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Abstract

Shyness and boldness has been considered a fundamental axis of human behavioural variation. At the extreme ends of this behavioural continuum subjects vary from being bold and assertive to shy and timid. Analogous patterns of individual variation have been noted in a number of species including fish. There has been debate on the nature of this continuum as to whether it depends on context. That is, whether it is domain-general (as in humans), or context-specific. The purpose of our study was to test if shyness and boldness depends on context in rainbow trout, *Oncorhynchus mykiss* and to this end we estimated boldness in five different situations. Our data provide evidence of a shy–bold behavioural syndrome in rainbow trout. Bold trout tended to be bold in four situations when the context was similar (when the context concerned foraging). However, in a different context, exploring a swim flume, the ranking was entirely different. We suggest that shyness and boldness depends on context in rainbow trout.

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Introduction

The shy–bold continuum has been considered a 'fundamental axis' of human behavioural variation (Wilson et al. 1994). Along this continuum individuals demonstrate consistent differences in their behavioural expression with some individuals being characterized by bold and assertive behaviour and others by comparatively shy and timid behaviour. Analogous patterns of individual variation have been noted in a number of species (e.g. Wilson et al. 1993; Réale et al. 2000; Svartberg 2002), suggesting that the shy–bold continuum may be widespread in many taxa, including fish (e.g. Coleman & Wilson 1998; Fraser et al. 2001; Sneddon 2003). An animal's position on this

continuum can influence how it reacts in a variety of situations (Sneddon et al. 2003). Thus, this continuum may have implications in understanding individual variation in movement and space utilization (Fraser et al. 2001), nociception and fear (Sneddon et al. 2003), as well as individual differences in learning (Kieffer & Colgan 1992). Variation in the propensity to take risks has the potential to create differences in survival by affecting how animals react to novel situations, evade predators, or interact in social and reproductive contexts (Réale et al. 2000).

There is debate as to whether the nature of the shy–bold continuum depends on context. In humans, shyness and boldness are often considered to be general personality traits (domain-general temperament) that are expressed in many different contexts (Kagan et al. 1988; Segal & Macdonald 1998). Thus, an individual that is bold in one context tends to be bold in others. In fish however, there is contrary evidence that suggests that this continuum depends on context. The context-specific temperament hypothesis (Wilson et al. 1994; Coleman & Wilson 1998) suggests that shy–bold behaviour may depend on the context of the situation (e.g. exploration of environment, predator–prey interactions).

While recognized since the time of Lamarck, the importance of behaviour's role in evolution has been underestimated (Gottlieb 2002). More explicitly, this applies to intraspecific differences in behaviour (e.g. temperament) that until recently, were considered to be non-adaptive variation around an adaptive population mean (Dall et al. 2004). However from an evolutionary standpoint, individual differences in behaviour (as seen in shy–bold) may represent the 'leading edge of evolution' (Gottlieb 2002) and may therefore provide a means by which rapid adaptive speciation can occur (Bolnick et al. 2003). Additionally, variation in temperamental traits have also been shown to have a substantial heritable component among animals such as the great tit, *Parus major* (Dingemanse et al. 2002, 2003). Réale & Festa-Bianchet (2003) showed that temperamental traits also were subject to natural selection in a predator–prey interaction between cougars, *Puma concolor*, and bighorn sheep, *Ovis canadensis*. Thus, understanding the nature of the shy–bold continuum as it relates to novel behavioural contexts is of importance to evolutionary biologists as well as ethologists, because it may provide a means to integrate evolutionary and ecological approaches to studying behaviour.

If the shy–bold continuum applies to rainbow trout and if it depends on context then we predict that latency to complete a task will be similar in tests with a similar context but not in those with a different context. The purpose of our study was to compare individual performance in measures of shyness and boldness in trout. We examined performance in five different situations to delineate the nature of these differences as well as to test if performance between measures was positively correlated. To this end we used the performance of subjects to generate rank data as a measure of shyness and boldness in rainbow trout.

