

# Unpredictability in food supply during early life influences boldness in fish

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Behavioral variation has been documented both between and within populations in a variety of traits. Many of these behavioral traits are phenotypically plastic and are conditional on the early environment an animal experiences, yet despite this the role of the environment in generating variation in boldness is not well understood. Here we investigate the importance of early and recent experience of temporal unpredictability in food supply on the behavior of a species of freshwater fish, the Trinidadian guppy *Poecilia reticulata*. We predict that individuals that experience temporally unpredictable food supplies will engage in more risky behavior than those experiencing a predictable food supply and find evidence to support this. Fish with early experience of unpredictable environments are generally bolder and more exploratory than fish reared in predictable environments, exploring a significantly greater proportion of a novel maze and spending less time in a refuge during the trial. Individuals with early experience of unpredictability also spent significantly less time associating with conspecifics in a shoaling tendency assay, again suggesting that they are bolder than guppies reared in predictable conditions. These findings suggest that early experience is important in shaping exploratory and shoaling behavior in this species and that unpredictability in early life can influence boldness in guppies. *Key words:* boldness, exploration, phenotypic plasticity, shoaling, unpredictable environment. [*Behav Ecol* 21:501–506 (2010)]

Intraspecific behavioral variation has been widely documented in the animal kingdom. Between-population differences in behavior are usually driven by spatial variation in environmental conditions (e.g., predation risk: Magurran 2005; food density: Dunbrack et al. 1995). Red-legged frog *Rana aurora* tadpoles from populations sympatric to predaceous bullfrogs *R. catesbeiana* display enhanced antipredator responses in comparison to individuals from low-predation populations (Kiesecker and Blaustein 1997). A study of the visual display behavior of sagebrush lizards *Sceloporus graciosus* found that communicative behavior differed between 3 populations of this species (Martins et al. 1997). Many examples of within-population variation between individuals can also be found in the literature, such as in competitive behavior over mates (Taborsky 2001) or food (Robinson and Wilson 1994). Explaining this variation remains a contemporary challenge in behavioral ecology.

One axis of individual variation that has received a great deal of attention in the past decade is the bold–shy axis. This behavioral range has been identified in a diverse variety of animal groups including mammals (Reale et al. 2000; Marchant-Forde 2002), birds (van Oers et al. 2004), fish (Ward et al. 2004), crustaceans (Rochette et al. 2001), and arachnids (Johnson and Sih 2005). Bold individuals are those willing to engage in behaviors that involve some degree of risk to attain a potential foraging or mating benefit, whereas shy individuals will attempt to avoid risky behavior. Bold individuals have been characterized as being relatively more exploratory (Drent et al. 2002), having a greater disposition to inspect predators (Godin and Clark 1997), interact with novel objects

(Frost et al. 2007), and recover after a fright stimulus (van Oers et al. 2004) than shy individuals. Conversely, shy individuals are relatively less exploratory, avoid interaction with predators and novel objects, and spend more time in a refuge than bold individuals. Variation in boldness is known to occur at the population level (Brown and Braithwaite 2004) and has also been documented within populations (Ward et al. 2004).

The question of how behavioral variation is generated has long been a focus of ecologists. Between-population variation can be explained in evolutionary terms, with natural selection acting to shape the behavior of individuals from populations experiencing different ecological pressures. The mean degree of individual boldness differs between populations of the field cricket *Gryllus integer* (Kortet et al. 2007) and the tropical poeciliid *Brachyraphis eciscopi* (Brown and Braithwaite 2004) that differ in predation risk. Furthermore, bold–shy behavior has a heritable component in some species, suggesting that it can be directly under selection (van Oers et al. 2004; Wright et al. 2006; Brown et al. 2007). A second mechanism—experience within an individual's lifetime (phenotypic plasticity)—has also been shown to play a role in the generation of phenotypic diversity (Pigliucci 2001). Experience can have a profound influence in shaping animal behavior (Stamps 2003; Chapman, Morrell, et al. 2008; Chapman, Ward, Krause 2008), and indeed, the role of development has received fresh attention in recent years from many animal behaviorists. Despite this revival of interest, our understanding of the experiential factors that shape boldness is poor, and with a few notable exceptions (e.g., Magnhagen and Staffan 2005; Frost et al. 2007), empirical studies investigating the environmental conditions that drive boldness are lacking. To improve theoretical predictions about the ecological and evolutionary consequences of individual variation within populations, it is essential to assess how dynamic these behavioral traits are and over what time scales environments must be experienced to impact on animal behavior (Dall et al. 2004; Neff and

