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Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata*

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KEYWORDS

Learning, personality, poeciliid, public information, social learning

ABSTRACT

The acquisition of information such as the location and quality of food, mates or shelter is a key survival requirement for animals. Individuals can acquire information through personal experience (private information) or through observing and interacting with others (social information). Environmental spatial and temporal heterogeneity can mean that sometimes social information conflicts with private knowledge. We tested how personality affected the importance placed on public versus private information in wild female guppies when these two information sources came into conflict. We found that boldness and sociality affected decisions to use conflicting social and private information. Bolder females used social information to avoid competition and/or potential patch depletion, whereas highly social individuals preferred the presence of conspecifics over rich foraging opportunities. There was no evidence of a speed-accuracy trade-off in a spatial associative learning task; rather, bold female guppies learned both more quickly and more accurately than shy females. We found no evidence of a behavioural syndrome between boldness and sociality which is consistent with previous studies on this population.

Learning is often the first line of defence when animals respond to environmental change (Brown, 2012). Individuals can acquire information by directly sampling the environment (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005) or through observation of the behaviour of others (Brown & Laland, 2011; Danchin, Giraldeau, Valone, & Wagner, 2004). While a strong reliance on socially acquired information could appear to be an optimal strategy in all contexts, this may not always be the case. The extent to which social learning is beneficial is dependent on the number of asocial learners in the population that directly sample the environment and hence the quality of the transmitted information (Giraldeau, Valone, & Templeton, 2002; Laland, 2004). Preferring to use social over private information may also impose costs on an individual. For example, individual fish may forgo opportunities to exploit foraging patches fully by following a shoal (Webster & Laland, 2012). Moreover, socially acquired information may not always be correct and its use may be maladaptive in some cases. Erroneous flight responses triggered by information cascades incur energetic costs (Giraldeau et al., 2002; Laland & Williams, 1998) and an overreliance on social information may lead to the continued use of a resource when better alternatives are available (Swaney, Kendal, Capon, Brown, & Laland, 2001). Although gathering information by

exploring the environment oneself may be energetically costly or risky, at least the individual gains direct and up-to-date information about the distribution of resources. Thus reliance on public or private information has a number of potential costs and benefits which an individual must weigh up when making decisions.

Conflict between personal knowledge and public information can occur when an environment is temporally or spatially variable. Laland (2004) suggested that individuals may be making optimal choices when they employ a 'copy when asocial learning is costly' strategy. Accordingly, animals may deploy a mixed information use approach in which uptake of public information could be influenced by a range of factors, including the quality of an individual's privately held knowledge. For example, nine-spined sticklebacks, *Pungitius pungitius*, modify their behaviour and give more weight to either public or private information depending on the reliability of an individual's private information (van Bergen, Coolen, & Laland, 2004). The perceived quality of social information is also important: female cactus bugs, *Chelinidea vittiger*, adjust egg production according to social cues indicating habitat quality (the presence of other eggs and nymphs) but only when these cues are indicative of recent reproductive success (Fletcher & Miller, 2008). It might be argued that the most adaptive response would be a completely plastic use of social information according to attendant costs and benefits. However, an increasing body of empirical evidence shows that social information use is not always totally flexible. For example, Trinidadian guppies and quail, *Coturnix japonica*, are both predisposed to favour one mode of information over another based on experiences during ontogeny (Boogert, Zimmer, & Spencer, 2013; Chapman, Ward, & Krause, 2008).

Personality has also been implicated in public information use. Personality may be broadly defined as interindividual differences that remain consistent over time and/or contexts (Wolf & Weissing, 2012) and can influence a range of processes, including the acquisition and use of information. Highly exploratory female zebra finches, *Taeniopygia guttata*, for example, are less likely to use social information in a foraging context (Rosa, Nguyen, & Dubois, 2012) while the opposite is true in male great tits, *Parus major* (Marchetti & Drent, 2000). Similarly, bold animals may be more likely to sample their environments more extensively than shy individuals and also less likely to act on social information (Kурvers et al., 2010). Personality, sex and social context have been shown to have a complex relationship in the risk-taking behaviour of great tits: van Oers, Klunder, and Drent (2005) found that whereas slow-exploring individuals became bolder when a companion was present, fast-exploring females became less bold. Sociality and social responsiveness could also be expected to play a significant role in public information use. Social conformity has been demonstrated in a social-learning context in which nine-spined sticklebacks copied the choices of demonstrator fish proportionately more as demonstrator numbers increased (Pike & Laland, 2010). In situations in which personal and public information conflict, however, Kendal, Coolen, and Laland (2004) showed that guppies adjust the importance they place on conformity according to potential cost.

The extent to which an animal prefers private knowledge over public information may be a result of the degree to which it samples its environment and its ability to learn the location of resources. Personality differences may affect cognitive style (reviewed in Carere & Locurto, 2011). For example, boldness and fast exploration have both been linked to better ability in learning foraging tasks (Boogert, Reader, & Laland, 2006; Dugatkin & Alfieri, 2003; Guillette, Reddon, Hurd, & Sturdy, 2009); however, these traits are also associated with a decreased ability in reversal learning when environments or signals change in quality or meaning (Guillette, Reddon, Hoeschele, & Sturdy, 2010; Sih & Del Giudice, 2012). Harcourt, Biau, Johnstone, and Manica (2010) found that shyer three-spined sticklebacks, *Gasterosteus aculeatus*, showed more variability in response times to social foraging tasks. Boldness and fast exploration might be favoured in tasks that are stable and routine forming whereas shyer and/or slower animals may do

better at tasks requiring greater flexibility (Exnerová, Svádová, Fučíková, Drent, & Stys, 2009; Guillette et al., 2010).

