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ORIGINAL PAPER

Personality and the response to predation risk: effects of information quantity and quality

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Abstract Within aquatic ecosystems, chemosensory cues provide valuable public information regarding the form and degree of risk, allowing prey to make informed behavioural decisions. Such cues, however, may vary in both relative concentration detected (i.e. 'quantity') and reliability of the information available (i.e. 'quality'), leading to varying response patterns. Moreover, prey species are also known to exhibit consistent behavioural tactics towards managing risk (i.e. personality), possibly shaping their use of public information. Here, we present two experiments examining the potential interacting effects of personality and the quantity (Experiment 1) or quality (Experiment 2) of public information on the short-term predator avoidance responses of wild-caught Trinidadian guppies under semi-natural conditions. Our first experiment demonstrated that personality shaped responses to a high concentration of alarm cues (high risk), with shyer guppies exhibiting stronger antipredator responses than bolder guppies. When exposed to either low risk or stream water controls, personality had no effect on the intensity of response. Our second experiment demonstrated that personality again shaped the response to high concentrations of alarm cues (a known risk) but not to a novel chemosensory cue (tilapia odour). When exposed to the unknown novel cue, guppies exhibited a relatively high intensity antipredator response, regardless of personality. Combined, our results suggest that individual risk-taking tactics shape the use of public information in a context-dependent fashion.

Keywords Personality · Threat-sensitive trade-offs · Trinidadian guppies · Public information · Predator–prey · Behavioural decisions

Introduction

Prey are often faced with the need to balance the conflicting pressures of early detection and avoidance of predation threats and the need to forage, defend territories and/or reproduce (Lima and Dill 1990; Brown 2003). As a result, prey are forced to make behavioural decisions, leading to threat-sensitive trade-offs (Brown et al. 2006; Helfman and Winkelman 1997) in order to reduce the potential fitness costs associated with these conflicting pressures. The ability to make flexible behavioural decisions is contingent upon the availability of reliable public information regarding local predation threats (McNamara and Dall 2010; Schmidt et al. 2010). Within aquatic ecosystems, chemosensory cues are widely used by vertebrate and invertebrate prey to assess local threats and to adjust response intensities according to perceived threat levels (Brown 2003; Ferrari et al. 2010).

Chemosensory cues are likely to vary both in the quantity (the relative concentration of cues detected) and

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quality (the reliability of the cue detected) of information conveyed to receivers. Initially, the quantity of cues detected can mediate threat-sensitive behavioural trade-offs, resulting in concentration-dependent predator avoidance responses to damage-released chemical alarm cues from conspecific donors (Dupuch et al. 2004; Brown et al. 2006, 2009), non-damage-released disturbance cues (Vavrek and Brown 2009) and learned predator odours (Ferrari et al. 2005). In addition, the quality of information may vary depending on the type of chemosensory cues available. Due to their nature of release following mechanical damage to the skin of fishes (Chivers and Smith 1998; Chivers et al. 2012), chemical alarm cues are highly reliable indicators of risk (Chivers et al. 2012). Likewise, acquired recognition of predator odours may also provide prey with additional reliable indicators of ambient risk (Ferrari et al. 2005; Ferrari and Chivers 2006). Conversely, under conditions of high and variable predation threat, prey may exhibit increased predator avoidance upon detecting novel chemical cues independent of prior experience (i.e. neophobic predator avoidance; Brown et al. 2013). For example, Trinidadian guppies (*Poecilia reticulata*) from high-predation populations exhibit increased predator avoidance towards novel cues under both laboratory and field conditions, while guppies from low-risk populations were indifferent to the same novel cues (Brown et al. 2013). Thus, while damage-released conspecific alarm cues and acquired predator cues are familiar 'known' sources of information sources, the reliability of information associated with neophobic responses ('unknown' cues) is likely lower to receivers (Brown et al. 2013, 2014).

