



Nest site choice: a potential pathway linking personality and reproductive success



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Animal personality has been linked to individual fitness across many taxa. However, the exact path by which personality translates into fitness is rarely identified. We tested whether nest site choice may serve as a potential pathway linking personality and reproductive success in a natural population of chestnut thrush, *Turdus rubrocanus*. Using path analysis, we found that human disturbance and choice of nest site with respect to nest density may both mediate the link between personality and reproductive success. Bolder females may choose nest sites with lower nest density, and the low nest density in turn may be responsible for a positive effect on nestling number, and have a negative effect on nestling mass. Bolder females may also prefer nest sites further from human settlements, resulting in a negative effect on nestling mass. Our findings provide rare exact mechanistic pathways by which boldness might be translated into reproductive success.

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Consistent individual differences in behaviour over time and across contexts, so-called animal personality, have been linked to fitness across animal taxa, and evidence that personality is subject to natural selection has begun to emerge (Carere & Maestripietri, 2013). Although personality may affect many different ecological and evolutionary factors in wild animals, such as dispersal, dominance, space use and habitat selection (Réale, Dingemanse, Kazem, & Wright, 2010), pathways by which personality are translated into fitness (such as reproductive success) are poorly understood (but see Mutzel, Dingemanse, Araya-Ajoy, & Kempenaers, 2013).

Habitat selection, and particularly the choice of nest site, may be important for reproductive success (Chalfoun & Schmidt, 2012; Martin, 1998) and individual differences in personality traits may be related to habitat choice (Seltmann, Jaatinen, Steele, & Öst, 2014; Sih, Bell, Johnson, & Ziemba, 2004). More specifically, individuals of some species may exhibit a personality-specific social tolerance with respect to population density (Cote, Clobert, Brodin, Fogarty, & Sih, 2010). For example, fast-exploring great tits, *Parus major*, disperse further (Dingemanse, Both, Noordwijk, Rutten, & Drent, 2003), so they could have access to nesting areas with lower

population densities. It is therefore possible that personality-affected nest site choice may act as a mechanism through which personality has an effect on reproductive success.

The trade-off between quantity and quality of offspring has been observed in numerous animal species (Allen, Buckley, Marshall, Clarke, & Whitlock, 2008; Lack, 1947). Selection tends to favour females producing higher numbers of offspring at low population density, while it tends to favour females producing higher quality of offspring at high population density (Both, 1998; Sinervo, Svensson, & Comendant, 2000). Based on this concept, we postulate that selection may drive parents nesting in high nest density areas to produce heavier (although fewer) nestlings, while in areas of low nest density selection favours the production of less heavy but more numerous nestlings. Thus, if personality affects nest site choice, it may also indirectly affect reproductive success.

Spatiotemporal variation in selection may play a key role in maintaining variation in personality (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Compared with several studies that have found evidence for temporal variation in selection pressures in natural populations (Dingemanse & Réale, 2013), spatial variation has rarely been reported (Nicolaus, Tinbergen, Ubels, Both, & Dingemanse, 2016; Quinn, Patrick, Bouwhuis, Wilkin, & Sheldon, 2009). The fact that some individuals are better in some habitats while others are better in alternative habitats is critical for

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explaining how different personality types can coexist (Sih et al., 2004). Moreover, habitats in turn may affect the trade-off in reproductive output. In bad environmental conditions, individuals that produce higher quality nestlings will most likely have more offspring surviving to the next breeding season (Fischer, Taborsky, & Kokko, 2011). Yet, in good years, most nestlings would survive, and then, it will be individuals producing a higher number of nestlings that will have more offspring surviving to the next breeding season (Messina & Fox, 2001). It is likely that this would yield equal fitness for each personality type in the long run. So habitat choice may be a potential factor to explain the maintenance of variation in personality.