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Received 16 May 2009; revised 10 November 2009; accepted 20 December 2009.

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Sherman 2004; Sih et al. 2004). Here we investigate the role of temporal predictability in food supply during early life and developmental timing in the expression of boldness in a model species of behavioral ecology, the Trinidadian guppy.

There are a number of ways in which one might predict experience of unpredictability would affect boldness. In resource acquisition, it may pay individuals facing an unpredictable food supply to focus on the short-term imperative of feeding by taking risks to acquire food when it is available. When individuals have a predictable food supply, the perceived benefits of engaging in risky behavior to obtain food may be lower than those facing an unpredictable food supply (as they have learned that food is predictably available). However, risky behavior is equally costly in both scenarios (e.g., via an increased chance of predation: Godin and Smith 1988). Delayed foraging impacts on an individual's nutritional state (van der Veen and Sivas 2000) and increases the probability of starvation (Sih 1997). Food-deprived (and potentially hungry) animals are likely to be more willing to take risks as the costs of hiding, and benefits of taking risks increase with increasing food deprivation (Damsgard and Dill 1998). Hence experience of a predictable environment with a guaranteed food resource and little experience of food deprivation may drive the development of less bold, more risk-averse individuals. Conversely, experience of unpredictability and food deprivation may drive the development of individuals that behave in a more risky manner when hunger levels are controlled for. This notion is supported by work on juvenile cod *Gadus morhua* carried out by Braithwaite and Salvanes (2005). They found that individuals reared with an unpredictable food supply left a refuge significantly faster in a novel environment than those reared with a predictable food supply. However, it is not clear whether unpredictability influences boldness across a broad range of contexts or whether associated behaviors such as social behavior and exploratory behavior are also affected.

Here we investigate the importance of experience of a temporally unpredictable and predictable food supply on the risk-taking behavior of the guppy, *Poecilia reticulata*. We assess the impact of the environment on boldness across a variety of contexts and also on related behaviors such as shoaling tendency and exploratory behavior. Finally, we also explicitly test the importance of early developmental environment versus recent experience in this system, assessing the importance of timing in behavioral plasticity.

## MATERIALS AND METHODS

### Rearing environment

All the fish used in this experiment were descended from wild-type guppies from the Tacarigua river in Trinidad (Trinidad national grid reference: PS 787 804; coordinates: 10°40.736'N, 61°19.168'W), a high-predation site. Guppies were collected in 2005; hence, experimental fish had been in captivity for 9–12 generations. Stockfish were reared at the University of Leeds in a 100 × 100 × 25-cm tank with gravel substrate and clumps of moss to provide refuge for fry. Controlled temperature (28 °C) and lighting conditions were maintained (18 W overhead fluorescent strips set on a 12:12 h light:dark cycle). Water depth was kept constant at 13 cm. All fish were fed daily ad libitum with dried flake food.