Methods

Experimental Animals

We used five juvenile rainbow trout, *Oncorhynchus mykiss* parr (fork length 6–8 cm, weight 2–5 g), from Rainbow Springs Hatchery in Tavistock, Ontario. Trout were held and tested individually throughout the study in 38 l rectangular (80 cm × 19 cm × 25 cm) glass aquaria in an environmental chamber. Room and water temperature were kept constant at 12°C, and photoperiod was 12:12. Tanks were opaquely painted on the bottom and sides to prevent interaction between subjects. Feeding took place only during daily conditioning trials with an apparatus using a paste consisting of gelatine and standard fish flakes or using commercial trout feed during the flume trial period.

We also used two Atlantic salmon, *Salmo salar* (fork length 28 and 29 cm, weight approx. 155 g), from the Atlantic Salmon Broodstock Development Program in St Andrews, New Brunswick. Salmon were held in 1 m round tanks throughout the study, except when being used during measure 3 trials, when they were placed in the experimental apparatus. Salmon were fed to satiation every other day using commercial feed throughout the study. Holding tanks for both salmon and trout were aerated continuously and given 30% water changes every other day. Fish were given a minimum of 24 h to adjust to their individual holding/experimental tanks prior to the onset of experimentation.

Experimental Set-up

The same experimental tank was used for every subject in all but one experiment to eliminate tank effects. The testing arena was identical to the holding tanks except it contained vertical constructs to hold a divider or barrier in the middle. The feeding apparatus was 7 cm to the right of the midline on the back wall and consisted of a cylindrical black PVC unit housing a tube for food delivery and a single red light emitting diode (LED) as a visual signal to condition for food reward. A syringe pump (Harvard Apparatus model 33, South Natick, MA, USA) delivered food (5.6 μl/s for 2 s) when the LED was on (3 s). All trials were performed in a darkened room, with a fluorescent (25 cm) light 8 cm above and just to the rear of the test tank. This lighting procedure, combined with painted tank sides prevented any outside stimulus from affecting the subject during trials. All fish were tested on the same day for a given measure. The order of individuals being tested was randomized within each measure to eliminate any risk of time effect or chemical signal influencing the outcome of the trial and therefore the ranking system. Trial length varied from 15 min (measures 1–4) to 1 h (measure 5) depending on the measure being examined. All trials were recorded with a Sony digital camcorder (DCRTRV18 miniDV, Sony, Japan) connected to a VCR. The camera's infrared setting (night vision) was used to facilitate recording in the low ambient light during trials. It was not necessary to mark the trout because they were held in separate holding tanks and tested separately.

Measures of Shyness and Boldness

Measures 1–4 involved foraging, that is, they involved using the feeding apparatus; measures 3 and 4 added the potential predation risk to the foraging context. Measure 5 did not involve foraging; rather it involved crossing a barrier in an artificial stream. Because we sought to insure that the subject's behaviour in each measure was independent we subjected the fish to varying contexts out of the order of measures presented here. Measures are listed as such to facilitate an understanding of the contextual nature of this experiment and the actual chronological arrangement of the measures is discussed in each section.

Measure 1: Latency to Explore and Find the Feeder

Our first measure was the latency to consume food at the feeding apparatus. We chose this as the fundamental test against which to compare other measures because it was the first test and its context clearly concerned foraging. To reduce stress level during transport, fish were transferred from their respective housing tank to the test arena in a bucket (as opposed to netting procedures). We used this procedure to familiarize fish with our transport procedure in all subsequent experiments. Fish were ranked according to latency to explore the feeding apparatus and consume the 'worm-like' novel food source. Fish possessing the shortest latency period were ranked as 1 and the fish with the longest latency were ranked as 5. Trials were repeated on three consecutive days to test for repeatability. Only the latency in the first trial was used to rank fish. Because a similar level of familiarity with the feeder was a prerequisite for later measures, we continued reinforcement of the conditioning procedure 5 d/wk for an additional 3 wk for all fish. We used the rank order results gained from measure 1 as a basis of comparison for all subsequent measures.