Here, using data from a chestnut thrush, *Turdus rubrocanus*, population in the wild we investigated several direct and indirect pathways between personality and fitness (Fig. 1a). The chestnut thrush population at our study site is very suitable for a nest site selection study. The study area encompasses mixed conifer–broadleaf woodland, farmland and edge (farm boundary) habitats. The local breeding density of the chestnut thrush population varies between and within habitats thus facilitating quantifying the relationship between personality and breeding density. We expected activity and boldness to be positively correlated and to form a behavioural syndrome (path 1; Garamszegi, Markó, & Herczeg, 2013). According to pace-of-life syndromes, a bold

individual (or one with a higher activity level) may exhibit lower social tolerance, so a bold female (path 2) or an active female (path 3) may nest in areas of lower nest density (Cote et al., 2010; Réale, Garant, et al., 2010). Nest density in turn may have a significant effect on reproductive output in the trade-off between offspring quality and quantity (path 4). For example, selection may favour females nesting in areas of high nest density to produce heavier nestlings that have a higher expectation of survival and recruitment in the breeding population (path 5; Both, Visser, & Verboven, 1999). Alternatively, nesting in areas of low nest density may result in higher numbers of fledglings (path 6; Sinervo et al., 2000).

Personality-dependent distributions may vary with levels of human disturbance. Martin and Réale (2008) found that docile eastern chipmunks, *Tamias striatus*, were more common in high-disturbance areas. In an earlier study, we found that chestnut thrushes nested closer to human settlements than any other sympatric bird species. The considerable interindividual variability in distances from nests to human habitations facilitated our examination of the putatively personality-dependent distribution of nests at the intrapopulation level. Both boldness and activity are negatively correlated with docility (Réale, Garant, et al., 2010), so we expected that bold and/or active females would choose to nest relatively far from settlements (paths 7 and 8), farmland (paths 9 and 10) and roads (paths 11 and 12). Moreover, predictable

