The effects of social conformity on Gouldian finch personality

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Abstract

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 adjust their behaviour according to personality of their partners: where a bird's partner is bolder, it becomes bolder; where a bird's partner is shyer, it becomes 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 finding bolder individuals are 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 hypothesise 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.

Keywords

boldness, colour polymorphism, *Erythrura gouldiae,* Gouldian finch, neophilia, personality, risk-taking, Social

Highlights

- We tested Gouldian finch personality in an asocial and social setting
- Our experiments show birds' behaviour changes according to their partners identity
- Shy birds take more risk when paired with bolder flock-mates
- Bold birds take less risk when paired with shyer flock-mates

INTRODUCTION

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, Kempenaers, & 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 whilst individuals may interact, their behavioural responses remain unchanged, and so the average behaviour of a social group should reflect these. For example, in threespine 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*) has 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 of all group members activity (Brown & Irving, 2014), and tests with mosquitofish (*Gambusia holbrooki*) have shown that individuals conforming to the speed of the group they are in (Herbert-Read et al., 2013). Similarly, Schuett & Dall (2009) studied pairs of zebra finches (*Taeniopygia guttata*) and found that the more 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 synchronise their behaviour in time and space (David-Barrett & Dunbar, 2012; King & Cowlishaw, 2009), altering their behaviour in line with their group-mates, and potentially suffering consensus costs (Biro, Sumpter, Meade, & Guilford, 2006; King, Douglas, Huchard, Isaac, & Cowlishaw, 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 effect group dynamics (e.g. during collective movements: Burns et al., 2012; Harcourt et al., 2009; King & Sueur, 2011; King, Sueur, Huchard, & Cowlishaw, 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 bird head colour (red or black) is related to different personalities when 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 behaviour in these tests varied, were repeatable over time, and were 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 behaviour 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 group-mates (conformity hypothesis), we expected to see birds' behavioural responses to converge: if birds are paired with a more exploratory, or more risk-taking partners, we expect them to become more exploratory, or more risk-taking (bolder) than when they were tested alone. Conversely, if birds are paired with a less exploratory, or a more risk-averse partners, they should become less exploratory, or a 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 behavioural responses diverge, i.e. the bolder

bird to become bolder, and 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; Mafli,Wakamatsu, & Roulin, 2011).

METHODS

Study Subjects

Forty-two wild-type and parent reared Gouldian finches were obtained from thirteen private breeders. Birds ranged in age from one to five years (information derived from closed rings and breeder information). Tarsus length (an indicator of body size, measured using callipers) ranged from 12.91cm to 15.84cm, and there were 20 males (12 red-headed; 8 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 at a temperature of approximately 24°C together in three 100 x 200 x 200cm 'free-flight enclosures' (14 birds, 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 x 120 x 100cm) 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 four days to habituate to their new surroundings. Birds took part in experiments from 8am until 1pm for three consecutive days on two occasions separated by four 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 (LJW) was absent from the room while the experiments were being conducted. All experiments complied with ethical and welfare guidelines for animals and the legal requirements of the University and the United Kingdom. In particular, holding and experimental aviaries conformed to Home Office codes of practice and were carried out in approved facilities in the University. All experiments carried out were non-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

All birds had been tested four 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 (ID: 9, 29) 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 to partner birds; one of the same head-colour and one of a different head-colour, and tested their responses with each partner four weeks apart; a time period over which novelty reactions are known to fully recover (Mettke-Hofmann et al. 2005). To ensure we controlled for sex/size differences, bird identities (IDs) 6, 8, 9, 10, 29 and 35 could be tested just once, and ID 21 was involved in three pairings; this resulted n=10 different-coloured pairs and n=10

same-coloured pairs taking part in our first round of tests, and n=10 same and n=9 pairs in the second round of tests (Appendix Fig. A1 provides full details).