In this study, we assessed how personality traits influence the decision to use public or private information when these two sources of information come into conflict. As discussed above, sex differences can play a role in the expression of personality traits in different contexts. We focused on females to eliminate potential behavioural differences as a result of differing predation pressure and sex-driven risk-taking behaviour (see Piyapong et al., 2010). Wild-born adult female guppies were trained to associate feeders with rich or poor foraging patches. We then allowed them to observe a shoal foraging at a feeder that either confirmed or contradicted their own private information regarding the quality of the foraging patch and allowed them to choose between patches after demonstrators and food had been removed. Specifically, we tested the following predictions. (1) When public information is in conflict with private knowledge, bolder fish will prefer private information gained as a result of personally sampling foraging patches, whereas shyer fish will be more likely to act on information gained by watching the foraging activity of other fish. (2) Fish with higher sociality scores should prefer public information over private knowledge compared to fish with lower sociality scores. Additionally, we analysed data gained from the training process to investigate the relationship between personality traits and learning speed and thereby tested the prediction (3) that personality traits will affect the rate at which female guppies acquire information.

METHODS

Animals

Feral guppies ($N = 140$) were seine netted from a drainage ditch opposite Fannie Bay Racecourse, Darwin ($12^{\circ}20'32.060''N$, $130^{\circ}50'46.510''E$) in the Northern Territory, Australia and transported by air (flight time = 4.5 h), in water-filled plastic bags, supplemented with oxygen, packed securely into insulated, polystyrene boxes, to Macquarie University in September and October 2012. Water temperature during flight was maintained at a constant $22^{\circ}C$. The collection site is upstream from an estuarine creek containing a number of large predators. The guppies were acclimatized to laboratory conditions in two large aquaria ($90\text{ cm} \times 35\text{ cm}$) filled with aged tap water to a height of 30 cm and provided with river gravel and plastic plants. Males were removed and housed separately in a third aquarium. All fish survived transport and acclimatization with no apparent ill effect. Because they had been collected from the field and had been in contact with males, all females tested in these experiments were assumed to be gravid (mean length \pm SE: $24.48 \pm 0.36\text{ mm}$; mean weight \pm SE: $342.08 \pm 17.95\text{ mg}$; $N = 95$). Water temperature was maintained at $25\text{-}28^{\circ}C$ and pH7 in all stock and experimental aquaria, with a 12:12 h light:dark regime (lights on at 0700 hours). Water quality was maintained by internal filters in each aquarium and monthly one-third water changes. Fish were given a minimum of 7 days to adjust to captivity before being tagged for identification (sensu Colléter & Brown, 2011; Irving & Brown, 2013). Briefly, each fish was weighed and measured after being anaesthetized with 0.1 g/litre tricane methane sulphonate (MS222) buffered with NaHCO_3 (Sigma-Aldrich Inc.), and then injected with Fluorescent Visible Implant Elastomer tags (North-West Marine Technology Inc.) into the dorsal epidermis at one of four different locations, using one of seven different colours (red, purple, orange, yellow, green, blue and pink). All fish rapidly resumed normal swimming behaviour after the procedure and no mortality was incurred as a result of the tagging process. Fish were sized matched and housed in groups of six in aquaria measuring $37\text{ cm} \times 20\text{ cm}$ and filled with aged tapwater to a height of 16 cm. A further two groups of 18 tagged fish were housed in two aquaria measuring $90\text{ cm} \times 35\text{ cm}$ and filled to a height of 12 cm. All fish were housed at a density of about 0.5 fish/litre. All aquaria had a river gravel substrate and plastic plants to provide shelter. Fish had views of other fish in neighbouring aquaria and the stock room in general. All fish were given at least 10 days to recover from the tagging process before testing began. In

all cases fish were transferred between aquaria and handled using a small clear plastic container (measuring 8 cm × 12 cm) to reduce stress caused by exposure to air.

All animals were fed once per day on commercial flake food (Tetramin tropical flakes) supplemented with algae pellets (Aquarian Algae Eater Chips). Prior to the social information experiments, females intended for testing received defrosted *Daphnia* spp. on alternate days. After completion of the social information experiments, food was limited to flake and algae only. In all cases, except when undergoing training, animals were fed at the completion of each day's testing. Fish that were housed overnight in experimental aquaria were fed in those aquaria. Fish that were being trained were fed during the training process (described below) on defrosted *Daphnia*.

This work was approved by the Macquarie University Animal Ethics Committee under ARA 2010/028. At the end of the experiment, all fish were retained for further experimentation and breeding.

Personality Tests

We used two tests to measure two personality traits: boldness and sociality. To establish repeatability, each test was carried out twice with an interval of 8 weeks (boldness) and 4 weeks (sociality) between the two rounds. A total of 79 fish completed all tests. All observations were recorded using EthoLog 2.2 software (Ottoni, 2000).

Boldness

Fish were placed individually into test arenas (45 cm × 23 cm) at least 20 h prior to commencement of testing. Arenas were covered in dark blue self-adhesive plastic on three sides; the fourth side was marked into a grid of squares, each measuring 6 cm × 6 cm. Each arena was filled with conditioned fresh water to the height of the top grid (i.e. 18 cm) and had a gravel floor, a heater and an airstone connected to an aerator. The room and experimenter were obscured from the subject's view during testing by a brown curtain and fish behaviour was viewed remotely via a webcam (Logitech c615 HD) connected to a laptop computer. Each subject was given 10 min to settle prior to commencement of the test. The test began when a novel object was introduced at one end of the arena by a remote pulley system. In the first round, the object was a pink or yellow plastic peg measuring 8 cm in length. In the second round, we used pink, blue, green or yellow pieces of Lego (measuring 5 cm × 3 cm × 2 cm). To increase the novelty effect, each fish experienced a different coloured object from that used in the first test. The object was introduced when the subject was at the far end of the tank from the object. Latency to approach and the amount of time that the fish spent in close proximity to the object (equivalent to two fish lengths or under, approximately 5 cm) was recorded. Trials lasted 10 min from the introduction of the object.

