Shy birds play it safe: personality in captivity predicts risk responsiveness during reproduction in the wild

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Despite a growing body of evidence linking personality to life-history variation and fitness, the behavioural mechanisms underlying these relationships remain poorly understood. One mechanism thought to play a key role is how individuals respond to risk. Relatively reactive and proactive (or shy and bold) personality types are expected to differ in how they manage the inherent trade-off between productivity and survival, with bold individuals being more risk-prone with lower survival probability, and shy individuals adopting a more risk-averse strategy. In the great tit (Parus major), the shy–bold personality axis has been well characterized in captivity and linked to fitness. Here, we tested whether ‘exploration behaviour’, a captive assay of the shy–bold axis, can predict risk responsiveness during reproduction in wild great tits. Relatively slow-exploring (shy) females took longer than fast-exploring (bold) birds to resume incubation after a novel object, representing an unknown threat, was attached to their nest-box, with some shy individuals not returning within the 40 min trial period. Risk responsiveness was consistent within individuals over days. These findings provide rare, field-based experimental evidence that shy individuals prioritize survival over reproductive investment, supporting the hypothesis that personality reflects life-history variation through links with risk responsiveness.

1. Introduction

Personality—defined as behavioural differences between individuals that are consistent over time and across contexts—is now widely considered to be ubiquitous in nature [1]. The reactive–proactive (or shy–bold) continuum represents the best-studied personality axis in non-human animals [2,3]. Work done largely on captive animals suggests that ‘proactives’ are bolder, more aggressive and more risk-prone in comparison with individuals at the ‘reactive’ end of the continuum [3]. How these behavioural correlations are maintained within populations remains puzzling, given the expectation that flexible behaviour should be favoured by selection [4]. Potential theories are diverse, but one adaptive explanation that is gaining increasing empirical support is that the shy–bold axis reflects life-history variation, specifically that bold individuals tend to sustain high productivity but at a potential cost to their survival, whereas shy individuals do the opposite [5–7].

One mechanism that is believed to play a key role in maintaining this link between personality and life-history variation is how individuals respond to risk—specifically how they negotiate the conflict between self-maintenance and other needs, for example, the trade-off between the risks of starvation and predation [6,8], and between survival and reproductive success [5,7]. Theory predicts that individuals who reserve resources for future reproductive success should be less willing to engage in risky behaviour that jeopardizes their survival than those who invest more in current fitness gains [5]. Studies exploring the fitness
consequences of personality largely support this theory, showing that bold individuals often have higher measures of reproductive success than shy individuals, but reduced survival (reviewed in [6,9]). However, there remains a lack of empirical work testing the assumption that risk management is an underlying mechanism linking personality and reproductive investment decisions [10].

In this study, we use a wild population of great tits (Parus major) to examine whether ‘exploration behaviour of a novel environment’ (hereafter EB), a captive measure of the shy–bold axis assayed during the winter, predicts risk-responsiveness during reproduction. Animals often show caution in response to novel objects or environments, which is thought to reflect avoidance of the unknown risks associated with novelty [11]. In high-risk situations, iteroparous animals such as great tits may reduce investment in or even abandon their reproductive attempt, favouring personal survival [12]. Here, we experimentally manipulated perceived risk by attaching a novel object to nest-boxes during incubation, and recorded the time it took females to resume normal behaviour. We predicted that relatively fast-exploring females would prioritize their reproductive attempt over personal survival and thus exhibit riskier behaviour by resuming incubation more quickly than slow females.

2. Material and methods

This work was conducted using a long-term study population of great tits (see [13]) at Wytham Woods, Oxford, UK (51°46′N, 1°20′W). During the winter, birds were trapped using mist nets, fitted with unique British Trust for Ornithology leg-rings and passive integrated transponder (PIT) tags and transported to the nearby field station. EB was assayed the following morning during an 8 min trial in a novel room, during which 11 activities and movement variables were recorded. The first component of these variables from a principal component analysis was used to derive individual EB estimates in a generalized linear model, controlling for the time in the season and the number of observations per bird (see [14] for further details). This trait has been shown to be repeatable across and between our seven-month data collection seasons (Sept–March each year) and correlated with a range of functional behaviours in the wild in our population [8,14–17]. All birds were released at their capture site within 24 h.