Exploration

We used a coloured plastic door-knob (4cm x 3.5cm) to test birds exploration of a novel object, following the same protocol used by Williams et al. (2012) . Half of the pairs were tested with a white knob, and half with a blue knob, which was swapped for the second round of tests four weeks later. We only changed colour but kept shape and size constant to provide objects as similar as possible since colour has been shown to have a strong novelty effect (Greenberg & Mettke-Hofmann 2001; Thomas et al. 2003). The object was hung with string from the mesh ceiling of the experimental cages, so it was in the middle of a neutral perch (a perch where no food or water was available) to give equal access to the object from both sides and thus reflect interest in the object (i.e. neophilia: Mettke-Hofmann, Ebert, Schmidt, Steiger, & Stieb, 2005). Latency to approach the object to within one body length (marked as a black line on the perch either side of the object) and latency to touch the object was recorded over a period of one hour. For all analyses, the mean of the two latencies was used (i.e. neophilia latency: Williams et al. 2012).

Risk-taking

The response of birds to a false predator-stimulus was examined either one or two days after the exploration test following the same protocol used by Williams et al. (2012) for single birds. All pairs were habituated to the predator-stimulus apparatus (line and pulley system) for 24 hours before testing. One hour before the test, the feeder was removed. When the feeder was replaced, latency to feed was recorded as a control measure for both birds. After both birds had been feeding together for 10 seconds a silhouette of an avian predator was pulled up and down in front of the cage, and each bird's latency to return to the feeder and feed was recorded. The difference between the control measure and latency to feed after the predator stimulus was taken as a measure of risk-taking. All birds returned to

feed within one hour after the predator stimulus. We had problems with collection of video data for pairs ID1-ID37, ID1-ID15, ID3-ID18; ID5-ID15 and ID18-ID3 thus reducing our sample to n=8 (instead of 10) same colour and n=8 (instead of 10) different coloured pairs for our second round of tests.

Effect of social context: Change in behaviour

We calculated the difference in the response times for an individual in the asocial and social context for both the exploration of the novel object and risk taking experiments. This change in behaviour (CIB) was calculated for every individual in each pair combination we observed (n=39 pairs) resulting in n=78 data points. Because we had a reduced sample for risk-taking trials and two birds did not have risk-taking scores as singletons (see above), risk-taking produced n=68 data points.

Inter-pair differences in personality

To test for any social conformity and social facilitation effects (or no change), we calculated, for each pair, the inter-pair difference (IPD) in birds' behavioural responses when tested alone for both the exploration of the novel object and risk taking experiments. This gave us an indication of how similar or dissimilar a pair of bird's personalities were.

Statistical Analysis

We tested for a general increase or decrease in CIB across our sample using non-parametric pairwise tests conducted in SPSS (v.17.0, 2009, SPSS Inc, Chicago, IL, U.S.A.). We examined individual CIB in the novel object (model 1) and risk taking (model 2) experiments using Linear Mixed Models (LMMs) conducted in MLwiN (v.2.26, 2012, Bristol University Centre for Multilevel Modelling, Bristol, U.K.). Because each trial resulted in CIB data for each bird in the pair, and birds could also appear in more than one pair (Appendix 1), we fitted focal bird identity (*i*), partner identity (*j*), and trial number as cross-classified random effects; this removed the independence assumption between responses belonging

to a particular bird (Browne, 2009; Goldstein, Browne, & Rasbash, 2002). For each model, we entered IPD when tested alone (in novel object, or risk-taking tests respectively) as a continuous fixed effect, and fitted an interaction between IPD and head-colour pairing (red-red, black-black, red-black, black-red) to see if any effect of IPD altered with respect to partner head-colour. Finally, we also tested/controlled for sex (male, female), age (continuous), size (tarsus length, continuous) by entering these as fixed effects. Models were run for 5 x 10^5 iterations using a Markov-chain Monte Carlo algorithm estimation (Browne, 2009, 2012). The significance of terms were tested using a Wald statistic, evaluated against the Chi-square distribution once estimates had stabilised and their SEs reached a constant value. In all cases we present full model results in our results, and the significance of all terms are unchanged if we use a model selection procedure, or the minimum adequate model.

