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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.

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 & Maestripieri, 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

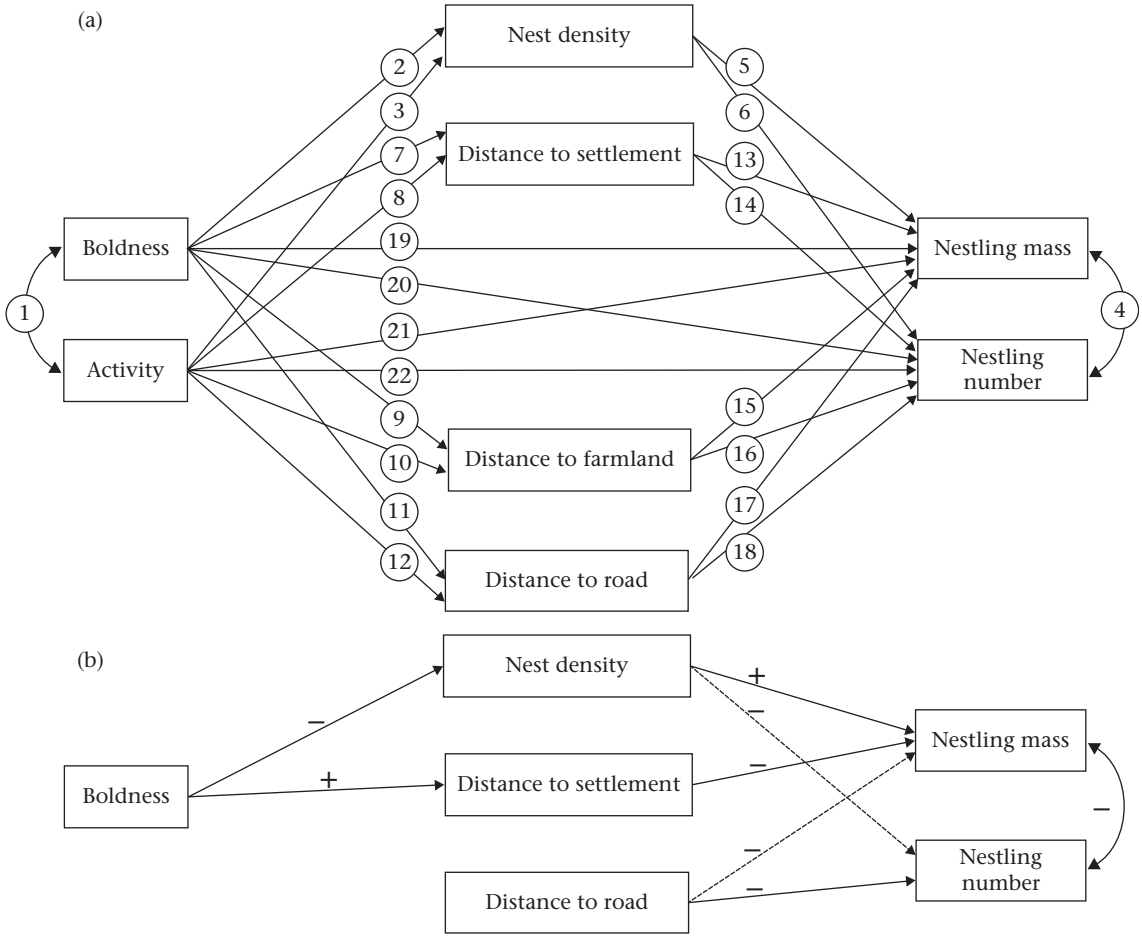

Figure 1. (a) Hypothesized path diagram representation of the path model fitted to estimate the relationships between two personality traits (activity, boldness), four nest site traits (nest density, distance to settlement, distance to farmland, distance to road) and reproductive success (nestling mass, 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 $P < 0.05$.