Measure 2: Latency to Pass Through a Net to get to the Feeder

Our second measure was the latency to cross through a mesh partition to gain access to the feeding apparatus. This measure began 48 h after the completion of the conditioning reinforcement from measure 1. The mesh partition fit within the vertical constructs in the centre of the tank and consisted of a black plastic outline and white nylon netting (5 cm^2 squares) spanning the width of the tank. The feeding apparatus was placed in the same location as the previous measure so that the fish would know its location. This task was intended to represent a novel object test that acted as a barrier to food acquisition. Fish were ranked according to latency to pass through the net to gain access to the feeding apparatus.

Measure 3: Latency to Feed Under Predation Risk by a Salmon

Our third measure was the latency to cross through the net to gain access to the feeding apparatus when there was a potential predator on the other side. This

measure began 48 h after the completion of the measure 2 trials. A salmon was placed on the opposite side of the partition, in the area containing the feeding apparatus. Trout were ranked according to their latency to feed from the feeding apparatus in the presence of the salmon. Risk of predation for subjects was minimal as salmon were fed to satiation before trials, were below previously observed average sizes (approx. 40 cm) for the onset of piscivory in Atlantic salmon (Salminen et al. 2001), and both predator and prey were naïve. We did not quantitatively assess the salmon's behaviour.

Measure 4: Latency to Feed Under Predation Risk by a Simulated Aerial Predator

Our fourth measure was the latency to consume food at the feeding apparatus in the presence of a simulated aerial predator. Chronologically, this measure took place 48 h after the completion of measure 5. This measure returned to the set-up of measure one as the net barrier was removed and only the feeding apparatus was left in the tank. To simulate an aerial predator, a 15 cm^2 piece of corrugated blue plastic was attached to a manual pulley system 18 cm above the testing arena. The pulley system allowed the drop and recovery of the 'predator' on the side of the tank holding the feeding apparatus, opposite the trout. Three seconds after the addition of fish to the test arena, the simulated predator was dropped on the surface water of the tank. Because of the material used in construction of this simulation, the 'predator' created an initial splash upon descent, and then afterwards created surface turbulence upon retrieval. This simulated predation attempt reoccurred upon a fish's approach to the feeder. If the subject did not approach the experimental tank midline, then the predator was dropped on random intervals varying from 3 to 10 s. Fish were ranked according to their latency to feed from the feeder in the presence of these simulated predation events.

Measure 5: Latency to Cross a Barrier in a Stream

Our fifth measure did not involve feeding or the feeding apparatus; it involved latency to cross a barrier in an artificial stream. This measure began 48 h after the completion of the measure 3 trials (and prior to measure 4 chronologically). Trout were placed individually in a 44 l glass flume apparatus consisting of two square pools (40 cm × 20 cm × 26 cm) connected by a narrow channel (34 cm × 8 cm × 13 cm). A rheotactic stimulus was created with re-circulating flow via a 2-horse-power pump. There was a 7.6 cm perforated PVC barrier in the center of the channel; water was 8 cm deep in the unobstructed channel. Water temperature in the flume was approx. 12°C (+/−2°C) for the duration of the test and trials took place in normal room light. A 1 l container (visible through the barrier perforations) was placed in the upstream pool to provide cover. Subjects were ranked according to latency to cross the PVC partition. During this experiment we fed subjects only in their holding tanks and not in the flume apparatus. In doing so, we insured that this measure was independent of the

context of feeding and only explored latency with respect to rheotrophism and potential cover.

Statistical Analyses

We used Kendall's coefficient of concordance in order to establish an association among measures of a similar context. We also used the Spearman rank correlation (one-tailed) to examine the relationship between rank scores of subjects between measures and used Pearson's correlation coefficient to examine the relationship between actual latency time data. The use of a one-tailed test was justified as we predicted a positive directional correlation between measures of a similar context based on a priori knowledge of literature on this continuum in fish (Wilson et al. 1994; Coleman & Wilson 1998). Our predictions were based on a simple yes/no approach in terms of positive correlations between contexts, therefore a one-tailed approach was appropriate.