RESULTS

We found that birds were not, on average, faster, or slower (Figure 1a; Figure 1b) in either the novel object test (Mann Whitney Test: n = 78, W = 6003; P = 0.34) or the risk-taking test (Mann Whitney Test: n = 68, W = 6139, P = 0.06), despite a trend for birds to get slower in the risk taking context (Figure 1b, d).

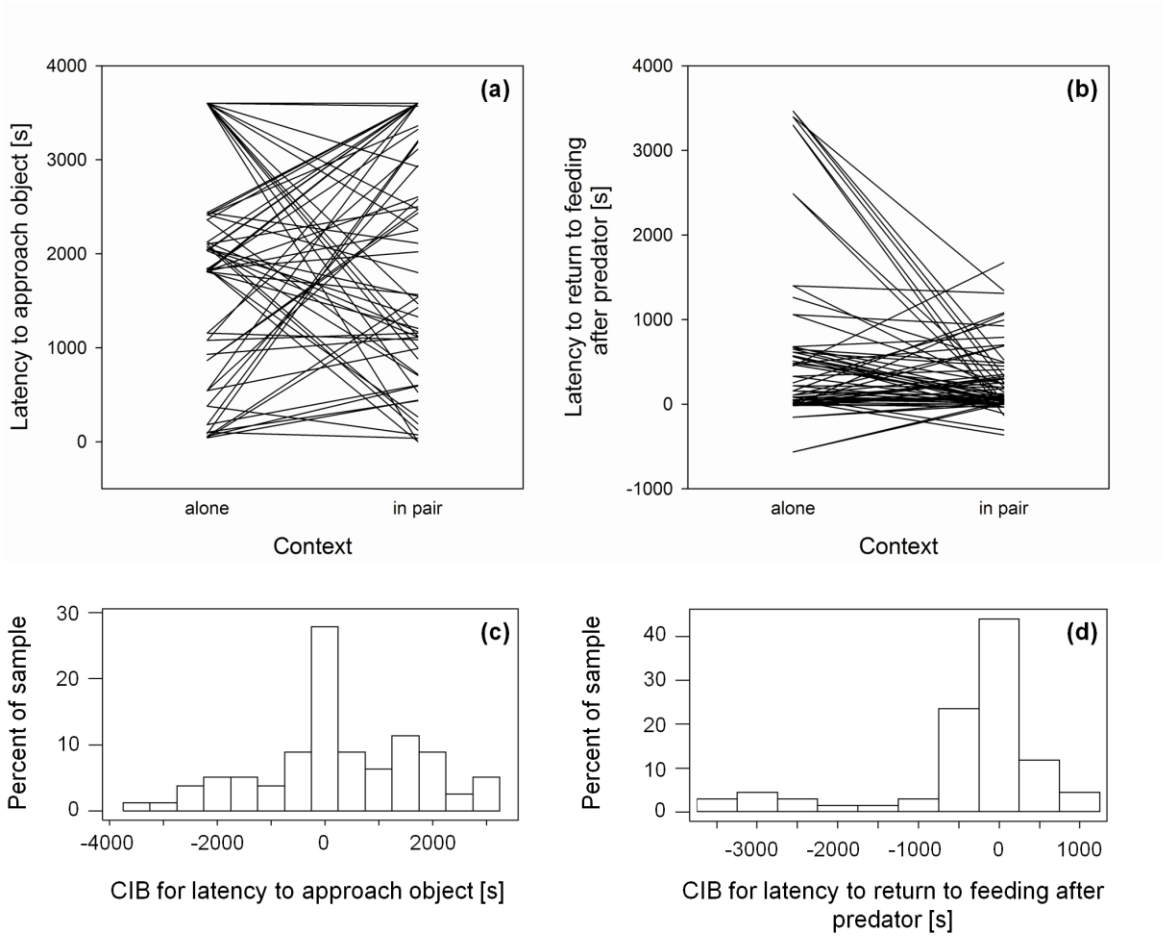

Figure 1. Behavioural response alone and in a pair. (a) Latency to approach a novel object (seconds) for birds tested alone, and as a pair (n=78). (b) Latency to return to feeding after a predator scare compared to a control condition for birds tested alone, and as a pair (n=68). (c) and (d) show frequency histograms illustrating the change in behaviour (CIB) for birds between the asocial and social contexts for the exploration and risk-taking experiments. The x-axis is the time difference (seconds) between the asocial and social contexts.