Sociality

Sociality was measured by the amount of time spent in proximity to stimulus fish. Testing commenced once all fish had undergone the boldness test. The two assays were separated by a minimum of 4 days. Fish were tested individually in an arena measuring 90 cm × 35 cm and filled with aged tap water to 15 cm. Water was heated and aerated with a filter overnight when fish were absent. The arena was divided into two chambers (stimulus and test) measuring 25 cm × 35 cm and 65 cm × 35 cm respectively, separated by a clear Perspex barrier. All sides of the arena were covered in dark blue plastic film and fish observed remotely via a webcam (Logitech c615 HD) mounted above the arena. The floor of the arena was clear glass resting on white polystyrene marked into four equal sections (measuring 16 cm × 35 cm) in the test chamber with section 1 closest to the stimulus chamber and section 4 furthest away. Five unfamiliar fish equivalent in size or larger than the subject were placed in the stimulus chamber and given 10 min to settle before the addition of test fish to the test chamber. Test subjects were confined

individually in a bottomless, removable plastic container (measuring 17 × 11.5 cm and 19 cm high) in section 4 of the test chamber. Each subject was given 60 s to recover from the transfer process and then the plastic container was removed remotely via a pulley system and the fish observed for 10 min. The time spent in each of the sections was recorded as well as the number of times a section was entered. We generated a measure of sociality based on the time spent in each section (effectively the mean distance from the stimulus shoal), that is, fish that spent the most time in section 1 (closest to the stimulus chamber) attained the highest sociality scores. Five fish were excluded from analysis following noise disturbances that affected behaviour during their trials. Stimuli fish were used for a maximum of 2 h (equivalent to 10 tests) and were then replaced with fresh stimuli fish and rested for the remainder of the day.

Social Information Experiment

Training

Fish were trained with their home aquarium companions in groups of six for 15 days (following Duffy, Pike, & Laland, 2009 with some modifications). The test arena measured 90 cm × 50 cm and was filled to 12 cm with fresh water that was filtered and heated overnight when fish were absent. The arena bottom was clear glass resting on white Styrofoam marked into regions (Fig. 1). The arena was divided into three chambers with removable Perspex barriers. Two foraging chambers (each measuring 45 cm × 20 cm) had a piece of coloured Perspex (green or purple) measuring 18 cm × 15 cm fixed to the wall close to a feeder. These colours were chosen on the basis that guppies are able to distinguish green from purple (Endler, 1991). The feeders consisted of a piece of white plastic rectangular conduit 15 cm in length and 2.5 cm wide and deep, with an open face partly enclosed by clear Perspex. These were mounted on a removable, white Perspex wall (20 cm × 16 cm) dividing the smaller chambers. Training groups experienced rich foraging conditions in one chamber and poor foraging conditions in the other. Seven groups ($N = 43$) were trained to associate green, and six groups ($N = 36$) purple, with rich foraging. For the first four training sessions, fish were confined to whichever foraging chamber they were being trained to; in subsequent sessions they had free access to the entire arena. Before training commenced, fish had at least 10 min in which to recover from the transfer process and acclimatize to the arena. Food for training sessions was prepared by defrosting cubes of *Daphnia* spp. (frozen weight 4 g) in 75 ml of conditioned fresh water. Training sessions lasted for 10 min and consisted of delivery of 10 mg (dry weight) of *Daphnia* suspended in 1.5 ml of water via a plastic pipette. Food delivery in the rich patch occurred every 90 s. In the poor patch, 1.5 ml of *Daphnia*-scented water was delivered every 90 s except at the 90 and 270 s marks when *Daphnia* was delivered as described above. Fish were trained twice per day with at least 10 min elapsing between training sessions, during which they remained in the training arena.

To test whether a fish had learnt to associate a feeding chamber with the rich foraging patch, each fish was removed from the home aquarium and placed in a bottomless plastic container at the far end of the test arena relative to the patches that had been associated with rich or poor foraging. After allowing 60 s for the fish to recover from the transfer process, we removed the container via a pulley system and allowed the fish to swim freely for 5 min while her activity was observed via a webcam (Logitech c615 HD) mounted above the arena. In contrast to training sessions, no food or chemical cues were provided during test assays. We noted the number of times a fish entered a rich or poor zone, the latency to enter the rich foraging zone, the time spent in each zone and the number of times a feeder was inspected to within two body lengths. Time spent in the rich zone was divided by total time in rich and poor zones to achieve a proportion. A fish was deemed to have passed the test if the proportion was >0.5 . All fish were tested on day 8 of their training (prior to that day's training) and again on day 11. Fish that passed the tests were not tested again; however, they continued to be trained with their group so as not to distort the training

process of their shoalmates. Fish that did not pass the second test were tested again on day 15; fish that still did not pass ($N = 22$) were excluded from the subsequent social information test that occurred on the following day. All fish were assigned a final training score, based on an average proportion of time spent in the rich foraging zone in all tests, as follows: 1 = <0.25 ; 2 = $0.25-0.5$; 3 = $0.5-0.75$; 4 = $0.75-1$. They were also assigned a latency score, based on an average across all trials, of the time it took to first enter the rich zone: 1 = $0-75$ s; 2 = $76-150$ s; 3 = $151-225$ s; 4 = $226-300$ s.