Ethical Note

The University of Guelph Animal Care Committee approved the study. The experiment was designed such that all interactions between trout and salmon occurred entirely on a volitional basis. The larger salmon could not penetrate the mesh barrier; however the smaller trout had no problem in doing so. Similarly, both salmon and trout were equally naïve at the onset of the experiment. Because of the feeder proximity to the net, our feeding regime with the salmon, and the subject's naivety, any risk of predation to our subjects was minimal. Trout were donated to another project at the completion of the study.

Results

We observed positive relationships for individual rank performance (Fig. 1) and for latencies (Fig. 2) among measures 1–4. The boldest fish (represented by the open circle in Figs 1 and 2) was invariably the boldest in measures 1–4 and the shyest fish (represented by the open square) was invariably the shyest in measures 1–4. There was an exact positive correlation between the two novel object measures (Fig. 1a) (measures 1 and 2), as well as between the two predation risk measures (Fig. 3) (measures 3 and 4) (Spearman rank correlation: $r_s = 1.0$, $p < 0.001$, one-tailed). Upon introduction of the context of predation risk, we observed a small change in rank (Fig. 1b,c). This change reflected two intermediate fish switching rank position during predation trials. However, a significant positive correlation still remained between rank orders (Spearman rank correlation: $r_s = 0.90$, $p < 0.037$, one-tailed).