We haphazardly assigned neonate fry of  $\leq 10$  mm ( $N = 144$ , mean  $\pm$  standard deviation [SD] =  $7.6 \pm 0.12$  mm) to 1 of 4 rearing treatments in a 2 × 2 experimental design: food availability was predictable or unpredictable at 2 different time scales, early and recent. As neonate fry were captured from a large stock population before assigning them to treatment, fry were unlikely to be from the same brood, ruling out the

influence of any maternal effects. Altogether fish were reared under these experimental feeding conditions for a period of 56 days before behavioral trials began. All tanks were given an equal amount of food each day (a single 5-mm<sup>2</sup> spatula of food once in the 2-h period: see below for details); to induce unpredictability, we varied the time fish were fed. We divided the day into four 2-h time slots: from 9 to 11 AM, 11 AM to 1 PM, 1 to 3 PM, and 3 to 5 PM. Fish in the predictable treatment were always fed in the 9–11 AM slot. Fish in the unpredictable treatment were designated daily feeding slots by generating a pseudorandom sequence of a number from 1 to 4 using Matlab (with 1 representing the first slot, 2 the second slot, and so on) for each day over the 56-day rearing period. To investigate the importance of early experience, we reared fish under their assigned feeding regime from birth to 49 days old. To investigate the impact of recent experience, we assigned fish a feeding regime from 50 to 56 days old (the final week prior to the beginning of behavioral trials). Hence we had 4 feeding treatments: fish that were always fed to an unpredictable schedule (for 56 days), fish that experienced an unpredictable early feeding regime (first 49 days) and a predictable recent regime (final 7 days), fish that were always fed to a predictable schedule, and finally fish that experienced a predictable early feeding regime and an unpredictable recent regime.

Fish were reared in small tanks (15 × 15 × 25 cm) at a density of 4 individuals per tank. Mortality during the rearing period was very low (5.9%). To ensure all fish that were behaviorally assayed experienced comparable conditions, individuals that died were not replaced. Each tank contained a gravel substrate and a filter to continuously aerate the water, had opaque sides to isolate visual contact from other fish, and minimize any impact of external disturbance. Water depth was maintained at 12 cm by checking water levels daily and renewing from an aerated source tank when necessary. Fish experienced a light:dark cycle of 12:12 h at a temperature of 24–26 °C. For the first 4 weeks, juveniles were fed daily on ZM200 fry food (one 5-mm<sup>2</sup> spatula/day). In weeks 5 and 6, fry were fed on crushed up flake food (Aquarian brand), again 1 spatula a day per tank. In the final 2 weeks of rearing (7 and 8), fish were fed 2 spatulas of flake food per tank per day. We reared 9 replicate tanks per treatment.

### Behavioral trials

To assess an individual's behavioral phenotype, we ran 3 different trials on the same individual: a novel maze task to measure exploratory tendency (day 57), a shoaling tendency trial (day 59) and a fright stimulus trial (day 61) in which we looked at responses to a simulated predator threat as a measure of boldness. In all trials, aerated water was used. We tested 2 individuals per tank for each of the 9 replicate tanks of the 4 treatments, controlling for pseudoreplication in the analysis using mixed-effects models (see Statistical Analysis). In between trials, we kept focal individuals isolated in a perforated, transparent 250-ml bottle within their rearing tank (following Chapman, Ward, Krause 2008). In all trials, all fish (focal and stimulus where appropriate) were fed 1 h prior to the trial to standardize motivation. This also controlled for differences in expectation between treatments. Trials took place between 9 AM and 5 PM.

#### Maze trial

To investigate individual exploratory tendency, we constructed a simple maze task (Figure 1) in a tank of dimensions 34.5 × 53.5 × 15 cm, with a water depth of 8 cm and a sand substrate. Fish were fed 1 h before the trial to standardize motivation. They began the trial in a refuge box constructed of white

plastic (dimensions  $25 \times 12 \times 10$  cm) with a door leading into the maze attached to a pulley system which meant that it could be remotely removed by an observer. Trials were illuminated by 2 lamps and filmed using a Sony handycam DCR-HC37. Initially, a focal guppy was placed in the refuge box and the lid attached to provide shade. Fish were allowed 2 min to acclimatize before the door was remotely removed. The time taken to leave the refuge was recorded and the trials lasted 5 min after the fish had first left its refuge box. We also recorded the proportion of time fish spent in the refuge during the trial. By dividing the 4 main corridors of the maze each into equal sized quarters, the maze was divided into 16 zones. Using these, we measured how many zones each fish ventured into the maze (with 16 representing a fish reaching the end of the maze) as an index of individual exploratory tendency. We converted this into proportion data for statistical analysis. After this, the focal fish was placed in a coded bottle and replaced to its rearing tank. Water was changed after each trial.