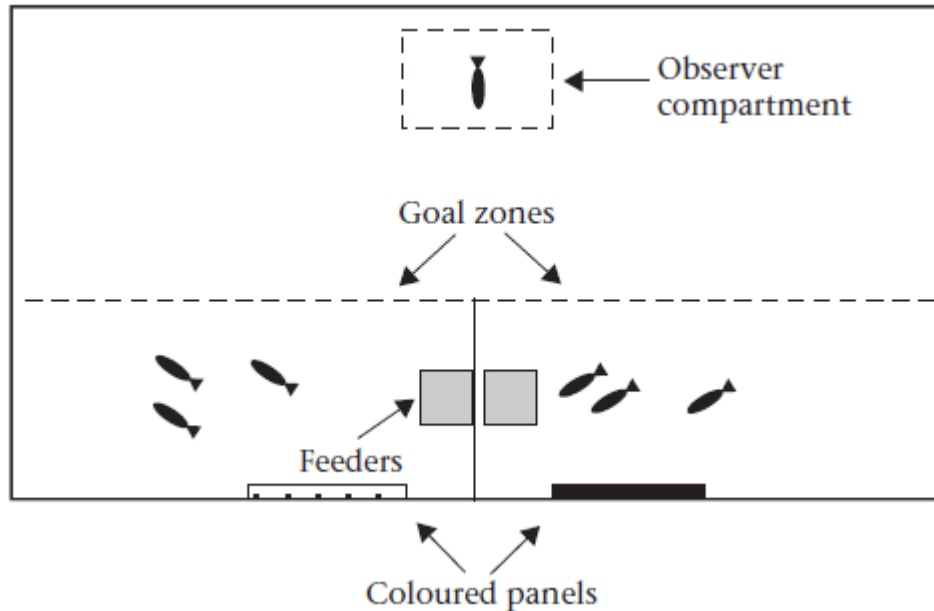


Figure 1. Diagram of training and social information arena. Dashed lines represent a removable clear barrier. Solid lines represent opaque barriers. Shown in set-up for condition C (social stimulus control) of the social information assay: demonstrators on right are receiving the rich foraging treatment in the poor zone; demonstrators on the left are receiving the poor foraging treatment in the rich zone.

Test for social information use

To test whether subjects preferred social information about the patch quality over their own private knowledge, they were confined in a clear container and shown three demonstrator fish being fed for 10 min in one of three conditions: in condition A public and private information coincided ($N = 19$; demonstrators were fed in the rich foraging zone); in condition B public and private information conflicted ($N = 19$; demonstrators were fed in the poor zone); and condition C was a social stimulus control ($N = 19$; demonstrators were present in both zones but the group in the poor zone experienced a rich foraging rate and vice versa). As with the training regime, demonstrator fish undergoing the poor foraging treatment received a limited amount of food and scent-laden water. During the demonstration phase, demonstrators were confined to their zone by a clear Perspex barrier. All demonstrators were mature, gravid females drawn from the long-term laboratory population and at least one member of each demonstrator group was larger (mean length \pm SE: 32.6 ± 0.3 mm) than fish being tested.

Following the demonstration, a white plastic barrier was placed in front of the subject to obscure her view and all demonstrators and food were removed from the arena. The clear barrier separating the feeding regions from the rest of the arena was also removed. The white barrier was then lifted and the plastic

container removed by remote pulley system. The subject fish was then at liberty to explore the entire arena. Subjects were observed via webcam for 5 min and their movements noted in the same way described in the feeder association test. Tanks were thoroughly cleaned between tests and demonstrators rotated so that no demonstrator group was used more than twice per day. Seven fish were excluded from analysis, either because they froze for the entire trial ($N = 5$) or because external noise disturbance affected their behavior ($N = 2$).

Statistical Analysis

All data were tested for normality. Sociality means (time spent in zone closest to stimulus fish) were squared to achieve a normal distribution. Spearman correlation tests were used to determine individual repeatability across time-separated personality trials. Linear regressions were used to compare personality means with training and social information use data. Where data included nominal variables, such as training and latency scores, and social information treatment, we used one-way analyses of variance (ANOVA) and covariance (ANCOVA) with the nominal variable as the main effect. To investigate fully the relationship between boldness and social information use, we performed a linear regression and then split it between treatments. All analyses were carried out using StatView 5.0.1 (SAS Institute Inc., Cary, NC, U.S.A.).

RESULTS

Personality Traits

Fish showed significant repeatability across two time-separated trials for boldness (Spearman rank correlation: $r^S = 0.287$, $N = 79$, tied $P = 0.017$). Sociality was also significantly repeatable over two time-separated trials (Spearman rank correlation: $r^S = 0.233$, $N = 74$, tied $P = 0.046$). Boldness and sociality were not significantly correlated (linear regression: $F_{1,72} = 0.86$, $P = 0.357$, $R^2 = 0.012$). Length and weight of test fish were highly correlated (growth regression: $Y = e(2.191 + 0.144X)$, $P < 0.0001$) so all analyses comparing size and traits were carried out using length as a covariate. Fish size was not an important factor in sociality (linear regression: $F_{1,72} = 0.003$, $P = 0.956$, $R^2 < 0.001$), but was highly correlated with boldness (linear regression: $F_{1,77} = 19.131$, $P < 0.001$, $R^2 = 0.199$).

Learning

Bolder fish were quicker to learn an associative task than shyer fish; they spent more test time in rich than poor foraging zones (linear regression: $F_{1,77} = 7.849$, $P = 0.006$, $R^2 = 0.093$) and entered rich zones more rapidly (linear regression: $F_{1,77} = 11.583$, $P = 0.001$, $R^2 = 0.362$). Training scores and boldness were also associated (ANOVA: $F_{3,75} = 2.757$, $P = 0.048$), as were latency scores and boldness (ANOVA: $F_{3,75} = 3.875$, $P = 0.012$; Fig. 2). The proportion of time fish spent in rich foraging zones was positively correlated with fish length (linear regression: $F_{1,77} = 5.182$, $P = 0.026$, $R^2 = 0.063$); however, multiple regression analysis showed that boldness remained close to significance once length was controlled for (length: $t_{78} = 1.191$, $P = 0.237$; boldness: $t_{78} = 1.983$, $P = 0.051$). Sociality did not affect the time fish spent in rich zones (linear regression: $F_{1,72} = 1.221$, $P = 0.273$, $R^2 = 0.017$) or the time taken to enter rich zones (linear regression: $F_{1,72} = 0.600$, $P = 0.441$, $R^2 = 0.008$).