We found that the IPD for birds tested alone significantly and positively predicted changes in behaviour; this was true of both the object exploration test (Figure 2a; Table 1) and the risk-taking test (Figure 2b; Table 2). Specifically, where birds were paired with a more exploratory, or more risk-taking partner, they themselves became more exploratory, or more risk-taking (bolder) than when they were tested alone. Conversely, where birds were paired with a less exploratory, or a more risk-averse partner, they became less exploratory, or a more risk-averse (shyer) than when tested alone. We also found that in the novel object test,

the significant effect of IPD was absent for black-headed birds paired with red-headed partners (Table 1; Figure 3), indicating that CIBs for black-headed birds could not be attributed to social conformity effects in these pairs. No such effects of head-colour pairings were seen in the risk-taking test (Table 2). Sex, age, or size did not predict CIB for either the novel object or risk-taking experiments (Table 1, 2).

Table 1. Factors affecting CIB between asocial and social conditions during a novel object test. Table shows Model Terms, Parameter Estimates (Effect), Standard Errors (SE), associated Degrees of Freedom (DF), Test Statistic (Wald), and P-value. b-b = black-headed birds paired with black-headed partner (Figure 3a); b-r = black-headed birds paired with red-headed partner (Figure 3b); r-b = red-headed bird paired with black-headed partner (Figure 3c); r-r = red-headed bird paired with red-headed partner (Figure 3d).

Model Terms	**Effect**	**SE**	**DF**	**Wald**	**P-value**
Sex			1	0.151	0.698
Female	0.000	0.000			
Male	0.039	0.100			
Age			4	4.321	0.634
5 yrs	0.000	0.000			
4 yrs	-0.414	0.291			
3 yrs	-0.123	0.236			
2 yrs	-0.175	0.238			
1 yr	-0.016	0.236			
Size	0.075	0.101			
Inter-pair difference (IPD)	**0.747**	**0.265**	**1**	**7.939**	**0.005**
Pair Type			3	1.447	0.695
b-b	0.000	0.000			
b-r	-0.144	0.134			
r-b	-0.129	0.138			
r-r	-0.112	0.131			
IPD*Pair type[λ]			**3**	**9.076**	**0.028**
PairDiff*b-b	0.000	0.000			
PairDiff*b-r	-0.771	0.309			
PairDiff*r-b	-0.472	0.313			
PairDiff*r-r	-0.157	0.321			
Intercept	-0.988	1.520			
Focal ID (random)	0.016	0.019			
Neighbour ID (random)	0.017	0.019			
Experiment no. (random)	0.119	0.029			

[λ] Pair-wise comparisons revealed the effect of IPD (i.e. social conformity) was significantly reduced for black-headed birds paired with red-headed partners (Figure 3b).