#### Shoaling tendency trial

In this trial, we used a classic dichotomous shoal choice design to assess individual shoaling tendency. The dimensions of the test tank was  $59 \times 21 \times 18$  cm with a water depth of 12 cm, and it was divided into 3 compartments with transparent glass walls. The central compartment (length = 29 cm) was flanked by 2 separate choice chambers (length = 15 cm) in which we could place a stimulus shoal versus an empty control. A 6-cm association zone was marked on the base of the tank contiguous to both choice compartments. This zone was approximately 4 body lengths wide, corresponding to interindividual distances documented by shoaling fish in the wild (Pitcher and Parrish 1993).

We then placed 3 naive stimulus females (sourced from a separate stock tank and therefore unfamiliar to the focal fish) in 1 of the 2 choice compartments and the focal guppy in the central compartment. After a 5-min acclimatization period, the 5-min trial began. We recorded the time spent in the association zone next to the compartment containing the stimulus fish as an index of shoaling tendency and from this calculated the proportion of time spent shoaling during the trial. After the trial, we replaced the focal fish in the holding container in its rearing tank and measured the stimulus fish. The location of the stimulus fish was alternated between each replicate. Within each replicate, one focal fish from each of the 4 treat-

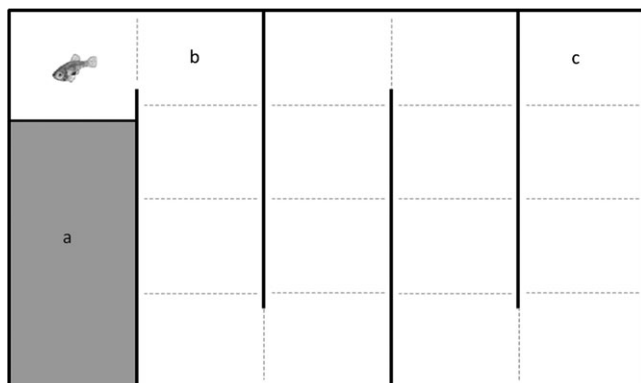
ments experienced the same stimulus shoal. The order between replicates was alternated systematically to control for any changes in the stimulus shoal behavior over time. Stimulus fish were only ever used once per day but were reused over the course of the trials.

#### Fright stimulus trial

We set up a fright stimulus trial by placing a tank beneath the path of a model aerial predator (Figure 2). The test tank was  $15 \times 15 \times 25$  cm with a water depth of 9 cm and had opaque back and sides but a transparent front to allow for filming to take place. The model predator was a simple piece of thick black card ( $10 \times 15$  cm), which had a tube attached to the topside of the card. Through the tube, a monofilament wire, was pulled taut at a  $20^\circ$  angle above the tank, which was lit from above by a single lamp. At the beginning of the trial, the model predator was attached to the frame holding the wire at the highest point. The focal fish was placed in the test tank and allowed 2 min to acclimatize. After this, we removed the clip holding the model predator in place and the model moved at speed down the wire over the tank, passing in front of the spotlight and so mimicking the movement of an avian predator passing overhead. Pilot trials indicated that this elicited a strong antipredator response in guppies: individuals responded by first dashing and then freezing on the bottom of the tank. We measured the time individuals took to return to movement (defined as once an individual was over one body length away from the initial freezing position). Finally, we measured the focal fish, recorded their sex, and returned them to a postexperiment stock tank.