To determine whether boldness simply increased the likelihood of fish engaging with the apparatus, we compared the relationship between boldness scores and latency to enter either foraging zone. Bolder fish tended to engage with the apparatus more speedily than shyer fish but this was not statistically significant (linear regression: $F_{1,77} = 3.419$, $P = 0.068$, $R^2 = 0.043$). However, when latencies to enter either the rich or poor zone were partitioned, it was evident that this result was driven principally by bolder fish demonstrating a shorter latency to enter the rich zone (linear regression: $F_{1,77} = 7.498$, $P = 0.008$, $R^2 =$

0.089). Bolder fish were not more likely to enter the poor zone more rapidly (linear regression: $F_{1,77} = 0.253$, $P = 0.617$, $R^2 = 0.003$).

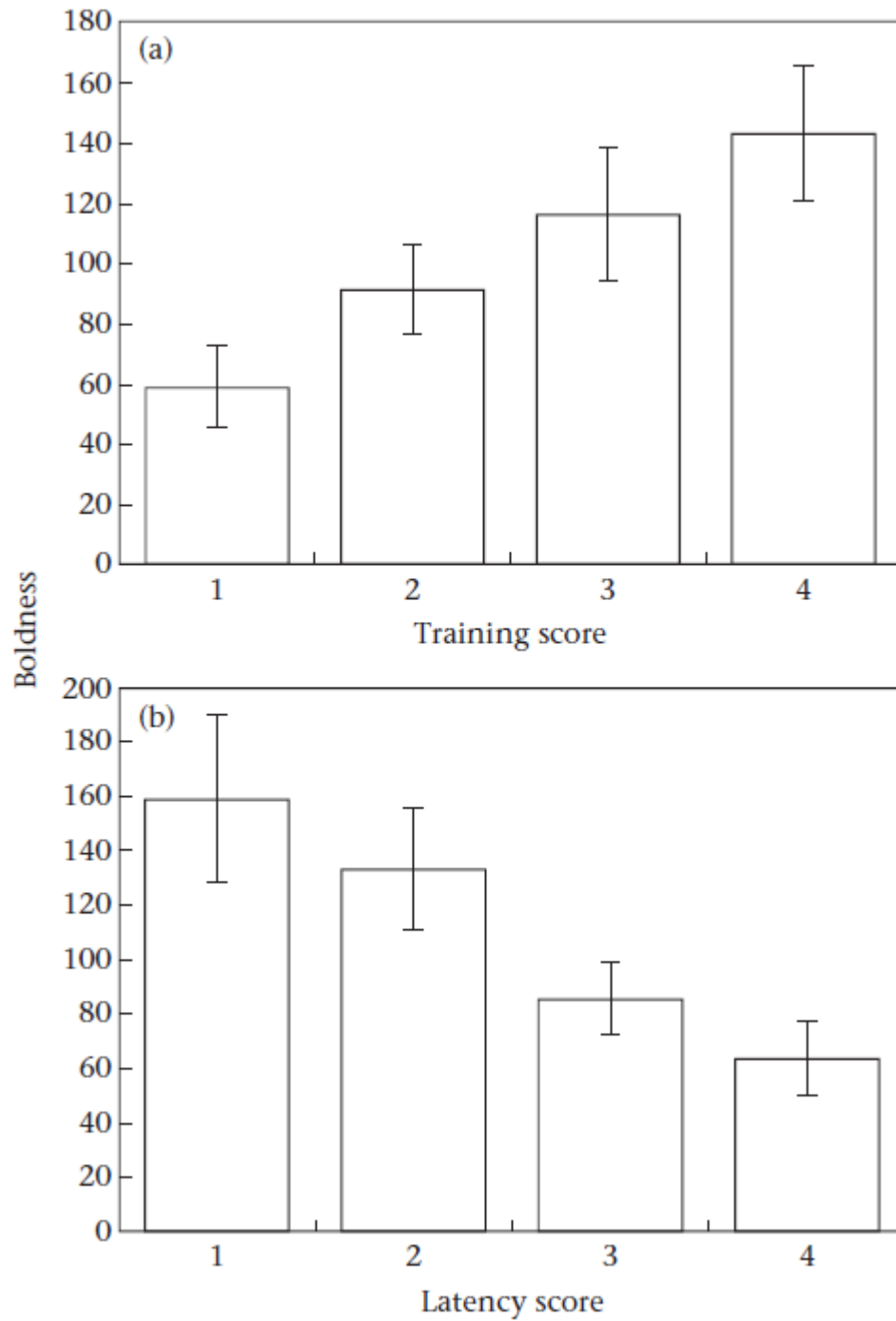


Figure 2. (a) Mean \pm SE boldness score (mean time (s) spent close to a novel object across two time-separated trials) and training score during a learning task based on average proportion of time spent in the rich foraging zone in all tests for feeder association (1 = <0.25 ; 2 = $0.25-0.5$; 3 = $0.5-0.75$; 4 = $0.75-1$; $N = 79$). (b) Mean \pm SE boldness score and latency score based on mean time to enter rich foraging zone in all tests for feeder association during a learning task (1 = $0-75$ s; 2 = $76-150$ s; 3 = $151-225$ s; 4 = $226-300$ s; $N = 79$).