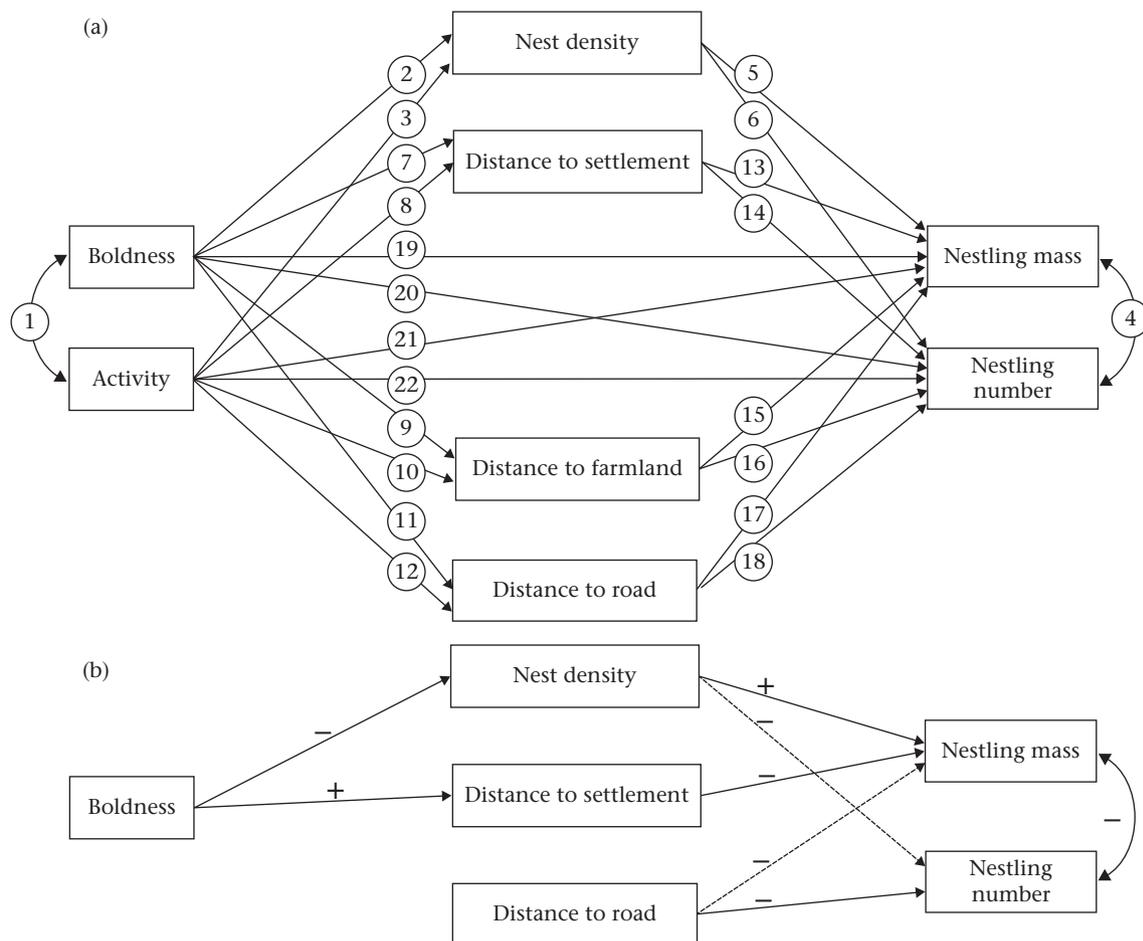


Figure 1. (a) Hypothesized path diagram representation of the path model fitted to estimate the relationships between two personality traits (activity, boldness), four nest site traits (nest density, distance to settlement, distance to farmland, distance to road) and reproductive success (nestling mass, nestling number) of female chestnut thrushes. Single-headed arrows indicate the direction of causal links. Double-headed curved arrows indicate simple correlations. Numbers in circles are path numbers. (b) Supported paths in the path analysis for female chestnut thrushes. Black arrows indicate that 95% confidence intervals did not overlap zero; dashed black lines indicate that 95% confidence intervals slightly overlapped zero but with $P < 0.05$.

anthropogenic food sources may increase reproductive success for nests near human settlements (Oro, Genovart, Tavecchia, Fowler, & Martínez-Abraín, 2013). Chestnut thrushes forage around residential areas where they particularly exploit larvae in livestock manure. We therefore expected that nests near human habitations would have higher reproductive success (paths 13 and 14; Marzluff & Neatherlin, 2006). Halfwerk, Holleman, Lessells, and Slabbekoorn (2011) showed a negative impact of traffic noise on avian reproductive success. Given that there was little traffic in the study area, and our observation that nesting chestnut thrushes often foraged for earthworms on wet roads, we hypothesized that nests close to roads would consequently have higher reproductive success (paths 15 and 16). Similarly, given the high availability of earthworms in agricultural areas, we expected nests near farmland to have higher reproductive success (paths 17 and 18).

Finally, the two personality traits we considered may directly affect reproductive success via unknown mechanisms (Mutzel et al., 2013). So, we also tested the potential direct association between boldness/activity and reproductive success (paths 19–22).

METHODS

Study Area and Subjects

We conducted this study in the breeding seasons of 2013–2014 in the highly fragmented agricultural landscape at the north edge of the Lianhuashan Nature Reserve, Gansu Province, in central China (34°40'N, 103°30'E). For a more detailed description of the reserve, see Sun, Swenson, Fang, Klaus, and Scherzinger (2003). In our study area, chestnut thrushes start building open-cup nests (primarily in hedgerows surrounding crop fields) in late April. Males usually defend the breeding territory, while females choose nest sites. Clutches are initiated from early May to late June. Clutch sizes range from two to five eggs (typically three or four) and only one brood per year is raised. The breeding population undertook altitudinal migration. They moved to nearby lower-altitude sites, travelling in small flocks in winter. Using mist nets, we tried to catch each bird twice: once before clutch initiation and once during the nestling period. For birds that we did not capture before the nestling period, we tried to catch them in the nestling period 7 days after the first capture. In 2014, some birds were also caught during the incubation period. For all captured birds, we measured tarsus length (0.01 mm) and body mass (0.01 g). We recorded the weight and number of all nestlings when they were 10 days old, in order to avoid premature fledging. The number of nestlings per nest and their average weight were considered to be measures of reproductive success for the parents.

