



Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*

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Despite burgeoning interest in consistent individual differences in behaviour (animal 'personality'), the influence of social interactions on the performance of different behavioural types is poorly understood. Similarly, the ecological and evolutionary consequences of personality differences in social contexts remain unexplored. Moreover, the possibility that the sexes differ in the degree to which they exhibit personality in both social and nonsocial contexts has not yet received serious attention, despite the sexes usually being subject to differing selection pressures. Using a highly gregarious species, the zebra finch, we tested for consistent behavioural differences (in exploration) between individuals of both sexes in both nonsocial and social contexts, the latter considering the behavioural influence of opposite-sex companions. We then investigated how exploratory tendencies relate to behaviour in a potentially risky foraging context in mixed-sex dyads of individuals with differing personalities. Males were not more exploratory on average but were more consistent in their exploratory tendencies than females. Additionally, males behaved more consistently across the social and asocial contexts than females, even though individuals of both sexes similarly influenced each other's exploratory behaviour within the social context: the more exploratory the companion, the more exploratory the focal individual (relative to its level of exploration in the asocial context). An individual's exploration also affected its performance in the social foraging context. Our results stress the importance of looking for sex differences in personality and of considering the influence of social context in animal personality studies. We discuss our findings and their implications in the light of the biology of the species and set them in a broader ecological and evolutionary context.

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Individuals often differ consistently in their behavioural expression from other members of the local population (Benus et al. 1991; Boissy 1995; Koolhaas et al. 1999; Gosling 2001). Such so-called 'personality differences' are frequently correlated among contexts, generating 'behavioural syndromes', that is, suites of correlated behavioural traits (Sih et al. 2004a, b). As personality differences are distributed nonrandomly along axes of behavioural variation and have fitness consequences (Gosling 2001; Sih et al. 2004a, b; Dingemanse & Réale 2005; Smith & Blumstein 2008), their ecological and evolutionary consequences are expected to be significant (Dall et al. 2004; Sih et al. 2004b). Most personality studies have thus far investigated consistent individual behavioural types and their consequences in nonsocial contexts (e.g. Dingemanse et al. 2003: relationship between individual exploration

under social separation and dispersal distance). Rarer investigations into social contexts mainly consider survival-competitive aspects, such as relationships between exploration and aggression (Verbeek et al. 1996) or dominance (Dingemanse & de Goede 2004), whereas other social aspects have attracted even less attention (but see Marchetti & Drent 2000; van Oers et al. 2005). So why are social influences worth investigating?

First, focal individual behaviour is likely to be influenced by the behaviour of other conspecifics (and individuals of different behavioural types might be influenced differently). Therefore, results obtained from nonsocial personality tests might not reflect individuals' responses under (more) natural social situations, particularly in highly social or gregarious species. Consequently, misleading conclusions might be drawn from studies restricted to asocial conditions. Based on contrasting results from social and nonsocial behavioural tests, some researchers have suggested that the social environment influences an individual's behaviour via fear reduction (Jones & Merry 1988; Jones et al. 1995; van Oers et al. 2005). Furthermore, a nonsocial context can simply limit the behavioural performance, as 'the social context is a necessary

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condition for the expression of a broad range of behaviour in organisms, including individual differences' (Malloy et al. 2005, page 643).

Second, social behaviour is important for individual survival in many circumstances. For instance, the social environment influences an animal's foraging performance (reviewed in Galef & Giraldeau 2001). Not only can the presence of conspecifics affect foraging strategies of individuals in general but it can also influence individuals differently, depending on their personality: Marchetti & Drent (2000) showed that individual great tits, *Parus major*, of different exploration types, differed in their tendency to copy a tutor's foraging decision. Besides effects on foraging decisions, the company of conspecifics can have impacts on perceived predation risk (Clutton-Brock et al. 1999; Lima et al. 1999; Krause & Ruxton 2002) and/or food competition (Janson & Goldsmith 1995). This probably affects the risk-taking behaviour of individuals differently (van Oers et al. 2005).