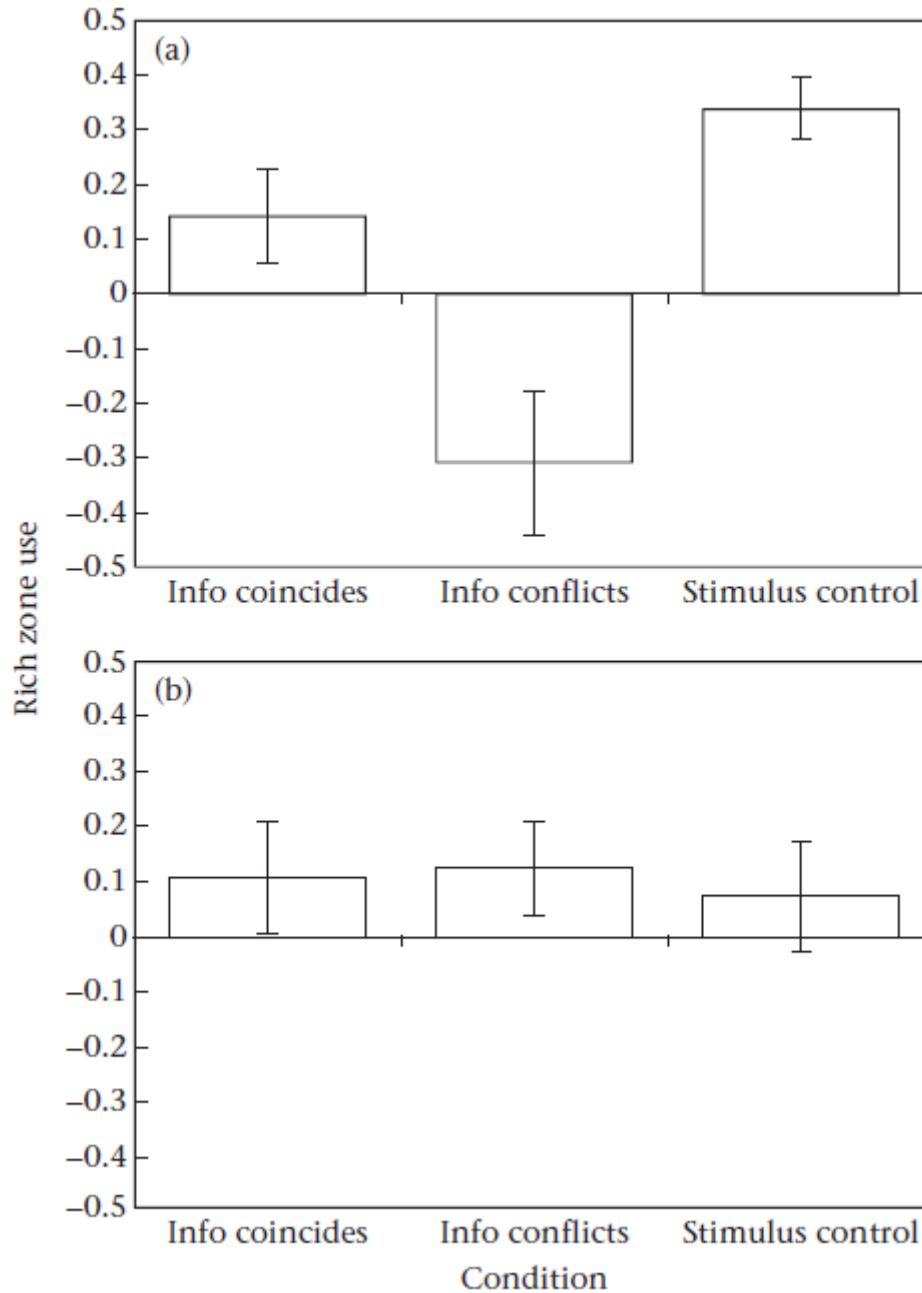


Figure 3. Fish with (a) a high ($N = 21$) and (b) a low ($N = 28$) sociality index and rich zone use (proportion of time spent in the rich foraging zone for each treatment during the social information trial). Negative values represent a greater proportion of time spent in the poor foraging zone.

Public versus Private Information Use

Linear regressions showed that fish length was not correlated with the proportion of time spent in the rich zone relative to time in both foraging zones in any of the treatments (condition A: $F_{1,15} = 0.005$, $P = 0.944$, $R^2 < 0.001$; condition B: $F_{1,13} = 1.643$, $P = 0.222$, $R^2 = 0.112$; condition C: $F_{1,16} = 1.329$, $P = 0.266$, $R^2 =$

0.077). An ANCOVA examining the effects of sociality and treatment on rich zone use was not significant (all P values > 0.1). To investigate further the potential role of sociality on social information use, we split fish into two groups based on their sociality scores. The more social fish ($N = 21$) showed a significant interaction with treatment in the proportion of time spent in the rich zone (ANOVA: $F_{2,18} = 9.771$, $P = 0.001$) and were more likely to follow public information rather than private knowledge (Fig. 3a). The less social fish ($N = 28$) were more likely to spend a greater proportion of time in the rich foraging zone irrespective of treatment (ANOVA: $F_{2,25} = 0.078$, $P = 0.925$; Fig. 3b).

Boldness scores also affected the patch choices that fish made in the context of public and private information use. An ANCOVA examining the effect of boldness and treatment on the time spent in the rich zone as a proportion of total time spent in either foraging zone showed that boldness was significantly related to social information use, which varied between treatments (treatment: $F_{2,44} = 5.551$, $P = 0.007$; boldness: $F_{1,44} = 0.791$, $P = 0.378$; treatment* boldness: $F_{2,44} = 4.585$, $P = 0.015$). To examine the two-way interaction, we conducted linear regressions for each treatment separately. In condition A (public and private information coincide), bolder fish spent less time in the rich zone than shy fish ($F_{1,15} = 5.271$, $P = 0.036$); in condition B (public and private information conflict), bolder fish spent more time in the rich zone than shy fish ($F_{1,13} = 5.511$, $P = 0.035$); whereas in condition C (social stimulus control), boldness scores were unrelated to patch preference ($F_{1,16} = 0.002$, $P = 0.961$; Fig. 4).

