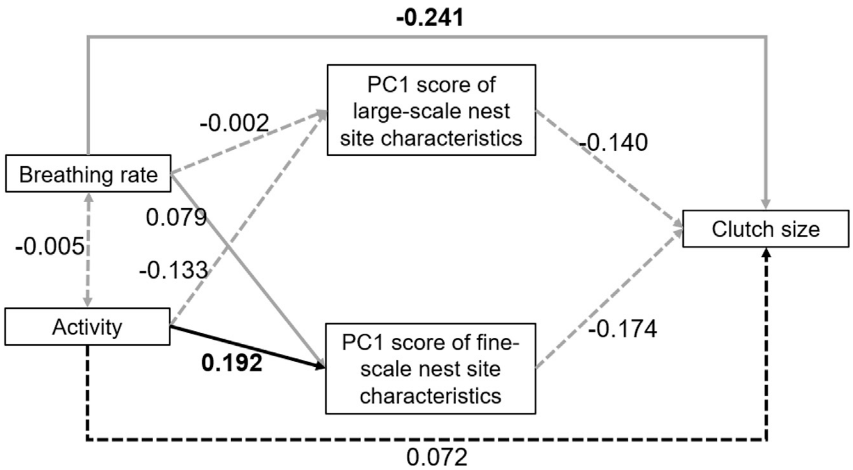

Figure 1. Effects of personality traits and nest site characteristics on clutch size in chestnut thrushes from piecewise structural equation model with individual identity as a random effect

Each box represents measured variables. Arrows represent relationships among variables. The dashed lines represent non-significant paths and solid lines represent significant paths. The gray lines represent negative relationships and black lines represent positive relationship. Significant paths are shown in bold. The piecewise structural equation models (pSEM) were conducted by piecewiseSEM package in R.[60]

Personality traits of females and nest success during incubation

From 2013 to 2016, nest fate during incubation was recorded in 129 nests (24 nests failed and 105 nests successfully hatched). Female breathing rate was the only significant predictor of nesting success during incubation. Nests of females with lower breathing rate had higher nest success during incubation (Table 2).

DISCUSSION

Our results show that there is proof for correlation between female personality trait and nest-site characteristics: more active females nested in areas with higher PC1 score of fine-scale nest site characteristics. Moreover, we found that clutch size was negatively associated with female's breathing rate, but we did not find that activity or any nest site characteristics were associated with clutch size. We also found that nest success during incubation was associated with female personality traits in chestnut thrushes.

We found that activity of female chestnut thrushes was positively related to lateral nest concealment, which mainly represents PC1 score in fine-scale nest site characteristics. Increased activity may make individuals more conspicuous to visual predators,[51] whereas greater lateral concealment of nests could reduce the ability of predators to locate nests. In our study area, numerous natural nest predators, such as Large Hawk Cuckoo (*Cuculus sparverioides*) and Elliot's Laughingthrush (*Garrulax elliotii*),[52] pose a particular risk for the eggs and nesting. Therefore, we hypothesize that more active female chestnut thrushes may be nesting in areas with greater concealment to overcome the constraint of higher visibility due to increased activity (e.g., entering and leaving of nests).

We found that female chestnut thrushes with lower breathing rate laid larger clutch size, while the activity was not associated with clutch size, a finding similar to that of Zhao et al.[53] However, some studies have found that female personality traits are not related with either clutch or brood size.[9,54,55] This variation in findings may be affected by the interaction of individual age and personality types. Dingemanse et al.[33] found that individuals with lower exploratory rates produced moderate-sized clutches throughout their lives, whereas faster-paced explorers produced moderate-sized clutch when young, but clutch size decreased with age. Currently, there is no suitable method to age chestnut thrushes in the field because we recaptured so few individuals across years, but further studies relating age and personality types are needed in the future.

