



The effects of social conformity on Gouldian finch personality



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Consistent individual differences in behaviour observed within a population are termed 'personality'. Studies of personality typically test subjects in isolation, ignoring the potential effects of the social environment, which might restrict the expression of individual behaviour via conformity, or enhance it by facilitation. The Gouldian finch, *Erythrura gouldiae*, exhibits polymorphism in head colour (red or black) which is related to different personalities: black-headed birds are bolder and less aggressive than red-headed birds. As such, this species provides a unique opportunity to investigate the effects of the presence of a social partner on the expression of individual behaviour. Using two behavioural tests that reflect individual 'boldness', exploration of a novel object and time taken to return to feeding following a predator threat, we show that Gouldian finches adjusted their behaviour according to the personality of their partners: where a bird's partner was bolder, it became bolder; where a bird's partner was shyer, it became shyer. This social conformity effect was reduced, however, for black-headed birds paired with red-headed partners in the novel object test; in keeping with previous research findings, bolder individuals were less plastic in their responses. Since variation in personality can promote group cohesion and improve the functioning of social groups in a variety of contexts, we hypothesize that head colour could act as a cue, facilitating preferential associations with those of similar or dissimilar personalities in large mobile flocks of Gouldian finches.

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Differences in behaviour are often observed in individuals within a species that are otherwise similar to each other in terms of sex, age and size (Koolhaas et al., 1999; Reale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, Johnson, & Ziemba, 2004). Consistency in these behavioural traits both within and between individuals represents a behavioural syndrome (Sih et al., 2004), which can be heritable (Drent, van Oers, & van Noordwijk, 2003; van Oers, Drent, de Goede, & van Noordwijk, 2004), and may have complex underlying genetic and physiological foundations (Carere, Caramaschi, & Fawcett, 2010; van Oers, de Jong, van Noordwijk, Kempnaers, & Drent, 2005). Understanding how these 'personality' types emerge, their causes and their consequences has become a major challenge in behavioural and evolutionary biology (Wolf, van Doorn, Leimar, & Weissing, 2007).

Studies of personality are usually performed with individuals in isolation (Webster & Ward, 2011). However, most species are at some point in their lives social, whether this is with a sexual partner, as part of loose aggregations with variable membership, or as part of a stable social group (Krause & Ruxton, 2002). Such social

interaction may have little or no effect on individual personality so that while individuals may interact, their behavioural responses remain unchanged, and so the average behaviour of a social group should reflect these. For example, in three-spined sticklebacks, *Gasterosteus aculeatus*, behavioural responses when tested alone reliably predict their behaviour in a social group, and individuals maintain their behavioural types despite the experience of repeated social interactions (Laskowski & Bell, 2014). However, the presence of conspecifics might restrict individual behavioural responses via conformity or enhance differences in behaviour by facilitation.

Social conformity is often examined from a social learning perspective, and recent experimental tests with wild vervet monkeys, *Chlorocebus pygerythrus*, have shown that individuals will abandon personal foraging preferences in favour of group norms new to them (van de Waal, Borgeaud, & Whiten, 2013). But social conformity may also act on personality. Recent empirical work with guppies, *Poecilia reticulata*, found that group activity scores correlated with that of the least active member of a group, rather than the average activity of all group members (Brown & Irving, 2014), and tests with mosquitofish, *Gambusia holbrooki*, have shown that individuals conform to the speed of the group they are in (Herbert-Read et al., 2013). Similarly, Schuett and Dall (2009) studied pairs of zebra finches, *Taeniopygia guttata*, and found that the more

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exploratory the partner a bird was paired with, the more exploratory this focal individual became. Overall, this 'conformity hypothesis' assumes that individuals will tend to synchronize their behaviour in time and space (David-Barrett & Dunbar, 2012; King & Cowlshaw, 2009), altering their behaviour in line with their groupmates, and potentially suffering consensus costs (Biro, Sumpter, Meade, & Guilford, 2006; King, Douglas, Huchard, Isaac, & Cowlshaw, 2008).

Rather opposite effects are expected in the case of facilitation processes (Dindo, Whiten, & De Waal, 2009; Harlow & Yudin, 1933; Hemelrijk & Wantia, 2005) where the presence of another individual can further enhance individual differences, to reduce direct competition and/or facilitate social coordination (Conradt & Roper, 2009; Sumpter, Krause, James, Couzin, & Ward, 2008). This facilitation effect can reinforce individual differences in personality (Burns, Herbert-Read, Morrell, & Ward, 2012; Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009; Kurvers et al., 2009) and may result in social roles (Flack, Akos, Nagy, Vicsek, & Biro, 2013; Harcourt et al., 2009) that are more consistently manifested and affect group dynamics (e.g. during collective movements: Burns et al., 2012; Harcourt et al., 2009; King & Sueur, 2011; King, Sueur, Huchard, & Cowlshaw, 2011; Kurvers et al., 2009; Nagy, Akos, Biro, & Vicsek, 2010). This 'facilitation hypothesis' therefore assumes individual differences in personality are enhanced in social settings.