This positive correlation was not observed for measure 5 when foraging behaviour was replaced by barrier passage as an entirely new context (Fig. 4) (Spearman rank correlation: $r_s = 0.00$, $p > 0.5$ with measures 1 and 2; $r_s = -0.22$, $p > 0.5$ with measures 3 and 4, one-tailed).
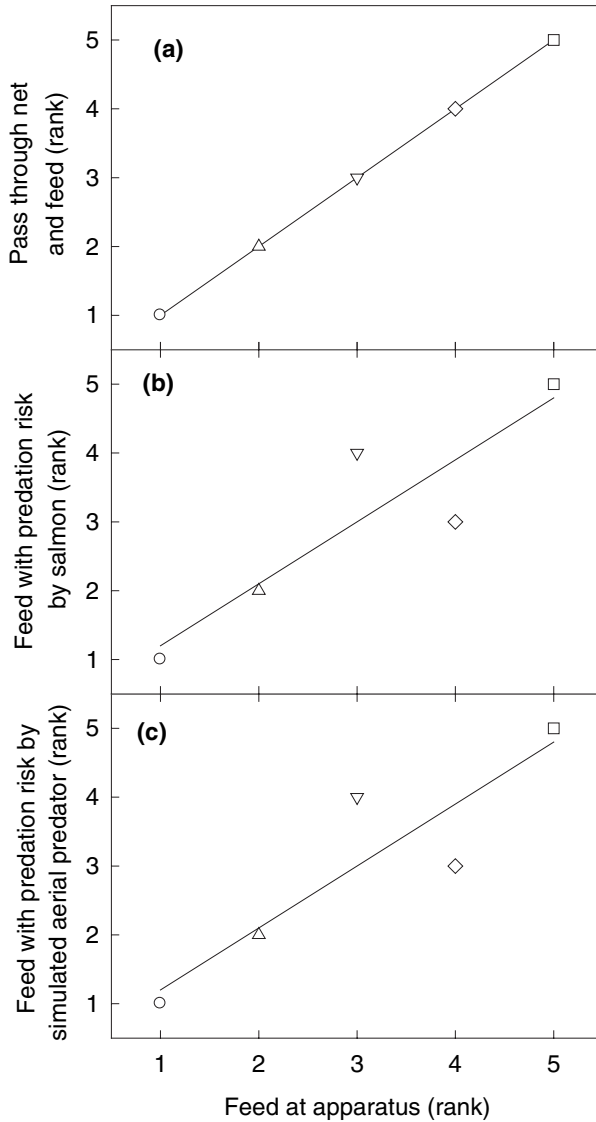
Fig. 1: Rank of latency to first success at: (a) passing through a net and feeding (measure 2), (b) passing through a net and feeding in presence of predation risk by a salmon (measure 3), and (c) crossing and feeding in presence of simulated aerial predator (measure 4) vs. rank performance of first feeding at the feeding apparatus (measure 1). In each case, latency to feed was explored in combination with other novel measures. The lines are least square fitted regressions. Fish are represented individually by separate symbols and can be followed through panels a, b, and c; open circle is boldest fish, open square is shyest fish
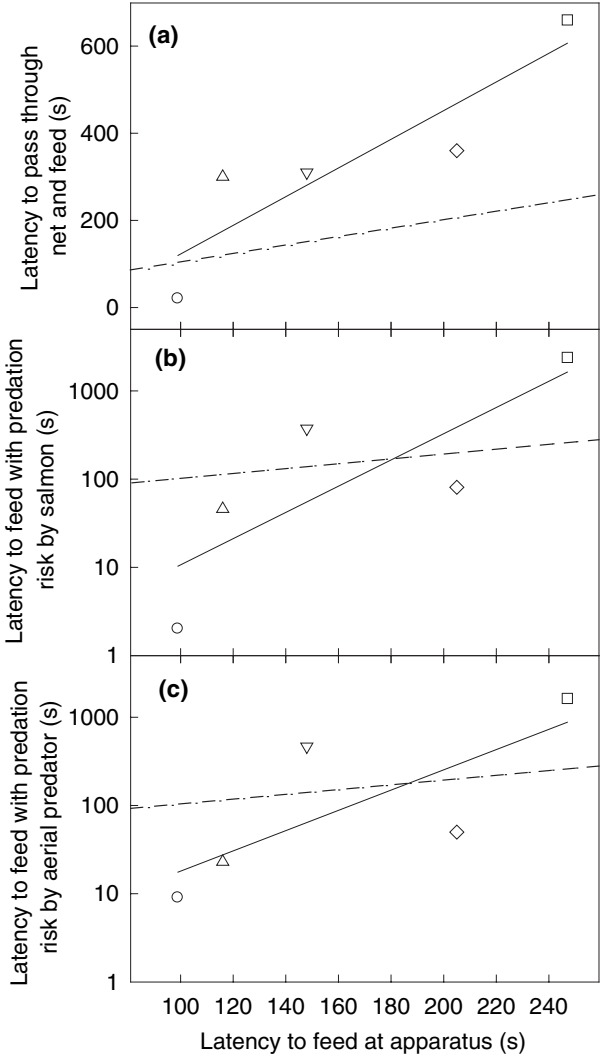
Fig. 2: Latency to first success at: (a) passing through a net and feeding (measure 2), (b) passing through a net and feeding in presence of predator (measure 3), and (c) crossing and feeding in presence of simulated aerial predator (measure 4) vs. latency of first feeding at the feeding apparatus (measure 1). In each case, latency to feed was explored in combination with other novel measures. The solid lines are least square fitted regressions. The dashed lines are unity lines; points below the line indicate decreased latency relative to the first measure, whereas points above the line indicate increased latency. It was necessary to place the times for measures 3 and 4 (b and c) on a log scale because the addition of the predation risk greatly increased latency to first crossing in some individuals. Fish are represented individually by separate symbols and can be followed through panels a, b, and c; open circle is boldest fish, open square is shyest fish
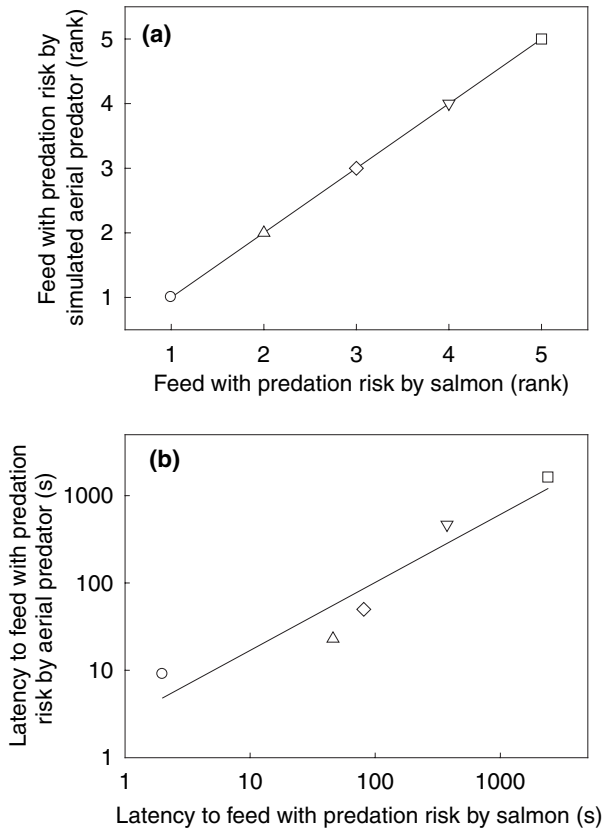
Fig. 3: Performance with potential predation risk. (a) Rank of latency to crossing and feeding in presence of predation risk by a salmon (measure 3) vs. rank of latency to crossing and feeding in presence of predation risk by simulated aerial predator (measure 4). (b) Latency in seconds to crossing and feeding in presence of predation risk by a salmon (measure 3) vs. rank of latency to crossing and feeding in presence of predation risk by simulated aerial predator (measure 4) (Pearson correlation coefficient = 0.991). In both measures, latency to feed was explored in combination with simulated/ actual predation risk. The line is a least squares fitted regression. Fish are represented individually by separate symbols and can be followed through panels a and b; open circle is boldest fish, open square is shyest fish