Personality Traits Assay

We quantified two personality traits: activity and boldness. Activity was measured using a simple cage test following Klue, Kuhn, Kempenaers, and Brommer (2012). We tested each bird separately in a simple cage (50 × 60 cm and 60 cm high) between 0900 and 1600 hours. After a habituation period of 10 min, we videoed the bird for 5 min. Activity was quantified from the videos using 'JWatcher 1.0' (Blumstein, Evans, & Daniels, 2006) which allowed us to count discrete behaviours and record the relevant times while playing the video. All video analyses were conducted by a single observer (Q.S.Z.). We attempted to account for the different energy expenditures involved in walking, hopping and flying by weighting numerical activity scores as follows: walks and hops × 2; short flights × 3 (for rationale, see Appendix 1).

Boldness was measured through a handling stress test immediately after the simple cage test, using the protocol of Brommer

and Klue (2012). The same observer (Q.S.Z.) caught each bird, and counted breast movements over a 60 s period; we considered this to be a measure of breathing rate and therefore of handling stress. Breathing rate has been associated with boldness and exploration in the great tit (Carere & van Oers, 2004; Fucikova, Drent, Smits, & Van Oers, 2009) and with activity in blue tits, *Cyanistes caeruleus* (Klue, Siitari, & Brommer, 2014). Here, we considered breathing rate as an index of boldness, being lower in bold individuals than in shy individuals (Carere & van Oers, 2004). We performed the simple cage tests and handling stress tests 208 times with 136 birds (62 males and 74 females) over the course of 2 years. We obtained repeated records for all traits on 57 individuals. Intervals between first and second tests ranged from 7 to 50 days (mean = 17).

Nest Site Characteristics Survey

Nest site characteristics were collected as soon as the nest was established. We recorded nest site coordinates using a Global Positioning System receiver and used ArcGIS 10.2 (www.esri.com) with Google Earth (www.google.com/earth/) satellite imagery to determine distances to settlement, road and farmland (see Appendix 2 for details). For each nest, we used the number of active nests within a 250 m radius as an index of nesting density (for rationale, see Appendix 3).

Ethical Note

All procedures on chestnut thrushes complied with the ASAB/ABS and the local, institutional and national rules concerning the care and use of animal subjects. The birds were captured under bird ringing licence from the China Bird Banding Center. This work was permitted by the Animal Care and Use Committee of the Institute of Zoology, the Chinese Academy of Sciences (Permission No. 2013/108). Bird trapping was done only under suitable weather conditions (no precipitation and low wind speed). For birds with nestlings, trapping was done when the nestlings were at least 3 days old and the temperature above 10 °C. Birds were trapped and released into the wild within 40 min near the trapping location. No trapping-related mortality was recorded for adults or dependent nestlings.

Statistical Analyses

To calculate the adjusted repeatability of personality traits, we used restricted maximum likelihood linear mixed modelling (LMM). Repeatability was calculated as the between-individual variance divided by the sum of the between-individual and the residual (within-individual) variances (Nakagawa & Schielzeth, 2010). We used the function `lmer` of R package `lme4` to fit the LMM (Bates, Mächler, Bolker, & Walker, 2015). Activity was square-root transformed in all models resulting in residuals not deviating from a Gaussian distribution. Continuous variables were mean centred and standardized. Information on individuals with only one measure was retained (Nakagawa & Schielzeth, 2010). As a random effect, the individual identity (bird ID) was included in the model. The intercept of each individual can be considered as the personality (so called BLUP, or best linear unbiased predictor; Henderson, 1975). To control for potential confounding factors, the following fixed effects were included in the LMM: 'year' (factor with two levels), 'date' (where 20 April = 0, 21 April = 1, etc.), 'sex' (male/female), 'order' (test sequence, first, second, etc.), 'time of day' (where 1200 = 0, 1300 = 1, 1100 = -1, etc.), 'temperature' (ambient temperature), context (context 1: before breeding; context 2: incubation; context3: nestling period). For breathing

rate, body mass was included as an additional fixed effect (Carere & van Oers, 2004). Statistical significance of the repeatability was tested by the likelihood ratio test (LRT) with one degree of freedom between the random effects model with and without the random effect (bird ID). For breathing rate, a negative BLUP indicated bolder birds. We multiplied both positive and negative BLUPs of breathing rate by -1 so that high scores represented individuals that were bold.