A growing body of research demonstrates that individual prey may show consistent risk-averse versus risk-prone tactics (Réale et al. 2007; Sih et al. 2004) while balancing trade-offs between predator avoidance and other fitness-related activities (Budaev and Brown 2011). Such consistent response patterns generally represent different tactics towards the optimization of behavioural trade-offs mediated by the perceived level of threat (Smith and Blumstein 2008; Budaev and Brown 2011; Mathot et al. 2012). Despite a wealth of studies examining animal personality within and between populations (Sih et al. 2004; Réale et al. 2007; Mathot et al. 2012), surprisingly little is known about the potential interactions between personality and threat-sensitive behavioural trade-offs. Recent studies have shown linkages between environmental uncertainty and individual personality (Chapman et al. 2010a; Mathot et al. 2012). For example, Trinidadian guppies held under conditions of temporally unpredictable foraging opportunities are consistently bolder than those experienced with predictable foraging opportunities (Chapman et al. 2010a). Similarly, the expression of bold (but not shy) phenotypes of rainbow trout (*Oncorhynchus mykiss*) is influenced by food availability and the intensity of perceived predation threats (Thomson et al. 2012). Thus, we might predict that the threat-sensitive behavioural trade-offs of prey individuals should be shaped by individual personality, and that the effects of personality will depend upon both the 'quantity' and 'quality' of public risk assessment information on risk detected by individual receivers.

Here, we evaluate the potential effects of an individual latency to escape task (as a proxy for personality) on the use of public information, using wild-caught Trinidadian guppies tested under semi-natural conditions. In the first experiment, we explore the role of personality on the predator avoidance response of individual female guppies exposed to high or low concentrations of conspecific alarm cues or a stream water control. In the second experiment, we explore the role of personality on the response of guppies to a known risk (high concentration of conspecific alarm cue), an unknown risk (a novel chemosensory cue) or a stream water control.

Methods

Study populations and stimulus collection

Observations were conducted along an approximately 500-m stretch of the Lower Aripo River, Northern Range Mountains, Trinidad and Tobago. The Lower Aripo site is characterized as a 'high-predation' site (Croft et al. 2006; Botham et al. 2008) containing several predators that prey on both juvenile and adult guppies, including the pike cichlid (*Crenicichla alta*), blue acara (*Aequidens pulcher*) and brown coscorub (*Cichlasoma taenia*). In addition, there are several predators that prey on smaller, juvenile guppies, including Hart's rivulus (*Rivulus hartii*) and the two-spot sardine (*Astyanax bimaculatus*).

We collected alarm cues for use in both experiments from non-gravid female guppies, collected using a beach seine (3 m length, 3 mm mesh size) from the Lower Aripo River populations. Alarm cue donors were killed via cervical dislocation (in accordance with Concordia University Animal Research Ethics Protocol #AREC-2011-BROW and AREC-2012-BROW). We immediately removed the head and tail (at the caudal peduncle) and manually extruded any remaining visceral tissue. The remaining tissue (skin and skeletal muscle) was immediately placed into 100 mL of aged tap water. We then homogenized the tissue samples, filtered through polyester floss and diluted to the desired final concentration ($0.1\ \text{cm}^2\ \text{mL}^{-1}$) with the addition of aged tap water. We collected a total of $31.26\ \text{cm}^2$ of skin from 30 donors (mean ± SD standard length = 17.93 ± 2.64 mm) for Experiment 1 and $41.50\ \text{cm}^2$ from 39 donors (19.92 ± 3.29 mm) for

Experiment 2. Guppy alarm cue was frozen in 20 mL aliquots at −20 °C until needed.

For Experiment 2, we collected tilapia (*Oreochromis niloticus*) odour as a novel potential predator cue. Tilapia do not occur in the Lower Aripo River, hence can be considered a 'novel' predator. Twenty-five adult tilapia (approximately 30 cm standard length) were held in a 600-L tank (filled with approximately 300 L of dechlorinated tap water). The tank was aerated but not filtered. Prior to stimulus collection, tilapia were fed commercial pellet food, twice daily. We collected 500 mL of tank water, filtered it through polyester floss and froze the resulting 'tilapia odour' in 20 mL aliquots at −20 °C until needed.