We failed to find any relationships between nest site characteristics and clutch size in chestnut thrushes, in contrast to several other passerine studies.[30,56] One potential explanation for this is that clutch size may be

Table 2. Predictors of nest success during incubation of chestnut thrushes

Predictors	Estimate	χ2	P
Breathing rate	−0.051	4.246	**0.039**
Activity	0.107	0.638	0.424
Julian date	0.016	1.626	0.202
PC1 score of large-scale nest site characteristics	−0.344	2.831	0.092
PC1 score of fine-scale nest site characteristics	0.314	2.393	0.122

Significant predictors are highlighted in bold.
The nest success during incubation was defined as the nests that survived until at least one offspring hatched.

mediated by predation risk.[57,58] Hu et al.[52] found that there are many predators in our study site, and almost 50% of chestnut thrush nests fail due to nest predation.[50] Chestnut thrushes produce greater clutch size at nesting sites with lower predation risk but lay smaller clutches in nesting sites with higher predation risk. In this scenario, such high nest predation risk may dilute the positive effects of nest site characteristics, and this needs to be verified in future research.

The nests of female chestnut thrushes with lower breathing rates were more likely to survival during incubation. Lower breathing rate females may be more successful at defending their nests against predators, thus contributing to lower nest failure and higher nest success rates.[40,59] Furthermore, boldness can covary with other personality traits, comprising a suite of behaviors or "behavioral syndromes",[2] such as aggression and exploration, which may further promote individuals to participate in nest defense.[37] Further investigations are needed to identify the direct relationship between breathing rate and the intensity of nest defense in chestnut thrushes.

In conclusion, this study provides some of the first evidence to show the relationship between personality traits and fine-scale nest site selection. Breathing rate was associated with clutch size, thus providing some support for the pace-of-life syndrome hypothesis. Our study also identified a relationship between nest success during incubation and personality traits. Collectively, these findings highlight an important linkage between fine-scale nest site selection and nest success with certain personality traits in birds, and make a valuable contribution to addressing the knowledge gap in our understanding of the roles of personality traits in animal reproduction.

Limitations of the study

Our findings revealed that female personality traits were associated with clutch size, nest site selection, and nest success during incubation, so the major limitation of the present study is the lack of data concerning the roles of both parents' personality traits during nestling period. Further studies are needed to explore how male and female personality traits affect the reproductive fitness.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability
  - Data and code availability
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
  - Study area and study species
  - Ethical statement
- METHOD DETAILS
  - Nest site characteristics
  - Measurement of personality traits
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2023.107419.

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AUTHOR CONTRIBUTIONS

Y.L. and Y.S. designed the experiment; Y.L., Q.Z., L.C., Y.H., and Y.F. performed the experiments in the wild, helped with data analysis and editing the manuscript; Y.L. and Y.S. wrote the first draft manuscript; H.L. helped with manuscript preparation and improved the English; all authors reviewed the work and approved the final version of the manuscript.

DECLARATION OF INTERESTS

The authors declare that they have no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental models: Organisms/strains		
Chestnut thrushes (*Turdus rubrocanus*)	Wild-caught in Lianhuashan Nature Reserve, Gansu Province, in China	N/A
Software and algorithms		
R software (v. 3.2.2)	R Core Team	https://www.rproject.org/
Deposited data		
Nest site selection data	This paper	Mendeley Data, V1, https://doi.org/10.17632/wtyvxwf7dh.1

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Yuehua Sun (sunyh@ioz.ac.cn).

Materials availability

DOIs are listed in the key resources table.