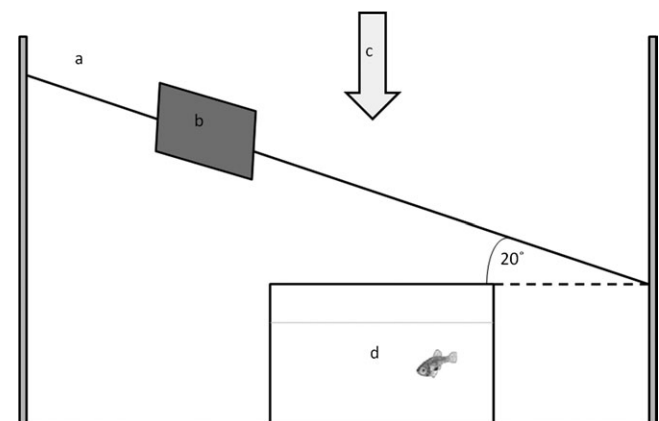
#### Statistical analysis

All data were analyzed using R 2.7.0. We used linear mixed-effects models (LMEs) to statistically assess the importance of rearing conditions on measures of boldness, exploratory tendency, and shoaling tendency. Our rearing conditions are “early experience” and “recent experience,” each of which contains 2 categories (predictable or unpredictable food supply). All these analyses included early and recent environment as main effects and all interaction terms and tank ID as a random effect in this repeated measures analysis to overcome pseudoreplication. We included all main effects and interaction terms in the initial model, which was then simplified by sequentially removing all nonsignificant terms to achieve the



**Figure 1**

The novel maze task. The refuge is in gray (a) and the 4 quadrants within each of the 4 arms of the maze are denoted by dashed lines. Hence if an individual reaches point (b), it will be scored as exploring 1/16th of the maze (i.e., exploratory tendency = 0.0625). If an individual reaches point (c) during the trial, it will be scored as exploring 16/16th of the maze (i.e., exploratory tendency = 1).



**Figure 2**

Simulated predator trial setup. The focal fish is placed into a tank (d) beneath a light source (c) and a monofilament line (a), angled at  $20^\circ$  above the tank. A model predator (b) is released and passes over the tank eliciting a fright response from the focal fish.

minimal adequate model. Throughout the results section, we only report significant interaction effects. Data required transformation to satisfy parametric assumptions: the time to initially leave the refuge in the maze trial was log-transformed, as was the response latency in the fright stimulus trial. All proportion data were arcsine square root transformed (maze trial: proportion of time spent in the refuge during the trial and proportion of maze explored; shoaling tendency trial: the proportion of time spent shoaling) prior to statistical analysis. One data point was lost from the maze trial due to a camera malfunction. To assess individual consistency in behavior, we tested for bivariate correlations using Pearson's product-moment correlation analysis, correcting for multiple testing using the Bonferroni correction. We used generalized linear models (GLMs) to investigate the effects of early and recent environments on tank mortality rate and mean (within tank) growth rates as only one data point per tank was analyzed here. These statistical models were fitted with Gaussian and quasipoisson error distributions, respectively.

## RESULTS

### Mortality and growth rate

Mortality was very low over the rearing period (8 of 136 individuals: 5.9%) and was not related to early or recent environment (GLM: early environment  $P > 0.05$ ; recent environment  $P > 0.05$ ). Similarly, we found no significant effect of early or recent experience on mean growth rates (GLM: early environment  $P > 0.05$ ; recent environment  $P > 0.05$ ).