Experiment 1: Risk-taking tactics and the response to the levels of perceived risk

Test arenas consisted of clear Plexiglas boxes (60 cm × 30 cm × 30 cm) bound at the corners with plastic zip-ties in order to allow the exchange of water between the enclosure and the stream. We positioned an isolation chamber (15 cm × 10 cm × 30 cm) constructed of opaque dark-grey Plexiglas near the upstream wall of the test arena. The isolation chamber was equipped with a dark Plexiglas cover (6 cm × 6 cm) and a hinged opening along the bottom edge. We positioned the test arenas in shaded pools, at least 1 m from the shore. Water depth in the enclosures ranged between 15 and 20 cm. Prior to behavioural observations, we collected non-gravid (assessed visually) female guppies from the pool using the seine net described above and placed them into a covered 16-L bucket filled with stream water. Guppies appeared to swim and forage normally in the holding bucket. Capturing guppies prior to testing ensured that we would not be observing individual guppies repeatedly. Females were chosen as the focal animals as they are generally more responsive to predation threats, especially under natural conditions (Magurran 2005; Brown et al. 2009).

Immediately prior to a trial, we placed individual female guppies (mean ± SD standard length = 22.80 ± 2.90 mm) into the isolation chambers, closed the cover and allowed a 5-min acclimation period. Prior to each observation, we provided ample food (freeze-dried tubifex worms, approximately 0.1 g) such that there was abundant food remaining following the trial. Tubifex worms were chosen as a forage items as they are easily visible and facilitated accurate counting of foraging attempts. Following the acclimation period, we raised the hinged door remotely and began the observation. We initially recorded the latency (seconds) for an individual to leave the isolation chamber and used this measure as a proxy for personality type, with latency inversely proportional to boldness (Brown et al. 2005). We recorded a guppy as having left the start box when more than half of its body was outside of the chamber. Latency to emerge has been demonstrated to be a highly reliable and repeatable proxy for personality in tropical poeciliids (Brown et al. 2005, 2007; Harris et al. 2010). Moreover, recent studies with Trinidadian guppies demonstrate that risk-taking tactics are repeatable (Harris et al. 2010; Smith and Blumstein 2010). As such, our measure of 'escape latency' is a robust measure of individual risk-taking tactics.

Pre-stimulus observations began at this point and lasted 5 min, during which we recorded time moving and the frequency of foraging attempts. Immediately following the pre-stimulus observation period, we introduced a high relative concentration of guppy alarm cue (10 mL of stock solution), a low concentration of guppy alarm cue (2.5 mL alarm cue + 7.5 mL stream water) or a 10 mL stream water control. During the 5-min post-stimulus injection observation period, we recorded time moving and foraging as above. We also recorded the latency to resume foraging (time until the first foraging attempt was observed) following stimulus exposure. Following each observation, the focal guppy was released and the observation arena was rinsed with stream water and repositioned. We conducted a total of 30 observations per stimulus and observations were made blind to treatment.

Experiment 2: Risk-taking tactics and the response to 'known' versus 'unknown' cues

Trials were conducted as described above except that following the pre-stimulus observations, we introduced 10 mL of guppy alarm cue (same as high concentration in Experiment 1), tilapia odour (a novel chemosensory cue) or a stream water control. Previously, we have shown that guppies from the Lower Aripo exhibit predator avoidance responses towards tilapia odour under laboratory and field conditions (Brown et al. 2013). We conducted 30 replicates per stimulus. Mean standard length (±SD) of guppies at the time of testing was 22.17 ± 4.61 mm.

Statistical analysis

For time spent moving and frequency of foraging attempts, we calculated the change (post–pre) and used these difference scores as dependent variables. In order to ensure normality, the latencies to escape the isolation chambers and to resume foraging following stimulus exposure were square-root transformed. As our behavioural measures are likely highly autocorrelated, we tested for the effect of stimulus type and personality (latency to escape) on the predator avoidance response using a multivariate GLM. Square-root-transformed latency to escape was included in the analysis as a covariate. All analyses were conducted using SPSS version 21.0.