A strong positive association was observed for individual rank performance for measures 1–4 (Kendall's coefficient of concordance: $\chi^2 = 15.2$, $p < 0.005$). Any other combination of four measures (i.e. any combination that included measure 5) was not significant (Kendall's coefficient of concordance: $\chi^2 = 8.8$ or 9.2 depending on the combination, $p > 0.05$).

All possible combinations of the raw performance data of actual latency times for contexts involving foraging (i.e. measures 1–4) had Pearson correlation coefficients ranging from 0.758 to 0.991 and were significant ($p < 0.05$). However, all correlations involving performance in the flume (measure 5) had
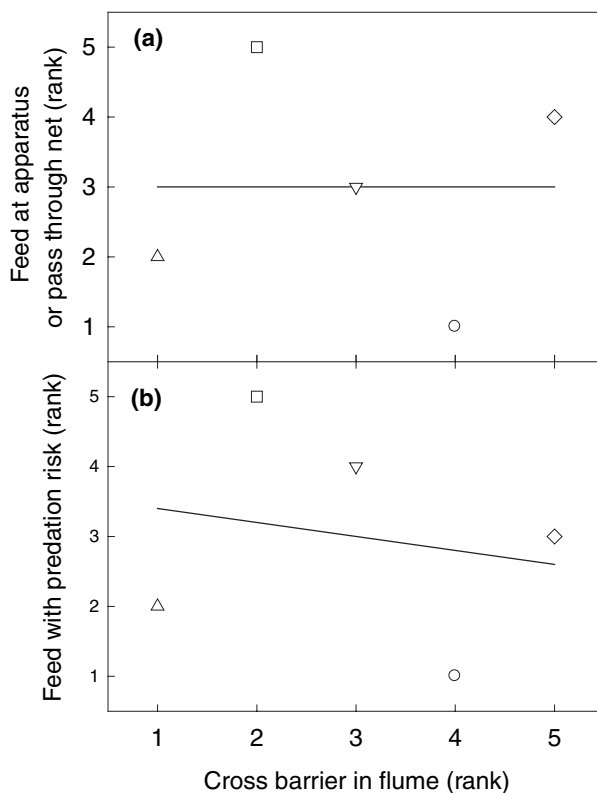
Fig. 4: Rank of (a) latency to feed at the apparatus (measure 1) or latency to pass through the net and feed at the apparatus (measure 2), and (b) latency to feed in presence of a potential predation risk by a salmon (measure 3) or latency to feed in presence of a potential predation risk by a simulated aerial predator (measure 4) vs. rank of latency to cross a barrier in a simulated stream (measure 5). The rank order in the novel measure (crossing the barrier in the simulated stream) was not correlated to the rank order in any of the other measures of boldness. The lines are least squares fitted regressions. Fish are represented individually by separate symbols and can be followed through panels a and b