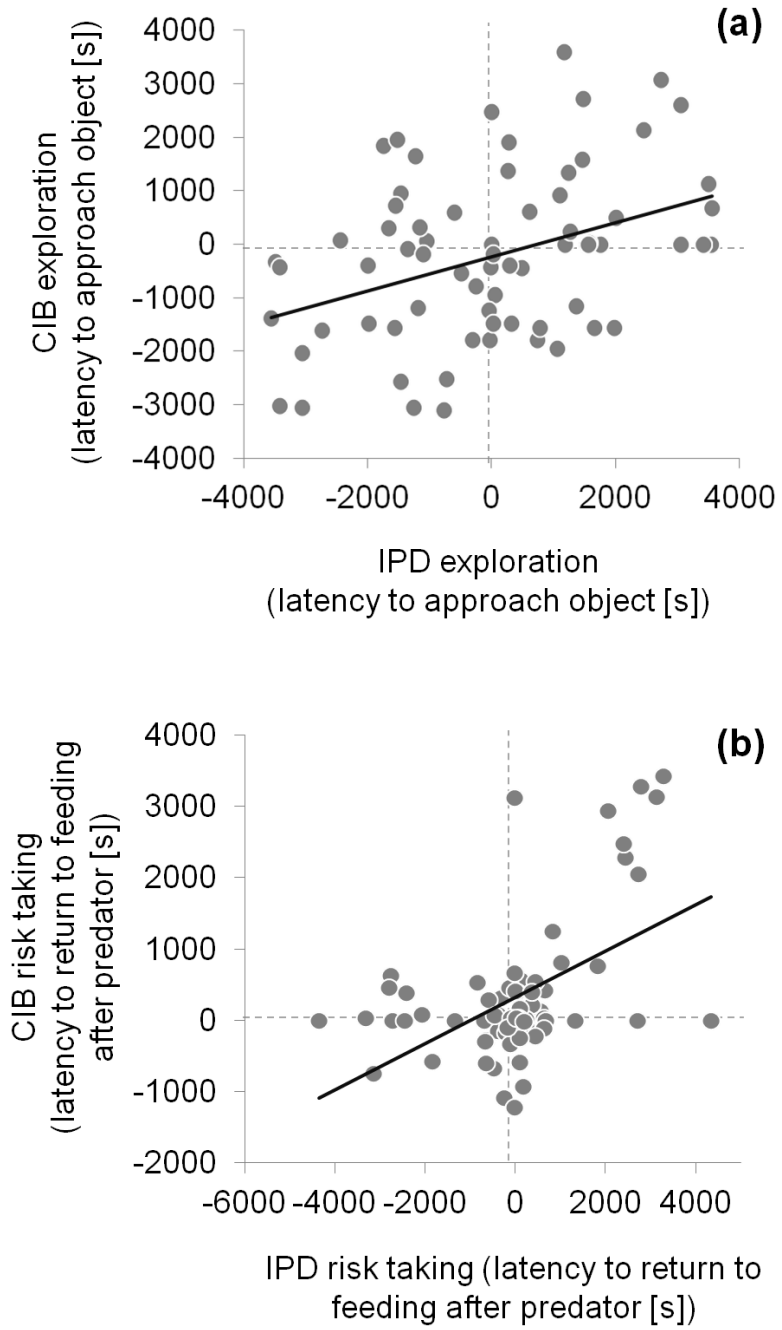

Figure 2. Social conformity. The CIB between the asocial and social contexts (see Figure 1) as a function of the inter-pair difference (IPD) in bird scores when tested alone for the (a) exploration (novel object) and (b) risk-taking (predator) tests. The fitted lines are the predicted effects from LMMs (see Tables 1 and 2). These relationships between IPD and CIB for the exploration and risk-taking indicate that for a given pair of birds, e.g. bold bird, *i* and shy bird, *j*, *i* will have a negative IPD score and tend to show a negative CIB, whilst *j* will have a positive IPD score and tend to have a positive CIB. If *i* and *j* are similar in personalities, they will both tend to score around zero for IPD and CIB.

Table 2. Factors affecting CIB between asocial and social conditions during a test of risk-taking. Table shows Model Terms, Parameter Estimates (Effect), Standard Errors (SE), associated Degrees of Freedom (DF), Test Statistic (Wald), and P-value. b-b = black-headed birds paired with black-headed partner; b-r = black-headed birds paired with red-headed partner; r-b = red-headed bird paired with black-headed partner; r-r = red-headed bird paired with red-headed partner.