DISCUSSION

Female guppies demonstrated personality as evidenced by repeatable variation in both boldness and sociality measures. In contrast with other studies that have found evidence of a boldness-sociality syndrome (e.g. Pike, Samanta, Lindström, & Royle, 2008), there was no correspondence between boldness and sociality in the present study. These results do, however, echo previous work that tested male and female guppies from the same population and found a syndrome between sociality and boldness in males but not females (Irving & Brown, 2013). Boldness was positively correlated with size in contrast to other findings (Brown & Braithwaite, 2004; Krause, Loader, McDermott, & Ruxton, 1998). Taken together these results suggest a complicated relationship between size, sex and personality in combination with other key environmental factors such as predation pressure. Most importantly, however, personality traits also affected reliance on social information.

Personality and Information Use

As predicted, both sociality and boldness were implicated in public information use when it conflicted with private knowledge. When public information coincided or conflicted with private information and when demonstrators were present in only one foraging patch, more social female fish preferred the patch that was previously occupied by the shoal. On the other hand, when demonstrators were present in both foraging zones and social information conflicted with private knowledge, females with a higher sociality index spent $84 \pm 5.7\%$ of total time in the rich zone, favouring private knowledge over public information. Females with low sociality scores showed no change in their behaviour across treatments. This suggests that fish with a high sociality index might be prioritizing the need to be with conspecifics over opportunities for rich foraging.

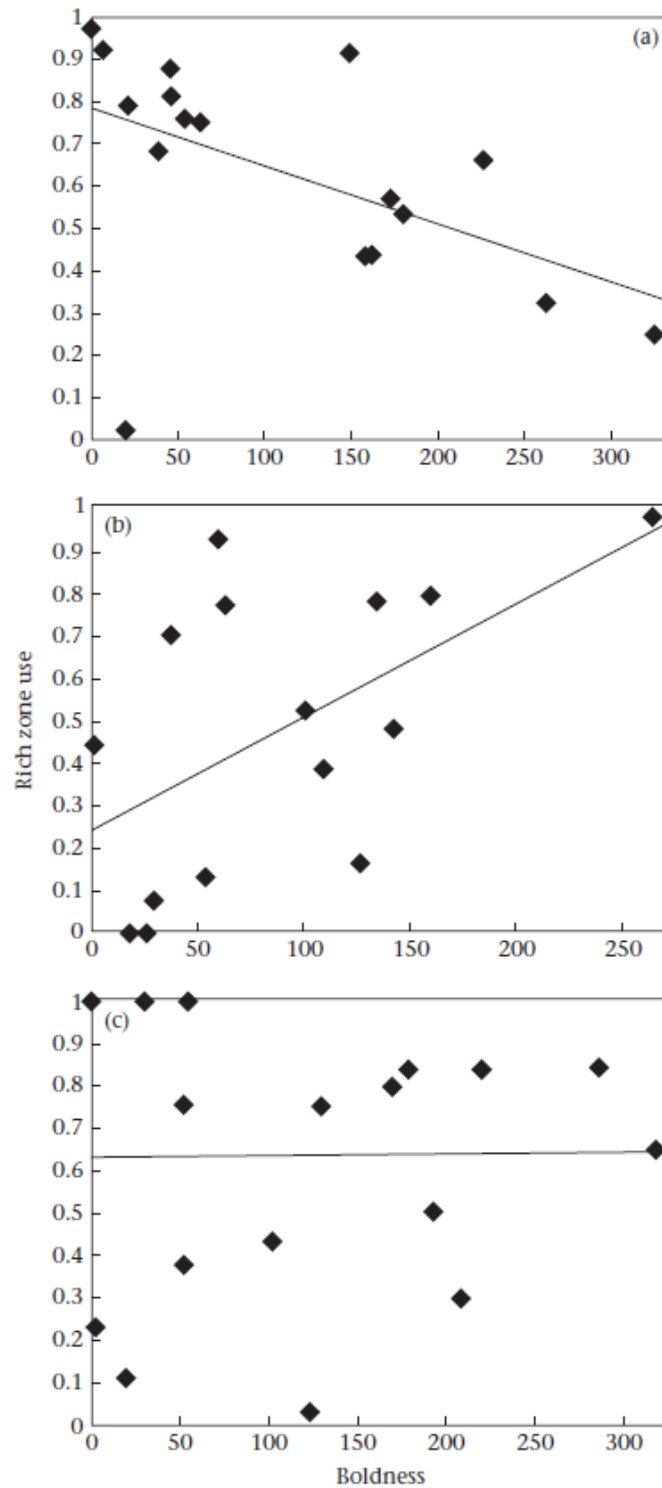


Figure 4. Boldness score (mean time (s) spent close to a novel object across two time-separated trials) and rich zone use (proportion of time spent in the rich foraging zone during the social information assay). (a) Condition A: public and private information coincide (N = 17); demonstrators fed in the rich foraging zone. (b) Condition B: public and private information conflict (N = 15); demonstrators fed in poor foraging zone. (c) Condition C: social stimulus control (N = 18); demonstrators present in both rich and poor zones, but fed only in the poor zone.