Pearson correlation coefficients ranging from 0.022 to 0.360 and were not significant ($p > 0.1$).

The rank order was repeatable and remained consistent when fish were tested on subsequent days in the same context (Fig. 5); the boldest remained the boldest, and the shyest fish remained the shyest. The latency tended to decrease in subsequent trials but the rank order tended to remain the same.

Discussion

A behavioural syndrome can be defined as a suite of correlated behaviours that reflect between-individual consistency in behaviour across two or more contexts (Sih et al. 2004). We documented between- and within-individual
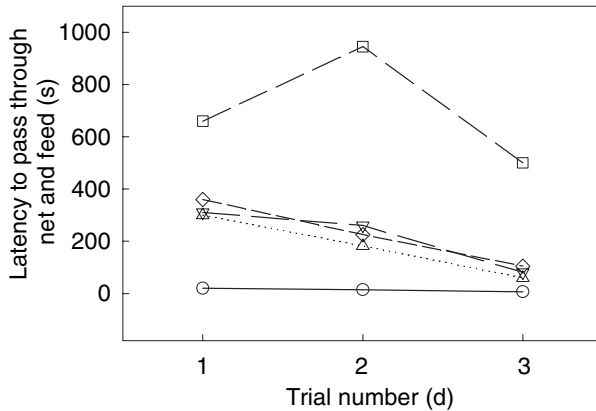
Fig. 5: Repeatability of trials using the same measure – latency to pass through a net and feed (measure 2) for trials on three consecutive days. Test order was random and was different for the three trials. The fish with the shortest latency remained the shortest; the fish with the longest latency remained the longest. Lines join points for individual fish; open circle is boldest fish, open square is shyest fish

consistency in behaviour across multiple novel contexts. Between-individual consistency was demonstrated through rank order performance among the first four novel measures. This positive correlation among measures of feeding, novel object, and predation risk can be interpreted as evidence for a shy–bold behavioural syndrome in rainbow trout.

In terms of shyness and boldness, behavioural syndromes are particularly relevant as subjects may demonstrate 'boldness' in contexts that would be seemingly ill advised (Riechert & Hedrick 1990, 1993). In our experiment this contextual 'difficulty' may be seen in subjects demonstrating decreased latency (boldness) in measures of novel object/food sources, as well as in measures of predation risk. While novel food and object exploration may convey a certain advantage for 'bolder' fish that are able to utilize novel resources, boldness in terms of predation risk potentially can have the opposite effect. In terms of predation risk a 'bolder', more exploratory fish may possess a greater chance of being preyed upon compared with a 'shy' counterpart that remains quiet and hidden until the danger has passed. However, from an evolutionary perspective, increased predation risk for bolder fish may not be overtly costly. When examining female mate choice in the guppy, *Poecilia reticulata*, Godin & Dugatkin (1996) found that females preferred bolder males, suggesting that bold males may seem more viable and may therefore offer indirect fitness benefits in terms of producing more viable offspring. Similarly, Fraser et al. (2001) documented that bold killifish, *Rivulus hartii*, disperse further, grow faster, and have greater overall fitness compared with their shy counterparts in predator threatened regions.