For path analysis we generally followed Mutzel et al. (2013). We only used the data of 64 females for which we had the nest site records. First, we ran a multivariate model using MCMCglmm (Hadfield, 2010) in a Bayesian framework with Markov chain Monte Carlo methods to extract variances and covariances between all hypothesized predictor and response variables. We used the BLUP of breathing rate and activity in the multivariate model and the variances and covariances matrix was used in the following path analysis (see Supplementary material, Table S1). For each analysis we used 130 000 iterations with a burn-in phase of 30 000 and a thinning interval of 100, resulting in a sample of 1000 values for each estimate. We ran the model with four different priors: (1) inverse Wishart ($V = \text{diag}(n)$, $\nu = n$), where n is the number of response variables in the multivariate model, (2) inverse gamma ($V = \text{diag}(n)$, $\nu = b.002$), where $b = n - 1$, (3) flat prior ($V = \text{diag}(n)$, $\nu = 1.002$) and (4) parameter expanded ($V = \text{diag}(n)$, $\nu = c$), where $c = n + 1$. Model output changed only slightly when using different priors, suggesting that the results were not influenced by our prior choice. The results presented in this paper are for models with the inverse Wishart prior. We then performed a path analysis within a Bayesian framework using package sem in R (Fox, Nie, & Byrnes, 2012), by running each of the specified path models once for each of the 1000 estimates. Using these 1000 estimates, we extracted path coefficient values and their associated 95% confidence interval for each specified path. We considered 95% confidence intervals not overlapping zero as statistically significant. When the lower or upper 95% confidence intervals slightly overlapped zero, we also checked for the number of times the estimate was positive or negative, thus giving the equivalent of a P value. To assess the indirect effect, we extracted path coefficients for compound paths by multiplying all coefficients along the focal path (Grace, 2006). To estimate the reliability of the analysis, we implemented sensitivity analyses based on simulated data sets (see Appendix 4 for details).

RESULTS

Activity (Table 1, Fig. 2a) and breathing rate (Table 1, Fig. 2b) were significantly repeatable across time. However, there was no significant correlation between activity and breathing rate (Table 2, path 1). Female boldness indirectly and negatively affected nestling mass via nest density (Fig. 1b; Table 2, compound path A). There was also a weak, but significant (Fig. 1b; Table 2, compound path B) positive indirect link between boldness and nestling number. The path model also provided support for a trade-off between offspring quality and quantity (Fig. 1b; Table 2, path 4), mediated by nest density, which positively affected nestling mass (Fig. 1b; Table 2,

path 5), and negatively influenced nestling number (Fig. 1b; Table 2, path 6). Moreover, female boldness again indirectly and negatively affected nestling mass through the distance from human settlements (Fig. 1b; Table 1, compound path C). The sensitivity analyses showed that the reported patterns were recovered reliably with simulated data sets. See Fig. S1 in the supplementary material for details.

DISCUSSION

We found that activity and breathing rate in chestnut thrushes were significantly repeatable over time. These two quantified behaviours could qualify as personality traits. However, they did not form a behavioural syndrome as expected. As expected, however, we found that bolder females preferred nest sites at lower density, which in turn was positively correlated with nestling mass and negatively correlated with nestling number. Moreover, bolder females also preferred nest sites away from human settlements, which in turn was negatively correlated with nestling mass. Contrary to our predictions, distance from road and farmland did not play a role in the pathway between female boldness and reproductive success. We did not find any correlation between female activity and all the four nest site traits either.