During the 2009 breeding season, females that had previously been assayed for EB were located in their nest-boxes using a hand-held PIT detector. Risk-taking behaviour was measured for 43 females at day 9 or 10 of incubation by video recording, from a distance of 10 m, the latency to resume incubation after a rigid black and white flag (148 x 105 mm) had been fixed to the nest-box (figure 1). After the flag was attached, the nest-box faceplate was removed to encourage the female to leave the nest. Trials were run only if the female was on the nest when the faceplate was removed. Males were very rarely heard near the nest while trials were initiated and were only observed during trials on four occasions. The flag was removed after 40 min; birds that did not return within this time period were scored as ‘non-returners’. We used a proportional hazards survival analysis to test whether latency to return to the nest could be predicted by EB, which accounted for non-returners. To control for motivational differences caused by variation in brood value, individual condition and environmental conditions, laydate, clutch-size, body condition and the hour of day the trial was run were included in the model. Females were trapped at the nest when chicks were approximately 8 days old, and their weight and wing length measured. Body condition was expressed as the residuals from a linear model of mass against wing-length and weighing time (both body size and weight are repeatable traits in great tits [18]). These data were not available for four experimental females whose breeding attempts failed before they were caught.

A random subset of individuals (n = 22) was given a repeat trial the following day to assess trait repeatability. The flag used for this repeat trial was patterned differently from the one used the previous day (either spotted or chequered, randomly assigned) to minimize habituation to the assay. To confirm that responses detected were caused by the novel object at the nest rather than the observer, a random sample of females (that had not undergone EB assays, n = 37) was assigned to a control treatment, in which the same assay procedure was followed, but no flag was used. These control trials were randomized over time with respect to the experimental trials, and control birds did not differ from the experimental birds in body condition (linear model: log 0.632, p = 0.641). All birds resumed incubation once the flag was removed, and all clutches hatched successfully.

3. Results

Females took significantly longer to return to the nest during the risk treatment than the control treatment (Mann-Whitney U-test: u = 2.190, p = 0.029, n = 80, figure 2a), which indicates that they were reacting specifically to the novel object. Return latency was also unrelated to the number of days since birds were assayed for EB, suggesting that the longer return time among experimental birds was not caused by these individuals becoming sensitized to human disturbance during EB assays (Spearman’s rank correlation: rs = −0.065, p = 0.754, n = 26, for birds assayed for EB the previous winter). Latency to resume incubation was repeatable within individuals over days (Spearman’s rank correlation: rs = 0.403, p = 0.031, n = 22), and birds did not differ in their latency to return in the two trials, indicating that there was no habituation to the assay across days (Wilcoxon matched-pairs test: w = 83, p = 0.913, n = 22). Relatively fast explorers resumed incubation sooner than slow explorers (z = 2.169, p = 0.030, n = 39, figure 2b). None of the other factors in the model were significant predictors of latency to resume incubation (laydate: z = 1.027, p = 0.304; clutch-size: z = 1.926, p = 0.054; body condition: z = 0.152, p = 0.879; time of day: z = −0.064, p = 0.949).
n = 39). Nine of the 43 birds did not return within the 40 min trial period, and there was a strong tendency for these birds to have lower EB scores than those that did return (Mann–Whitney U-test: $u = 1.941, p = 0.053, n = 43$, figure 2c).

4. Discussion

We demonstrate that EB, a repeatable personality trait measured in captivity in the winter, predicts risk-responsiveness during reproduction in the wild—a behaviour that was itself repeatable across days. Relatively slow-exploring females took longer than fast explorers to resume incubation after a novel object was attached to their nest-box, with some slow individuals not returning within the 40-min trial. This relationship could not be explained by differences in brood value or body condition between personality types.

During incubation, female tits leave their eggs for time spans of approximately 10 min in order to feed [19]. Evidence has shown that more attentively incubated clutches hatch sooner and have a higher hatching success [20]. In response to risk at the nest, 90% of females in our study remained away from the nest for longer than 10 min and 21% did not resume incubation until after the novel object had been removed. Although it is not known how long these birds would have stayed away if the threat had not been removed, tits have been observed to abandon their breeding attempt for prolonged periods in response to novelty at the nest (E. Cole 1999; personal observation). Our findings therefore suggest

that when faced with risk owing to uncertainty, shy females may jeopardize their reproductive attempt, providing support for the theory that these individuals prioritize survival over current productivity, whereas bolder individuals do the opposite [5–7]. One alternative hypothesis is that bold and shy females inherently differ in the duration of their foraging bouts during incubating, resulting in shy birds taking longer to resume incubation in our trial. However, previous work in our population has shown that average foraging trip duration while provisioning nestlings is unrelated to EB [21], suggesting that this is unlikely.

The results presented here represent rare, field-based support for the hypothesis that personality and reproductive life-history variation are linked through risk sensitivity. Furthermore, they support evidence from other studies in this species linking EB to risk responsiveness in a range of ecological contexts [8,16,22,23], suggesting that personality is likely to have broad significance for risk management strategies in animals.

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Data accessibility. We provide the dataset via the Dryad repository (doi:10.5061/dryad.58142) [24].

References