In addition to fitness considerations, boldness in view of predators may also have proximate advantages. Dugatkin & Alfieri (2003) documented that bold

guppies, demonstrated a positive relationship between predator inspection and increased performance in associative learning tasks. It has also been suggested that being shy or bold is instead interchangeably favoured in a population depending on environmental factors such as resource abundance (Dall 2004). Thus, an animal's tendency to demonstrate either shyness or boldness may have significant implications for understanding the evolution of behavioural variation among individuals.

Our experiment demonstrates limited behavioural plasticity in measures involving foraging, regardless of other introduced contexts such as novel objects or actual/simulated predation risk. This constancy in the correlation between different contextual measures is termed behavioural 'carryover', and is rarely studied (Sih et al. 2003). The concept of behavioural carryover and its implications across contexts is critical to understanding the evolution of behavioural syndromes, as it implies that these traits may evolve not as separate characteristics, but as a combined 'package' (Price & Langen 1992; Sih et al. 2004). Similarly, the notion of why some individuals do well in certain contexts and not others may have an important role in explaining the maintenance of individual variation in a population over time (Sih et al. 2004); a critical factor in speciation (Bolnick et al. 2003). The suggested processes responsible for maintaining individual variation differ among studies but might include fluctuating selection pressures due to environmental variability (Dingemanse et al. 2004), frequency-dependent selection (Wilson et al. 1994), and sexual selection through mate preference (Godin & Dugatkin 1996). Thus, understanding how performance between contexts is correlated is critical to studying both the evolution as well as the behavioural ecology of animals as each animal experiences a myriad of contexts during their lifetime that influence their overall fitness.

Our fifth measure did not demonstrate the same trend as that seen between our first four measures. There are two possible explanations for this lack of correlation. The first possibility is that the proposed 'shy–bold behavioural syndrome' may encompass a suite of positive correlations among behaviours (measures 1–4) that carryover across some but not all situations. The second possibility is that these behavioural differences may be attributable to context-specific differences. Our first four measures demonstrated that 'bold' individuals (subjects with shorter latencies) tended to remain bold over several novel contexts; it is important to note that these measures shared foraging as an underlying component of each novel test. Thus, while it is possible to demonstrate carryover between measures 1–4 with shy (longer latency periods) and bold (shorter latency periods) fish, it may not occur with measure 5. It can only be said that this positive correlation exists for measures involving novel objects, feeding behaviour and predation risk. Fish that were previously bold in terms of novel objects and predation risk were not in an entirely new environment. Thus boldness in terms of foraging (measures 1–4) and novel environment (measure 5) measures may be context-specific. In this sense our results tend to support the context-specific temperament hypothesis (Wilson et al. 1994; Coleman & Wilson 1998). In addition, our fish that demonstrated the longest latency (shyest fish) also fit the

behavioural definition of a 'shy' fish described by Wilson et al. (1993). Shy fish characteristically responded to unfamiliar situations by retreating or becoming quiet and vigilant during experimental measures. In contrast, subjects that demonstrated the shortest latency between measures (boldest fish) either acted normally (similar activity level to that seen prior to introduction of novel stimulus) or became actively exploratory in the same context.

While there was a positive correlation for each of the first four measures, there was also a significant increase in latency in two fish when exposed to measures 3 and 4. This increase in latency necessitated the log transformation latency (Fig. 2b,c). Because this change in rank was present for both fish and both predation measures, it may be a further indication of context-specific differences within the shy–bold behavioural syndrome.

The concept of behavioural syndromes advocates a holistic approach that considers the many contexts and situations an animal encounters over its lifetime that affect its overall fitness (Sih et al. 2004). Our data provide compelling evidence of a shy–bold behavioural syndrome in rainbow trout. We demonstrated consistent positive correlations in both between- and within-individual variation in novel objects, predation risk and foraging contexts. Our results also suggest that the shy–bold syndrome may be context-specific and that further work should be performed to understand how these suites of correlated/uncorrelated behaviours evolve and are maintained in natural populations.

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