Model Terms	**Effect**	**SE**	**DF**	**Wald**	**P-value**
Sex			1	2.711	0.100
Female	0.000	0.000			
Male	0.120	0.073			
Age			4	4.702	0.319
5 yrs	0.000	0.000			
4 yrs	-0.057	0.229			
3 yrs	-0.088	0.193			
2 yrs	0.087	0.192			
1 yr	0.028	0.193			
Size	-0.049	0.068	1	0.519	0.471
Inter-pair difference (IPD)	0.508	0.221	**1**	**5.264**	**0.021**
Pair Type			3	1.516	0.218
b-b	0.000	0.000			
b-r	0.042	0.069			
r-b	-0.002	0.075			
r-r	-0.030	0.080			
IPD*Pair type$^{\lambda}$			3	1.987	0.575
PairDiff*b-b	0.000	0.000			
PairDiff*b-r	0.028	0.165			
PairDiff*r-b	-0.184	0.185			
PairDiff*r-r	-0.006	0.168			
Intercept	0.747	1.078			
Focal ID (random)	0.021	0.015			
Neighbour ID (random)	0.020	0.018			
Experiment no. (random)	0.011	0.007			

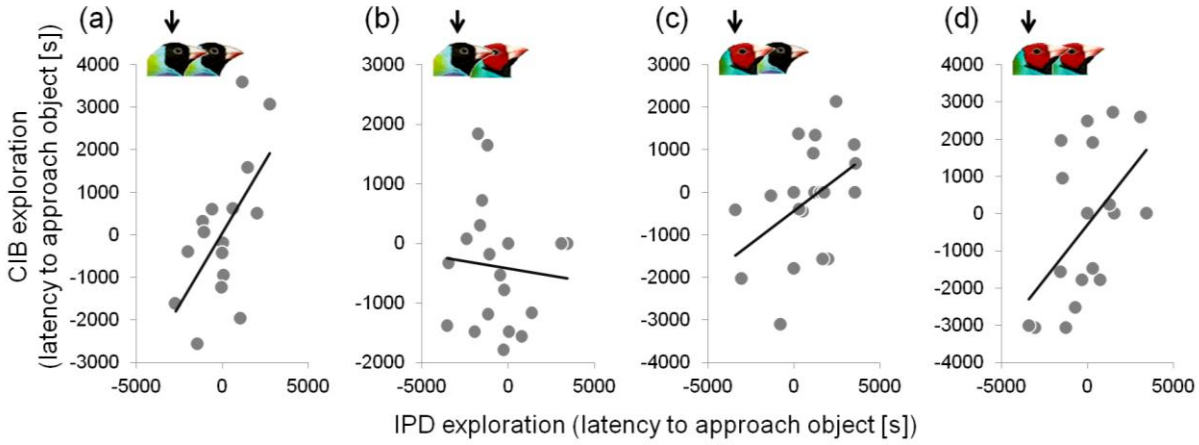

Figure 3. Social conformity and pair head-colour combinations (exploration). The CIB between the asocial and social contexts as a function of the inter-pair difference (IPD) when tested alone for exploration tendency (novel object). Panels show CIB for the birds indicated by the arrow, i.e. black-headed birds paired with a black-headed partner (a), black-headed birds paired with a red-headed partner (b), red-headed birds paired with a black-headed partner, and red-headed bird paired with another red-headed bird (e). Lines are best fit linear regression lines. See Table 1 for statistical tests of the effect of IPD and head-colour pairing.

DISCUSSION

We examined pairs of Gouldian finch's tendencies to explore a novel object, and return to feeding following a predator threat, and compared these data to the same birds' behaviour when tested alone. We found that birds were not, on average, faster to approach the novel object or resume feeding after a predator scare, as might be predicted in accordance with reduced perception of risk, or increased levels of competition with increasing group size (Krause & Ruxton, 2002; Magnhagen & Bunnefeld, 2009; Webster, Ward, & Hart, 2007). Instead, we found that some birds got faster, some got slower, and some were relatively unchanged. Our investigations of the effect of differences in personalities within a pair upon birds' changes in behaviour revealed that birds were adjusting their behaviour predictably according to personality of their partners: Where a bird's partner was bolder, it became bolder; where a bird's partner was shyer, it became shyer. Thus, our results offer support to social conformity rather than any facilitation processes.