We found no evidence for a relationship between breathing rate and activity, contrary to what has been previously reported in blue tits (Kluen et al., 2014). However, our findings were in line with observations in zebra finches, *Taeniopygia guttata* (David, Auclair, Dechaume-Moncharmont, & Cézilly, 2012). It is possible that the boldness–activity syndrome is domain specific (Sih et al., 2004) and that the correlations between boldness and activity did not occur in the contexts we tested.

We showed that bolder females chose nest sites with low nest density as expected. Several hypotheses can explain this finding. First, bold individuals may disperse in order to avoid crowded populations (Cote et al., 2010). In this case, the correlation between boldness and sociability should be negative. Second, bolder individuals are less able to use social or ‘public’ information (Montiglio, Ferrari, & Reale, 2013). The inefficient use of such information may cause these individuals to choose a nest site in areas of low conspecific nest density. Finally, personality and nest site choice might coevolve to reduce conflicts resulting from competition for resources such as food and space. Personality traits could be affected by social interactions with conspecifics, and be linked with social niche specialization (Montiglio et al., 2013). Furthermore, since ecological niche specialization relates to choice of nesting sites, it could be associated with personality traits. Under this scenario, individuals of certain personality types may prefer habitats with low competitor abundance but also low resource availability (Montiglio et al., 2013). Consistent with this, bold female chestnut thrushes seemed to prefer nesting areas with both low nest density and lower food abundance further from human habitations.

The trade-off between nestling quantity and quality according to different nest densities is consistent with our prediction. Birds

Table 1
Repeatability and descriptive statistics of two personality traits of chestnut thrushes

Trait	N_{ind}	N_{obs} (mean \pm SD)	Mean (SD)	Range	R	χ^2	P
Sqrt activity	136	1.73 \pm 0.91	6.99 (3.92)	0–19.05	0.31	6.85	0.009
Breathing rate	136	1.73 \pm 0.91	97.79 (24.03)	57–195	0.70	34.47	<0.001

‘Sqrt activity’ is the square root of the number of movements in the simple cage test. ‘Breathing rate’ is the number of breaths during 60 s while being handled. Data are from a total of 208 observations of 136 individuals. The table shows the total number of individuals (N_{ind}), the mean number of observations per individual (N_{obs}) \pm SD, the mean and SD for each trait, the range and repeatability (R). Statistical significance of the repeatability was tested using a likelihood ratio test on the log likelihood of models with and without the random effect (Bird ID), using a χ^2 distribution with 1 degree of freedom.

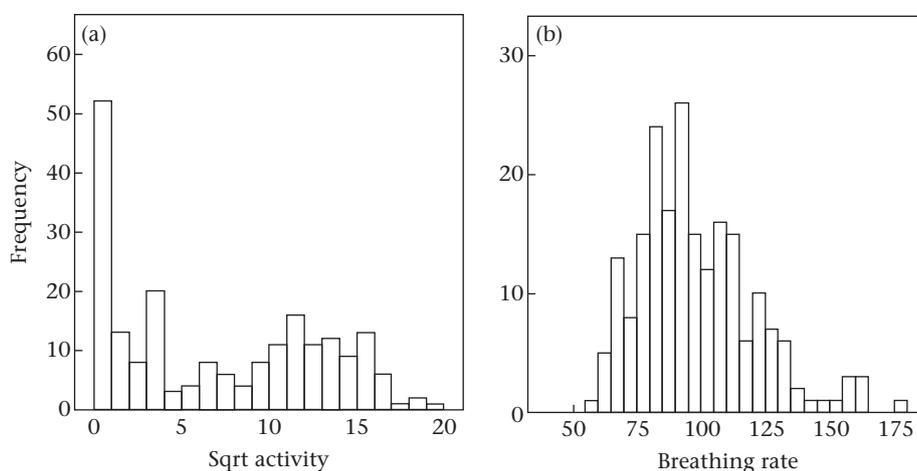


Figure 2. Two behaviours measured in the cage and handling stress tests for 136 chestnut thrushes. (a) Frequency plot of activity (square root of sum of the hops and short flights of the subject in the baseline session for 5 min, displayed in bins of 1. (b) Frequency plot of breathing rate (count of the breast movements during 60 s) displayed in bins of 5.