### Sex ratio and focal fish body length

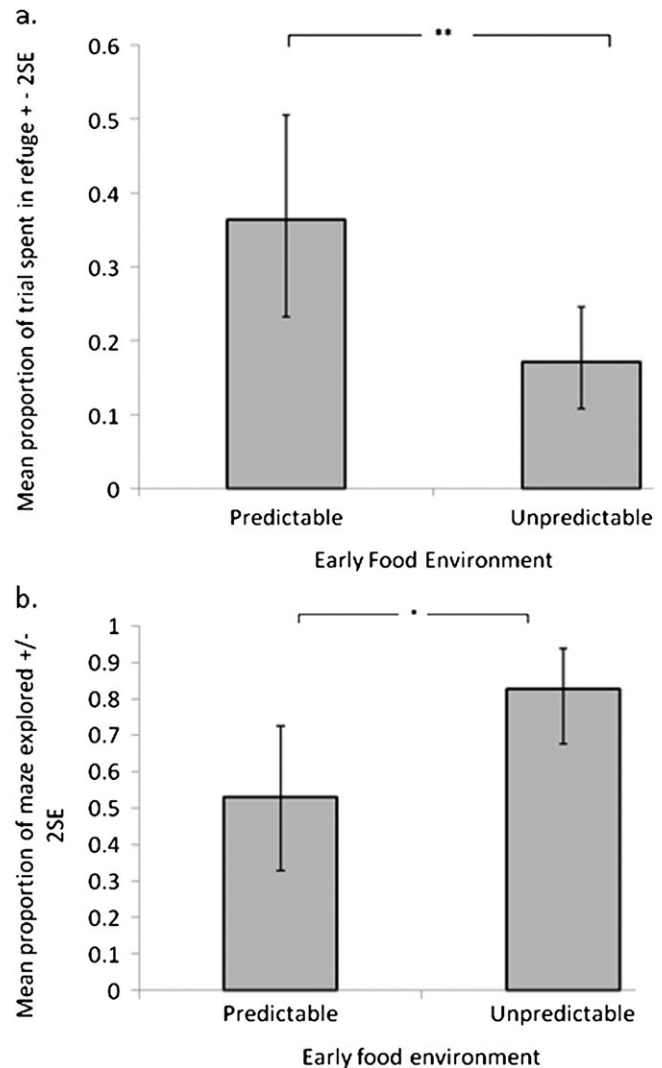
The overall sex ratio of focal fish was 22 males and 45 females. We found no difference in sex ratio between early experience treatments ( $\chi^2 = 0.38$ , degrees of freedom [df] = 1,  $P > 0.05$ ) or between recent experience treatments ( $\chi^2 = 0.36$ , df = 1,  $P > 0.05$ ). Similarly, there was no effect of early or recent experience on focal fish body length (LME: early experience  $F_{1,64} = 0.65$ ,  $P > 0.05$ ; recent experience  $F_{1,64} = 0.6$ ,  $P > 0.05$ ; mean  $\pm$  SD =  $14.1 \pm 1.88$  cm). Therefore, in the following analyses, we excluded sex and body length.

### Maze trial

We found no effect of either early or recent experience on the time taken to initially leave the refuge (LME: early experience  $F_{1,31} = 0.85$ ,  $P > 0.05$ ; recent experience  $F_{1,31} = 0.48$ ,  $P > 0.05$ ). However, fish with early experience of a predictable environment spent a significantly greater proportion of the trial within the refuge than fish with early experience of an unpredictable environment (LME:  $F_{1,31} = 8.02$ ,  $P < 0.01$ ; Figure 3a). Recent environment had no significant impact on refuge use during the trial (LME:  $F_{1,31} = 0.42$ ,  $P > 0.05$ ). Fish reared in unpredictable early environments explored a significantly greater proportion of the maze during the trial than those reared in predictable early environments (LME:  $F_{1,31} = 4.29$ ,  $P < 0.05$ ; Figure 3b). Recent experience had no effect on the proportion of maze explored (LME:  $F_{1,31} = 0.008$ ,  $P > 0.05$ ). No significant interaction effects were evident in these analyses ( $P > 0.05$ ), and they were removed from the models during simplification.

### Shoaling tendency

Fish reared with early experience of unpredictable environments spent a lower proportion of time shoaling with a stimulus shoal than fish reared with early experience of predictable environments (LME:  $F_{1,31} = 6.67$ ,  $P < 0.05$ ; Figure 4). Recent



**Figure 3**

(a) Mean proportion of time spent in the refuge during the trial (showing 2 standard errors [SEs]). (b) Mean proportion of experimental maze explored during the trial (showing 2 SEs). Note that the data in Figures 3a, b were arcsine square root transformed for analysis: these figures show back transformed means and 95% confidence intervals (\*\* indicates  $P < 0.05$ ; \*\*\* indicates  $P < 0.01$ ).

experience did not affect an individual's shoaling tendency ( $F_{1,31} = 2.15$ ,  $P > 0.05$ ). No significant interaction effects were evident in this analysis ( $P > 0.05$ ), and they were removed from the model during simplification.