The Gouldian finch, *Erythrura gouldiae*, is a colour-polymorphic social bird species that exhibits two main discrete, genetically determined head colour morphs, red and black, found at a stable 3:7 ratio in wild populations, in addition to a rare yellow-headed morph (Brush & Seifried, 1968; Gilby, Pryke, & Griffith, 2009). In its natural habitat the Gouldian finch lives in open, subtropical woodland in Australia, where they nest in loose colonies, and forage mainly on grass seeds (Dostine, Johnson, Franklin, Zhang, & Hempel, 2001), forming mobile flocks (of mixed morphs) of between 10 and 400 individuals outside the breeding season (O'Malley, 2006). In a previous study, we showed that head colour (red or black) is related to different personalities when birds are tested individually: black-headed birds were bolder as measured by their latency to explore a novel object and the time taken to return to feeding following a predator threat. Moreover, individual behaviours in these tests varied, were repeatable over time and correlated with each other (Williams, King, & Mettke-Hofmann, 2012). As such, the Gouldian finch provides an opportunity to test how the presence and personality of a social partner effects the expression of individual personality.

We examined pairs of Gouldian finch's tendencies to explore a novel object ('exploration'), and return to feeding following a predator threat ('risk taking'), and compared birds' responses in a pair to their responses when tested alone. Because we were interested in how the behaviour of a social partner may mediate individual personality, we calculated any change in behavioural response we observed for birds between the asocial and social contexts. If individuals altered their behaviour in line with their groupmates (conformity hypothesis), we expected to see birds' behavioural responses to converge: if birds were paired with a more exploratory, or more risk-taking partner, we expected them to become more exploratory or more risk taking (bolder) than when they were tested alone. Conversely, if birds were paired with a less exploratory or a more risk-averse partner, they should become less exploratory or more risk-averse (shyer) than when tested alone. However, if the presence of another individual enhances individual differences (facilitation hypothesis), we expected to see individuals' responses diverge, i.e. the bolder bird to become bolder and the shyer bird to become shyer. Since head colour might prove a useful cue in mediating any conformity/facilitation, we also tested whether the head colours of interacting birds increased or decreased any

changes in behaviour we observed as a function of interacting birds' individual personalities, since there is accumulating evidence of links between colour phenotype and social interactions (Healey, Uller, & Olsson, 2007; Maffi, Wakamatsu, & Roulin, 2011).

METHODS

Study Subjects

Forty-two wild-type and parent-reared Gouldian finches were obtained from 13 private breeders. Birds ranged in age from 1 to 5 years (information derived from closed rings and breeder information). Tarsus length (an indicator of body size, measured using callipers) ranged from 12.91 cm to 15.84 cm, and there were 20 males (12 red-headed; eight black-headed) and 22 females (12 red-headed; 10 black-headed).

Housing and Care

Birds were provided with a full-spectrum light source with a cycle of 13:11 (light:dark), and kept together at a temperature of approximately 24 °C in three 100 × 200 cm and 200 cm high 'free-flight enclosures' (14 birds in each) in mixed head colours and sex groups for a year prior to social experiments. Aviaries contained a variety of perches (artificial and branches), food hoppers, bowls and water dispensers. Birds were fed Amadinen-Zucht Spezial (seed mixture for Gouldian finches), canary and millet seed, grit (all from Blattner Heimtierfutter, Ermengerst, Germany), eggshells and water ad libitum. Once a week they were given millet spray and supplemented with minerals and vitamins (Nekton MSA and Nekton S). Birds were checked daily for health and injuries.

Experimental Tests

Tests were conducted in six experimental cages (80 × 120 cm and 100 cm high) which contained three perches and food and water provided ad libitum the same as in the holding aviaries. For testing, six pairs of birds were moved to experimental cages at a time and were given 4 days to habituate to their new surroundings. Birds took part in experiments from 0800 to 1300 hours for 3 consecutive days on two occasions separated by 4 weeks. Between tests birds were kept in their holding aviaries. Subjects did not have visual access to neighbours during experiments, and all experiments were recorded by digital video cameras using GeoVision 1480 for later analysis. The experimenter (L.J.W.) was absent from the room while the experiments were being conducted. All experiments complied with ethical and welfare guidelines of Liverpool John Moores University. In particular, holding and experimental aviaries conformed to Home Office codes of practice and were carried out in approved facilities in the Liverpool John Moores University. The experiments carried out were not regulated by the Home Office and an Inspector's advice was sought to confirm this. After the experiments birds were returned to their holding conditions.

Pairing Birds

Birds were tested in the social context in February to June 2011, having been tested 4 months earlier as singletons (Williams et al., 2012) and shown to have repeatable behaviour with regard to the time it took them to approach a novel object ('exploration') and return to feeding after presentation of a false predator (risk taking). Two of these birds (ID9, ID29) only had exploration scores and not risk-taking scores (Williams et al., 2012). We compared bird scores in these asocial contexts to their behaviour in a social setting by matching birds for sex and size, and then assigning them randomly

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