In the context we have studied here, conformity may arise as a consequence of negotiating risks (Hellström, Heynen, Oosten, Borcherding, & Magnhagen, 2011; Magnhagen & Bunnefeld, 2009; van Oers, Klunder, & Drent, 2005), where the faster bird slows down in its response as it reacts to the behaviour of the more cautious partner, and slower birds speed up, in response to the faster exploring bird. Such social conformity is in accordance with previous work that has shown socially induced change in individual behaviour (Grand & Dill, 1999; Greenberg & Mettke-Hofmann, 2001); for example, in rainbow trout (*Onchorhyncus mykiss*), bolder fish observing the behaviour of shyer fish became more shy by increasing their latency to approach a novel object (Frost, Winrow-Giffen, Ashley, & Sneddon, 2007) and recent experiments by Herbert-Read et al. (2013) with mosquitofish (*Gambusia holbrooki*) reported repeatable individual locomotion behaviours (i.e. median speeds, variance in speeds and median turning speeds) to disappear at large group sizes. Specifically, fish in larger groups (n=8 compared to n= 2 or 4) tended to reduce their speed, and variation in speed compared to when alone. In practical terms, for the birds in this experiment, and the mosquitofish that Herbert-Read et al. studied, social conformity means individuals tend to move together, rather than independently. This process results from birds compromising their individual tendency to explore and/or return to feeding following risk; thus, where differences in individual tendencies are large, so was the degree of compromise we observed.

Since head-colour might prove a useful cue in mediating any conformity/facilitation, we also tested whether the head-colours of interacting birds had an independent effect of the change in birds' behaviour, or if there was an interaction between the pair head-colour combination and any conformity/facilitation effects observed. We did not find that head colour combinations predicted CIB, and conformity effects were consistent across pairs with the exception of black-headed birds paired with red-headed partners in the novel object test. Here, the CIB for black-headed birds was not reliably predicted by the IDBs of interacting birds. Therefore, future work needs to examine the interaction dynamics (Burns et al., 2012;

Harcourt et al., 2009; Kurvers et al., 2009) among the pairs of birds we have studied, rather than just their overall responses. For instance, the fact that black-headed birds show reduced social conformity when paired with a red-headed partner suggests the behaviour of black-headed birds – which are usually more explorative and take greater risk – would not be affected by their shyer red-headed flock mates and may could act as producers in exploring new resources. Conformity in red-headed birds, in contrast, would benefit them in mixed head-colour flocks by starting exploration of novel resources earlier. Therefore, where flock size and composition is variable and opportunity for engaging and monitoring the behaviour of others is limited, head-colour might prove a useful cue mediating interaction/association patterns since head colour of Gouldian finches can be used as a signal of dominance Pryke & Griffith (2006). Moreover, experiments with wild great tits (*Parus major*) have shown that variation in personality promotes within-patch movement while maintaining group cohesion (Aplin, Farine, Mann, & Sheldon, 2014), and a mix of personalities can improve the functioning of social groups in a variety of other contexts (Dyer, Croft, Morrell, & Krause, 2009; Harcourt et al., 2009; Pruitt & Riechert, 2011).

Overall, our experiments demonstrate how social context can mediate the expression of an individual's personality: Where a bird's partner was bolder, it became bolder; where a bird's partner was shyer, it become shyer. To more fully understand the functional role of individual differences in a social context experiments considering (and measuring) the costs and benefits regarding some activity (e.g. collective defence, foraging, or predator avoidance) and investigations of interaction dynamics in larger social groups is surely the way to go. Recent field experiments with social birds investigating patch exploitation and group movements using automated tracking techniques (Aplin et al., 2014) sets a benchmark for such investigations, and it will now be interesting to explore whether the conformity in behaviour we observe here relates to work describing how different personalities adopt specific social roles, e.g. leader-follower dynamics (Flack et al., 2013; Harcourt et al., 2009).