Data and code availability

- All data reported in this paper are available at Mendeley, and the DOI is listed in the key resources table.
- All original code in this paper are available at Mendeley, and the DOI is listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Study area and study species

This study was conducted during 2013-2016 on a wild breeding chestnut thrush population located at the north edge of the Lianhuashan Nature Reserve, Gansu Province, in central China (34°40′N, 103°30′E). More detailed information about the reserve and local climate can be found in Sun et al.[61] In our study area, only female chestnut thrushes select nest sites, in which they build open-cup nests in trees and shrubs beside the roads and farmlands[50,52] and also near human residence during early May to late June. The nest height ranges from 0.90 m to 4.50 m.[50] We searched for nests of chestnut thrushes from late April to early July in each year of the study. The clutch size ranges from 1 to 5 (typically 3- 4 eggs), and incubation period and nestling period were 13-15 days, respectively. The chestnut thrushes renest when their nests are depredated, but only few individuals produce more than one brood in a year.

Ethical statement

All birds were captured under a bird ringing license issued from the China Bird Banding Center. All methods were carried out in the study were in accordance with the guidelines and regulations of the Animal Care and Use Committee of the Institute of Zoology, the Chinese Academy of Sciences. All experimental protocols were approved by Institute of Zoology, the Chinese Academy of Sciences, Permission number 2013/ 108. To reduce human disturbance during the incubation period, only one person checked each nest at a distance of over four m from the nest. We only checked nests during good weather conditions, when the ambient temperature was relatively high. Mist netting was done only under suitable weather conditions (no precipitation and low wind speed). Birds were trapped and released into the wild within

70 minutes near the trapping locations. No trapping-related mortality or nest abandon were recorded for females.

METHOD DETAILS

Nest site characteristics

Generally, the nests of chestnut thrushes were positioned 1-3 m above the ground,[52] and we collected seven nest site characteristics when the nest failed or successfully fledged.[52] During previous field observations, we found that chestnut thrushes nested closer to human settlements than other sympatric bird species, and are able to use some anthropogenic food resources. We also found that chestnut thrushes often foraged for food alongside the roads following rain. Furthermore, the nest height and nest concealment were also associated with reproductive success.[30,62,63] Therefore, in our study, two scales of nest site characteristics were measured: large-scale which included distance of nest to human residences (m), distance of nest to farmland (m), distance of nest to the nearest road (m); and fine-scale measurements which included nest height (to the nearest 0.1 m), nest lateral concealment, and concealment above and below the nest. To minimize variation estimated by different observers, the same person (YB Hu) measured all nest site characteristics. All measurements followed Hu et al.[52]: nest height was defined as the distance from the nest to the ground, to the nearest 0.1 m; nest lateral concealment was measured as the estimated vegetation cover from the most visible direction at a distance of 3 m after the observer checked from all directions. Concealment above and below the nest were recorded by estimating the percentage of vertical vegetation cover at 1 m above and 1 m below each nest, respectively. In addition, we recorded the location of all nests using a Global Positioning System (GPS) receiver, and then used the ArcGIS 10.2 (ESRI, Inc., Redlands, CA, USA) to measure the distances to human residences, roads and farmland habitat (to the nearest 1 m).

Measurement of personality traits

We captured birds by using mist nets which we positioned two meters away from the nest. In order to calculate the repeatability of personality traits, we tried to catch individuals twice during three breeding stages, including before clutch initiation, incubation and nestling period. The interval between two measurements was at least 7 days. Two personality traits, activity and breathing rate, were measured in 2013-2016. Activity was measured between 0900 and 1700 by using a simple cage test based on Kluen et al.[64] and adapted by Zhao et al.[25] and Lou et al.[15] We recorded the activity behaviors (such as walk, hop and fly) for 5 min after a 10 min acclimatization in the cage (size: L 60 × W 36 × H 60 cm) using JVC (GZ-E265AC). JWatcher software was used to analyse all recorded activity data.[65] We calculated weighted activity scores using the following formula, to account for differences in energy expenditure: activity score = walks × 1 + hops × 2 + flights × 3.[15,25] Breathing rate was measured by using the handling stress test, and we recorded the total number of breast movements within 60 seconds.[15,25] In general, we assumed that birds with lower breathing rates are bolder than those with higher rates.[25,66] The body mass (to the nearest 0.1 g) was measured before release.