Finally, sex is social and required for reproduction and is therefore crucial for individual fitness. Social interactions between mates are widespread, particularly in species in which partners stay together after fertilization of the female's gametes. As the sexes have different roles in reproduction and/or are often subject to distinct selection pressures, arising from, for example, intrasexual competition or mate choice, we should also expect the sexes to differ consistently in their behavioural performance and to be influenced by their social environments differently. That males and females respond differently in social versus nonsocial contexts is evident in risk-taking behaviour in the great tits studied by van Oers et al. (2005). However, in this study all individuals experienced nonsocial tests before social tests which could have confounded any influence of social context per se. Also, all companions were males and therefore only the influence of male companions on focal females but not the influence of females on males was assessed. Yet, distinct sex-of-partner effects on the response of the focal individuals of different sexes have been shown in mice, *Mus musculus*, (Malloy et al. 2005) and zebra finches (Benskin et al. 2002). In the latter, females copied foraging decisions more frequently from male rather than female tutors, whereas males did not appear to distinguish between the sex of the demonstrator.

Hence, there is some evidence that personality differences can have substantial impacts on social performance and vice versa and these implications seem to differ for males and females, but further work is needed to shore up these findings. We focused on how the sexes differ in their personality and how personality differences influence the social performance of the sexes. The latter may have implications for behavioural coordination both in mated pairs (e.g. for providing food for the offspring) and in social contexts in general (e.g. via risk dilution when feeding/moving together in groups), which could be particularly crucial in contexts important for survival such as foraging.

Our first aim in this study was to investigate consistent behavioural differences (in exploration) between individuals and between the sexes in nonsocial and social contexts, considering the influence of opposite-sex companions in the latter (experiment 1). We also investigated how a priori established exploratory tendencies affect behaviour in a potentially risky foraging context in mixed-sex dyads (experiment 2): we measured individual leadership and foraging behaviour as influenced by the combination of focal individual and companion exploratory tendencies recorded in experiment 1. We also recorded the proportion of time the male and female companions spent together at a risky novel food source as influenced by the combination of their exploration types. The latter may reflect behavioural synchronization in a risky situation which can affect individual fitness (see above: offspring

provision, risk dilution). The highly gregarious zebra finch was used as a model study species. In these birds partnerships are socially monogamous and characterized by biparental care (Zann 1996).

Given the general issues discussed above and the biology of the study species, we predicted the following. First, because of their different roles and/or distinct selection pressures we expected males and females to differ in the levels of and/or consistency in exploration. More specifically, male zebra finches usually lead their female through the colony except during breeding when the opposite occurs (Zann 1996). Based on the leadership role of males during most of the year, it may be advantageous for a female to have a male who is consistent and therefore predictable in its exploration and leadership behaviour. It could be crucial for a female to be led to feeding sites in a reliable manner to gain access to food at a regular rate. Consequently, we expected males (1) to be more consistent in their exploration and leading than females, (2) to influence females' exploratory behaviour more than the other way round and (3) to show a generally higher level of exploration and leading behaviour than females given that tests were conducted outside the breeding season. Second, as more exploratory and active individuals are likely to lead more often (see Beauchamp 2000, for tests on mostly males), we expected the two measures to be correlated. Finally, for relationships between the combination of exploratory tendencies in a group and its influence on male and female tendencies to spend time together at a novel risky feeder, we predicted one of two scenarios: exploratory individuals will rarely join their companions (see also Budaev 1997) and should therefore spend more time on their own at the feeder if they have a behaviourally similar companion. However, less exploratory individuals are predicted to join companions more often, resulting in an increased proportion of time spent with a companion (regardless of its exploration tendency). Alternatively, (dis)similar behavioural types may coordinate their foraging and spend more time together at the feeder (for reasons see above, Burley 1983).

METHODS

Ethical Note

Methodological and animal welfare issues were approved by the Ethical Committee of the University of Exeter and discussed with our Home Office inspector, who agreed that no special licence was required. The condition and health of all birds were monitored on a daily basis.

Housing and Study Species

We used sexually experienced, adult wild-type zebra finches (1–1.5 years old). They originated from different commercial suppliers in the U.K. but were kept for more than 6 months in the University of Exeter, Cornwall Campus, aviaries prior to the experiments. All focal birds were housed outdoors in two mixed flocks in free-flight enclosures (84 × 215 cm and 263 cm high). These holding enclosures contained a number of perches at two locations across the width of the cages as well as nestboxes, feeders and drinkers. Commercial seeds (Foreign Finch Mixture; J. E. Haith, Cleethorpes, U.K.), cuttlebone, grit and water were available ad libitum. Supplementary conditioning food (a mixture of Rearing and Conditioning Food (J. E. Haith), Daily Essentials vitamin supplement (The Birdcare Company, Nailsworth, U.K.) and water) was provided once a week.

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