The presence or absence of conspecifics also appears to be a determining factor in the foraging decisions of bolder female fish. We predicted that bolder fish would be more likely to rely on private knowledge when this conflicted with public information. This appears to be the case when we look at the results in which demonstrators were located in the poor zone; bolder fish spent significantly more time in the rich zone than shyer fish. When we look at the results for the condition where demonstrators were located in the rich zone, however, it becomes apparent that bolder fish were actually avoiding patches recently vacated by demonstrators and, conversely, that shyer fish might have been seeking out demonstrators. When a social stimulus was present in both foraging zones there was no apparent relationship between boldness and patch preference. There are several explanations for why this might be the case. There is evidence to show that bolder animals take risks by being the first to move away from a group (Franks & Marshall, 2013; Michelena, Sibbald, Erhard, & McLeod, 2008). However, we failed to find a relationship between boldness and sociality in these fish. Alternatively, it may be that the bolder fish were more sensitive to potential competition. While boldness has been found to be positively correlated with competitive ability (Ward, Thomas, Hart, & Krause, 2004; Ward, Webster, & Hart, 2006), size, strength and familiarity are also likely to be important to the outcome (Brown, Jones, & Braithwaite, 2007; Warburton, 2003; Ward et al., 2006). Focal fish witnessed a large number of aggressive interactions between stimulus conspecifics and bolder focal fish might have been avoiding potentially aggressive encounters with similar-sized demonstrator fish. However, this is a tenuous connection given that, unobserved by the focal fish, all demonstrators (and food) were removed from the test arena prior to release of the focal fish. A third possibility is that bolder fish were motivated by higher levels of hunger; however, this is unlikely given that boldness was positively correlated with size. Smaller fish tend to have higher metabolic rates (Clarke & Johnston, 1999) and so could be expected to be faster to forage. Furthermore, the total amount of food available to each training group during the course of the day (dry weight = 10 mg) was sufficient to satiate all group members regardless of size. Thus foraging motivation is not likely to be the reason for performance variance. A more parsimonious explanation is that bolder females indirectly infer patch depletion from the presence of other fish. Fish are capable of flexible decision making and adjust foraging strategies to account for changes in patch richness (reviewed in Warburton, 2003); fish are also able to remember the location of previous encounters with predators and avoid potentially dangerous locations in future (Brown, 2003; Odling-Smee & Braithwaite, 2003). The bolder females tested in these experiments might have been seeking out the alternative foraging zone to that recently occupied by demonstrators on the basis that this foraging patch, even when it is associated with poor foraging, is less likely to be depleted. Recent work with wild great tits supports this idea: Cole and Quinn (2012) found that good problem-solvers were poor competitors and suggested that, rather than successfully compete for a single resource, innovative foragers may rely on a range of food sources and alternative foraging strategies. Our results also show that bold female fish solve this foraging task more efficiently than shy females, adding further weight to this argument.

Personality and Learning

Boldness, but not sociality, affected female guppies' ability to learn an associative task. Dugatkin and Alfieri (2003) found positive correlations between learning speed and boldness in male guppies and our results show a similar outcome for females. Fish that were bolder were faster to enter the rich zone and showed greater learning accuracy (measured as the proportion of time they spent in the rich than the poor foraging zone). In contrast to other work that has found learning speed-accuracy trade-offs in bold phenotypes (reviewed in Sih & Del Giudice, 2012), our results show that bold female fish have the capacity to demonstrate both speed and accuracy when learning an associative foraging task. This disparity may be a result of the environmental context of the experiment. One context in which speed-accuracy trade-offs have been found in guppies is between low- and high-predation environments (Burns & Rodd, 2008). The guppies we tested were drawn from a high-predation population which might suggest

the fish favour lower speed in return for higher accuracy. However, at the time of the learning assays, the fish had been maintained in a predator-free environment for at least 6 weeks. Furthermore, fish were fully acclimatized to the test arena as learning trials took place after a minimum of 7 days, during which time fish spent a minimum of 40 min per day with shoalmates in the test arena undergoing training. Low-level natural lighting was used during training and testing, and the trainer was mostly out of sight. These two factors (high-predation origin and low-predation current context) may have decoupled any trade-off between speed and accuracy in this population. Alternatively, because female guppies are less affected by predation pressure in the wild than males because of their coloration and lower risk-taking behaviour (Piyapong et al., 2010), speed-accuracy trade-offs may be less important.

The test process itself presented a stressful context, in that fish were first transported from home aquaria and confined to a settling zone before being released and tested in the absence of any shoalmates. Bolder fish might have been less affected by these stresses or better able to recover; indeed, previous studies show negative correlations between stress levels and boldness in fish (Huntingford et al., 2010; Raoult, Brown, Zuberi, & Williamson, 2012). Because of this, it is possible that, rather than actually learning the location of the rich foraging zone, bolder females were simply quicker to encounter the rich zone because they were quicker to recover and move from the initial settling zone and engage with the apparatus. Bolder animals may accomplish new tasks not through general learning ability per se but because they are more likely to move and explore in a novel environment (Shettleworth, 2010). This possible effect was also discussed (but discounted) by Dugatkin and Alfieri (2003). To investigate this possibility we compared boldness with latency to enter either the rich or poor zone first. Results were statistically nonsignificant but did point to a trend indicating shyer animals were slower to enter either foraging zone. Thus the possibility that learning was confounded with recovery speed cannot be ruled out without further investigation. Notwithstanding, these results do support other evidence that points to differences in learning styles between different personality types. Variations along a bold-shy axis can be correlated with innovation and social learning. For example, bold bottlenose dolphins, *Tursiops truncatus*, are more likely to approach new objects and to engage in innovative behaviours that are then learned by shyer individuals (Kuczaj, Yeater, & Highfill, 2012). Dominant breeding male carrion crows, *Corvus corone corone*, also model new behaviour to neophobic conspecifics (Chiarati, Canestrari, Vera, & Baglione, 2012); and exploratory male Carib grackles, *Quiscalus lugubris*, are quicker and more effective at solving novel problems (Overington, Cauchard, Côté, & Lefebvre, 2011).

In conclusion, we found that boldness and sociality both affected information acquisition and use by female guppies. Bolder fish appeared to use the presence and activity of other fish as cues to suggest patch depletion and subsequently avoid an area. In contrast, fish at the most social end of the spectrum were attracted to the patch that had been recently occupied by others. The mechanisms by which this is mediated may be a complex cocktail of cues, including competition potential, relative size and aggression levels and estimations of patch richness that are traded off against predation risk and shoaling tendencies. Disentangling these factors to examine relative influences could be a fruitful area for further work. In addition, we showed that learning may be influenced by boldness. Future work could examine the interplay between personality and environmental influences on plasticity in decision making.

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