know who their neighbours are, and may even adjust their responses according to their neighbours' personalities (Amy, Sprau, Goede, & Naguib, 2010). They may also be able to adjust their reproductive decisions based on the perception of the abundance of neighbours. In addition, bold females are unable to track environmental changes efficiently or to produce optimal brood sizes (Nicolaus et al., 2015) and consequently produce more numerous but lighter nestlings. Moreover, personality is integrated within a pace-of-life syndrome (Réale, Garant, et al., 2010). Bolder females lead fast-paced lives, and are also characterized as investing in current, rather than future reproduction, so they produce more offspring (Wolf, van Doorn, Leimar, & Weissing, 2007). Accordingly, bolder female chestnut thrushes produced more nestlings. In contrast, previous studies in great tits found that males lead fast-

paced lives (fast-exploring) and produce fewer offspring in low-density habitats (Quinn et al., 2009). Interestingly, boldness, not activity, seems to be the density-dependent selection target in our study population. This contrasts with populations of common lizards, *Zootoca vivipara*, in which selection for activity, not boldness, is density dependent (Le Galliard, Paquet, & Mugabo, 2015). Moreover, a recent study on great tits found that density-dependent selection acted on exploratory behaviour via adult survival rather than offspring recruitment (Nicolaus et al., 2016). Thus, density-dependent selection appears to be species specific.

As expected, bolder females prefer to nest away from settlements, and produce lighter nestlings. A large body of research has reported that urban individuals are bolder than rural conspecifics (reviewed by Miranda, Schielzeth, Sonntag, & Partecke, 2013) and

Table 2
Estimated partial regression coefficients of the path model for female chestnut thrushes

Path number	Hypothesized link	N	Path coefficient	95% CI
1	Boldness → Activity	64	-0.070	-0.223, 0.267
2	Boldness → Nest density	64	-0.309	-0.509, -0.082
3	Activity → Nest density	64	-0.006	-0.184, 0.263
4	Nestling number → Nestling mass	41	-0.233	-0.367, -0.052
5	Nest density → Nestling mass	41	0.351	0.140, 0.537
6	Nest density → Nestling number	41	-0.306	-0.491, 0.017
7	Boldness → Distance to settlement	64	0.351	0.111, 0.536
8	Activity → Distance to settlement	64	-0.103	-0.302, 0.134
9	Boldness → Distance to farmland	64	0.100	-0.143, 0.330
10	Activity → Distance to farmland	64	-0.040	-0.280, 0.185
11	Boldness → Distance to road	64	-0.068	-0.218, 0.245
12	Activity → Distance to road	64	-0.126	-0.329, 0.155
13	Distance to settlement → Nestling mass	41	-0.558	-0.665, -0.132
14	Distance to settlement → Nestling number	41	0.215	-0.261, 0.471
15	Distance to farmland → Nestling mass	41	-0.080	-0.334, 0.095
16	Distance to farmland → Nestling number	41	0.079	-0.233, 0.315
17	Distance to road → Nestling mass	41	-0.235	-0.388, 0.024
18	Distance to road → Nestling number	41	-0.301	-0.545, -0.020
19	Boldness → Nestling mass	64	0.109	-0.088, 0.293
20	Boldness → Nestling number	64	0.057	-0.210, 0.272
21	Activity → Nestling mass	64	0.023	-0.148, 0.202
22	Activity → Nestling number	64	-0.004	-0.210, 0.256
Compound path	Individual path number			
A	2 × 5		-0.101	-0.221, -0.017
B	2 × 6		<i>0.063</i>	-0.015, 0.197
C	7 × 13		-0.174	-0.274, -0.022

Path coefficients of the path models shown in Fig. 1. Bold numbers indicate that 95% confidence intervals (95% CI) did not overlap zero. Italicized numbers indicate that 95% CI of coefficients slightly overlapped zero but with $P < 0.05$.

these results support the so-called 'disturbance-induced habitat selection balancing selection' hypothesis which suggests that individuals may choose nest sites depending on their susceptibility to human disturbance (Carrete & Tella, 2010). Our results did not support this hypothesis. Recently, another study has suggested that individuals with relatively higher behavioural flexibility will be better at coping with human disturbance (Carrete & Tella, 2011). Bold individuals are generally less flexible (Koolhaas et al., 1999) and bolder chestnut thrushes may be unable to cope with human-driven changes in rural habitats which would explain why they choose nesting areas further from human habitation.