QUANTIFICATION AND STATISTICAL ANALYSIS

We constructed linear mixed models (LMMs) with individual identity as a random variable to calculate the repeatability of breathing rate and activity.[15,53] Before the analysis, activity was square root transformed to meet Gaussian distribution of residuals. To control for confounding factors, seven predictor variables were included in each model: date (Julian date), year, sex, test sequence of activity and breathing rate (i.e., 1: first, 2: second or 3: third test), time of day (where 1200 = 0, 1300 = 1, 1100 = -1, etc.), context (i.e., 1: before breeding, 2: incubation or 3: nestling period) and body mass. All continuous variables were mean centered and standardized. The results were shown in the Table S1. Likelihood ratio test (LRT) between the models with and without the random effect (individual identity) was used to test the statistical significance of the repeatability. We used the LMMs of breathing rate and activity to run 1000 simulations using the *arm* package,[67] and the average best linear unbiased predictors (BLUPs) for the intercepts of each individual were used as personality profiles (breathing rate and activity) in the following data analysis, since a recent study found that the estimates of average BLUPs was less precise but unbiased.[33]

To minimize the number of nest site characteristics, the principal component analysis (PCA) was performed on the large- and fine-scale nest site characteristics, respectively. We kept the first components extracted with eigenvalues > 1 (see table below), which could reflect important information in nest site characteristics. We used the factor scores from PCA (hereafter PC1 score) for individuals in the further analysis. In large-scale nest site characteristics, higher PC1 score corresponded to longer distance among nests, human settlement and farmland. In the fine-scale nest site characteristics, higher PC1 score corresponded to greater lateral concealment.

Principal component analysis (PCA) of large- and fine-scale nest site characteristics in chestnut thrushes

Rotated factor loading				
Large-scale nest site characteristics	PC1	PC2	PC3	PC4
Distance to human settlement	0.656	−0.147	−0.740	
Distance to farmland (m)	0.602	−0.488	0.631	
Distance to road (m)	0.454	0.860	0.232	
Eigenvalues	1.088	0.980	0.926	
% of variance	0.394	0.714	1	
Fine-scale nest site characteristics				
Nest height	0.289	0.925	−0.190	0.154
Nest lateral concealment	0.601	−0.003	0.296	−0.742
Concealment above the nest	0.572	−0.192	0.463	0.649
Concealment below the nest	0.477	−0.327	−0.814	0.063
Eigenvalues	1.356	0.972	0.851	0.702
% of variance	0.460	0.696	0.877	1

In order to investigate the relationships among female's personality traits (breathing rate and activity), large- and fine-scale nest site characteristics and clutch size, a piecewise structural equation model (pSEM) was used. The pSEM has the ability to propose causal relationships between predictor and response variables.[60] Individual identity was incorporated in all models as a random factor.

The pSEM was conducted by piecewiseSEM package in R,[60] which represents a list of generalized linear mixed models (GLMMs), and each pSEM was represented by a list of models which considered different variables as response variables. For the response variables, we built models which included potential paths between key variables, and the models were selected by Akaike information criterion (AIC). The best-fit model has the lowest AIC value[68] (Table S2). Fisher's C was used to assess the goodness of fit of the pSEM[60] and $P > 0.05$ indicated no missing paths among variables and that these models represented the data appropriately.

A GLMM with binomial distribution was used to investigate whether nest success during the incubation period (success was defined as at least one egg successfully hatched; failure was defined as the nest was depredated) was affected by PC1 scores of large- and fine-scale nest-site characteristics, Julian date, females' activity and breathing rate. Collinearity of fixed effects were examined to ensure the Variable Inflation Factor (VIF) with values < 2.5.[69] We included female ID as random effect because of some repeated measurements of females among years. We also added year as a random effect to reduce the effects of environmental variations among years. All LMMs and GLMMs were fitted with *lmer* and *glmer* functions from the *lme4* package.[70] All statistics were performed with R software (v. 3.2.2).[71]