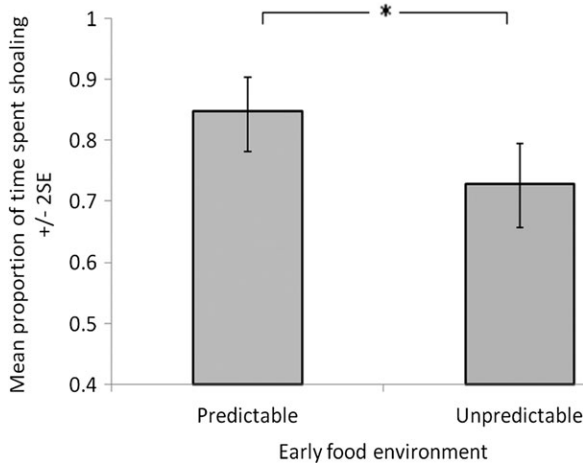
### Fright stimulus trial

Neither early experience nor recent experience of predictable or unpredictable environments had an impact on the response latency to a model aerial predator (LME: Early experience  $F_{1,31} = 0.04$ ,  $P > 0.05$ ; Recent experience  $F_{1,31} = 0.73$ ,  $P > 0.05$ ). Again, no significant interaction effects were evident in this analysis ( $P > 0.05$ ), and they were removed from the model during simplification.

### Behavioral correlations

We found no evidence for any behavioral correlations between trials ( $P > 0.05$ ).





**Figure 4**  
Mean proportion of time spent shoaling with stimulus shoal (showing 2 standard errors). Note that the data were arcsin square root transformed for analysis; this figure shows back transformed means and 95% confidence intervals ("\*" indicates  $P < 0.05$ ).

## DISCUSSION

Our experimental results show that environmental stochasticity is a powerful force shaping behavior in fish. Our principal finding was that individuals experiencing unpredictable environments during early ontogeny exhibited generally more risky (i.e., bolder) behavior. They explored a greater proportion of a novel "maze" task, spent less time beneath a refuge during the maze trial and spent less time shoaling with conspecifics than fish reared under predictable conditions. All these behaviors are likely to involve some degree of risk in the wild. Exploring a novel environment may increase the probability of encountering a predator and spending less time in a refuge may increase the probability of being detected. Many animals (including the guppy) form social groups principally to reduce predation risk through mechanisms such as the dilution effect (Krause and Ruxton 2002). Individuals isolated from the shoal are more at risk of attack: predators in numerous studies have been shown to have a preference to strike isolated individuals, most likely to reduce the confusion effect associated with attacking groups of prey (Milinski 1977; Morgan and Godin 1985; Parrish 1989). Hence spending a greater amount of time away from the safety of the group in order to explore the novel setting of the experimental tank is potentially a risky business and implies individual boldness.

It is likely that the differences in boldness we report between early experience treatments are driven by differences in individuals' experience of the payoffs involved in risky behavior. In predictable environments, where food is available at a set time, it may not pay individuals to take further risks such as exploring novel environments or leaving the shoal. Conversely, individuals reared in unpredictable environments cannot rely on regular food supplies and, hence, may benefit more from taking risks and actively seeking out foraging opportunities. Hence the trade-off between risk and reward is different for fish reared under different conditions. Our data show that early rather than recent experience is important, which suggests a certain degree of inflexibility in responding to conditions when they change later in the animal's life. The importance of early rather than recent experience suggests that animals may be able to adapt to environmental conditions given that the rate of environmental change is not too rapid. Short-term perturbations may not have strong effects on underlying behav-