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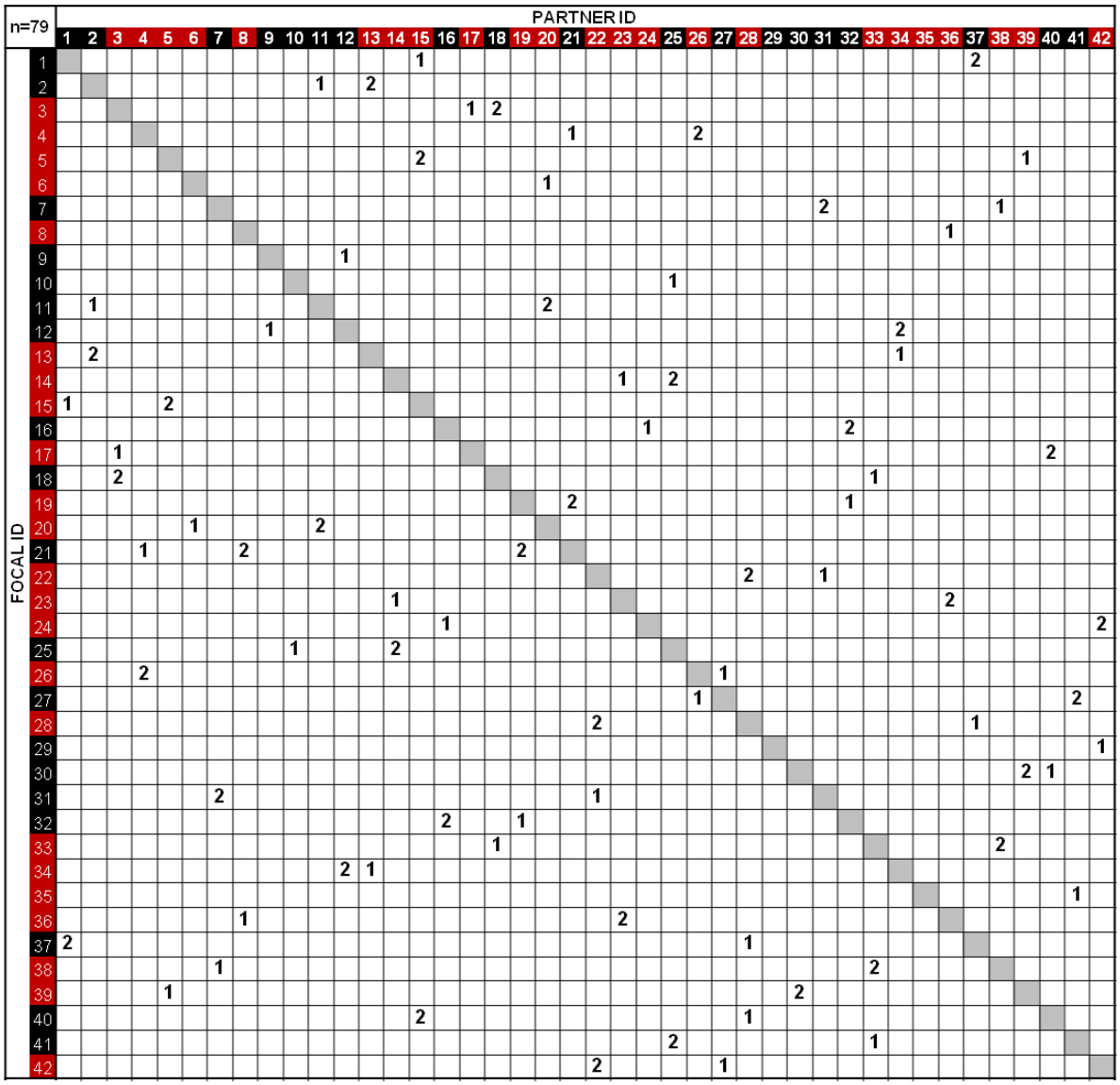

Appendix 1. Matrix showing how pairs were matched for sex and size and tested on two occasions (trial 1 and 2 are indicated in the cells); once with the same coloured head partner and once with a different coloured head partner, otherwise birds were paired randomly. The colour of the bird ID indicated its head colour red, or black (note that red birds' identity will appear grey in the journal version).