Nests near settlements and roads, but not near farmland, produced heavier nestlings. Although birds have easy access to anthropogenic food in urban areas, they have lower reproductive success, perhaps because of less abundant native insects (Chamberlain et al., 2009). In our study area, chestnut thrushes have access to both anthropogenic and natural food. So, moderate levels of human settlements may have a positive effect on avian reproduction (Marzluff & Neatherlin, 2006). As expected, nests close to roads produced heavier nestlings. The availability of earthworms in farmland was dependent on rainfall and the effect of farmland may therefore be constrained by rainfall.

In conclusion, nest site choice could serve as a possible mediator between boldness and reproductive success. We also revealed the trade-off between offspring quality and quantity, mediated by nest density. Moreover, the survival of heavy versus light nestlings may be inversely frequency or time dependent, yielding equal fitness for each personality (Sinervo et al., 2000). The whole pathway provided a 'snapshot' of individual life histories and ecological processes, and would facilitate the understanding of how personality variation is maintained in a natural population.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.05.017>.

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APPENDIX 1. CALCULATION OF ACTIVITY SCORE

The cage we used was similar to that used by Klueen et al. (2012), who quantified activity by only using cage-wide movements through the three zones, because the majority of their blue tits tended to move around continuously. However, most chestnut thrushes tended to stay in the lowest zone. They moved through two of the three zones when they jumped or hopped, and through the three zones when they made short flights. Energy is the same as work, that is force times distance (Norberg, 1996). To simplify the estimation, we did not consider the take-off angles and horizontal movement distance, and only used the vertical movement distance. So it may be reasonable to weight activity scores in this way.

APPENDIX 2. CLASSIFICATION OF 'SETTLEMENT', 'ROAD' AND 'FARMLAND'

We classified 'settlement', 'road' and 'farmland' based on detailed surveys during the field season and satellite imagery. As farm buildings were scattered in the study area, we considered the distance of the chestnut thrush's nest from the nearest cottage or courtyard as 'distance to settlement'. We considered the distance of the nest from the nearest road (at least 3 m wide) as 'distance to road'. We considered the distance of nest from the nearest farmland as 'distance to farmland'. After digitizing the map in ArcGIS 10.3, we used the measurement tool to obtain the distance.

APPENDIX 3. RATIONALE FOR CHOOSING 250 M RADIUS TO ASSESS NEST DENSITY

Using the number of neighbours within a radius as an index for nest density has a long history in bird studies (Dexheimer & Southern, 1974; Kovacs & Ryder, 1983) and is still widely used (Bentz, Navara, & Siefferman, 2013; Kamp et al., 2014; Minias, Wojczulanis-Jakubas, & Kaczmarek, 2014). According to our observations, chestnut thrushes typically remain within 150–250 m of the breeding site when foraging in the breeding season, so a 250 m radius should encompass the area within which a female could come into contact with a conspecific. This is also the area within which a female could perceive the abundance of neighbours and other information.

APPENDIX 4. SENSITIVITY ANALYSIS

To determine the reliability of our pathway analyses, we generated 100 simulated data sets with the same structure (the same correlation matrix as in Table S1) and sample size ($N = 64$) as our own data using function 'rsmvnorm' in R package 'SimCorMultRes' (Touloumis, 2015). Then we performed the same path analyses. For each path, the 95% confidence intervals that were estimated using 100 simulated data sets were stable, so the parameters could be recovered reliably. The results are shown in Fig. S1 in the Supplementary material.