iors, with individuals maintaining behaviors that fit the "usual," background environment. Persistent variation, however (i.e., a temporally unpredictable food supply), experienced throughout ontogeny effectively "sets" patterns of behavior to allow individuals to respond adaptively to unpredictability in the environment by exhibiting more risky behaviors. Although it is plausible that the development of bold behavior in unpredictable food environments is driven by learning, it could also be attributed to differences in underlying physiology or life history. Our data cannot distinguish between these different hypotheses; future work might concentrate on evaluating the mechanisms driving boldness in animals. In our experiments, early and recent experiences were of different durations (7 weeks and 1 week, respectively). Hence we cannot rule out that differences in boldness and exploratory tendency are attributable to the time fish were exposed to an unpredictable food supply rather than an effect of early experience per se. Further experiments to test these hypotheses would be interesting and valuable, as would trials that quantified the ontogeny of traits such as boldness.

These results also suggest that phenotypic plasticity may at least partially buffer individuals against the increased environmental unpredictability. We show that guppies become bolder and more exploratory in response to an unpredictable environment, which is likely to allow them to maximize food intake under these conditions. Furthermore, an increased exploratory tendency may increase dispersal and allow individuals to colonize new habitats more effectively. Intraspecific comparisons of both great tits *Parus major* and killifish *Rivulus hartii* showed that bolder individuals dispersed further than shyer conspecifics (Dingemanse et al. 2003; Fraser et al. 2001, respectively), supporting this idea. When searching for new feeding areas, bold behavior may be advantageous, but as new habitats may be more risky, exploring should be avoided if an animal can acquire equivalent resources from known or less risky habitats (Abrahams and Dill 1989). This rise in exploratory tendency may also have negative ecological implications, for example, increasing the invasiveness of species. Invasiveness has been linked to dispersal tendency (Lodge 1993; Rehage and Sih 2004), which in turn has been linked to boldness in some species (Fraser et al. 2001; Dingemanse et al. 2003). The putative benefits of boldness in an unpredictable environment we discuss here could be tested empirically using a mesocosm approach, rearing fish in both environments and monitoring patterns of survival and dispersal.

Interestingly, increases in boldness in the early unpredictability treatments were not ubiquitous across context, nor did we find evidence for consistent differences between individuals (Bell 2007). In the simulated aerial predator trials, we found no evidence for any differences in response latency between treatments. This may be due to a number of factors: first, it is possible that our preconceptions of what constitutes general "boldness" are inaccurate or at least lack definition. Exploring a novel environment, leaving a shoal and returning to movement following a predator encounter all involve potential risk, but they are unlikely to involve the same degree of risk. It is plausible that although early experience of unpredictable environments increases an individual's boldness in situations of intermediate or low risk, these differences are lost in situations of high risk (such as an actual or perceived predator encounter). One might then predict that individuals experiencing higher levels of risk during early ontogeny (e.g., experience of being chased by a pseudopredator [Brown et al. 2007]) would respond in a bold way to both high and intermediate risk (e.g., a simulated predator encounter and exploration of novel environments). This hypothesis would be relatively simple to test by varying the type or degree of risk

animals experienced during development and then assaying individuals across a suite of behavioral trials.

In conclusion, we have shown the importance of an animal's early experience in the development of boldness. Individuals that experienced an unpredictable food supply developed more risky behaviors in exploratory tendency, refuge use, and also shoaling behavior. Contrary to some other recent research in this area (Frost et al. 2007), we have also shown that recent experience does not impact on boldness. Although here we have focussed on temporal predictability, in wild populations, animals are likely to experience variance in spatial predictability of food supply and also variance in the size of the food pulse received: future work could investigate the role of these different factors. Finally, it is likely that the differences in behavior we report here are linked to individual differences in underlying physiology and life history. Research into the mechanisms that underpin individual differences in boldness would undoubtedly provide valuable insights for animal behaviorists.

## FUNDING

University of Leeds (B.B.C.); NERC fellowship (NE/D008 921/1) to L.J.M.

Thanks to Jolyon Faria for help feeding the fish.

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