Results

Experiment 1: Risk-taking tactics and the response to the levels of perceived risk

Latency to escape was not correlated with either baseline (pre-stimulus) foraging ($F_{(1,90)} = 0.63$, $P = 0.43$) or time spent moving ($F_{(1,90)} = 2.77$, $P = 0.10$); hence, we are justified in using the difference scores as dependent variables. Our overall analysis (multivariate GLM) revealed a significant interaction between escape latency and cue type ($F_{(3,86)} = 8.80$, $P < 0.001$). To further investigate this interaction, we compared the response of guppies exposed to stream water and low concentrations of alarm cue and found a significant effect of cue type ($F_{(3,56)} = 28.68$, $P < 0.001$) but no cue by escape latency interaction ($F_{(3,56)} = 1.16$, $P = 0.33$). When exposed to stream water or a low concentration of conspecific alarm cue, we found no effect of personality on the response patterns of guppies (Fig. 1). However, there was a significant effect of personality on the response towards high concentrations of guppy alarm cue. Bolder guppies (i.e. shorter escape times) exhibited weaker responses than did shyer guppies (i.e. longer escape times).

Experiment 2: Risk-taking tactics and the response to ‘known’ versus ‘unknown’ cues

As in Experiment 1, latency to escape was not related to baseline foraging ($F_{(1,88)} = 0.11$, $P = 0.75$) or movement ($F_{(1,88)} = 0.49$, $P = 0.49$). Our overall multivariate GLM revealed a significant cue × escape latency interaction ($F_{(3,84)} = 40.67$, $P < 0.001$). As above, we compared the response of guppies exposed to tilapia odour versus stream water and found a significant effect of cue ($F_{(3,55)} = 31.16$, $P < 0.001$) but not a cue × escape latency interaction ($F_{(3,55)} = 0.38$, $P = 0.77$). The responses of guppies towards the conspecific alarm cue treatment appear to be shaped by individual risk-taking tactics. As in Experiment 1, bolder guppies exhibited only weak response to the high concentration of alarm cues, while shyer guppies showed strong avoidance behaviour (reduced time moving, increased latency to resume foraging and reduced number of foraging attempts; Fig. 2). There was no effect of individual risk-taking tactics on the response of guppies towards the novel predator odour (tilapia); all guppies tested showed a strong avoidance response independent of latency to escape.

Discussion

Combined, these results clearly demonstrate that the expression of individual risk-taking tactics (personality) is shaped by both the ‘quantity’ (Experiment 1) and ‘quality’ (Experiment 2) of publicly available information used to assess risk levels. Our first experiment suggests that individual personality shapes the response of guppies to high, but not low-intensity acute threats. When exposed to the high-risk alarm cue (but not the low risk or control) treatment, shyer guppies exhibited much stronger anti-predator responses than did bolder guppies. Previous reports have shown that guppies exposed to high ambient predation risks exhibit strong graded threat-sensitive trade-offs (Botham et al. 2008; Brown et al. 2009). Our results suggest that these threat-sensitive response patterns are subject to individual personality. Moreover, the results of our first experiment support the hypothesis that behavioural flexibility may be limited by individual personality (Dingemanse et al. 2010; Mathot et al. 2012). For example, shyer chaffinches (*Fringilla coelebs*) and juvenile brown trout (*Salmo trutta*) are better able to respond to variable foraging opportunities under high-risk conditions than do bolder conspecifics (Quinn and Cresswell 2005; Adriaenssens and Johnsson 2011a, b). While shyer guppies tested here exhibited a graded (proportional) threat-sensitive response pattern to increased concentrations of conspecific alarm cue, bolder guppies had similar response intensities to both low- and high-risk alarm cues. Such differences in the degree of behavioural flexibility may arise if shy prey individuals are more susceptible to short-term changes in environmental factors (i.e. predation threats or foraging opportunities). Bolder prey may have a lower sensitivity to environmental fluctuations (i.e. the costs of not responding to short-term changes in some factor are relatively low); thus, they may be less likely to alter their behaviours in response to short-term variance in environmental factors (Luttbeg and Sih 2010; Mathot et al. 2012). While we did not test directly for individual repeatability and behavioural plasticity in the current study, our findings are consistent with the earlier hypothesized links between personality and behavioural plasticity (Dingemanse et al. 2010; Mathot et al. 2012).

The sensory complementation hypothesis (Ferrari et al. 2008; Kim et al. 2009; Elvidge et al. 2013) predicts that the reliability of risk assessment by prey is enhanced through the integration of complementary information sources. By extension, additional sensory inputs may provide confirming information regarding an individual’s initial assessment

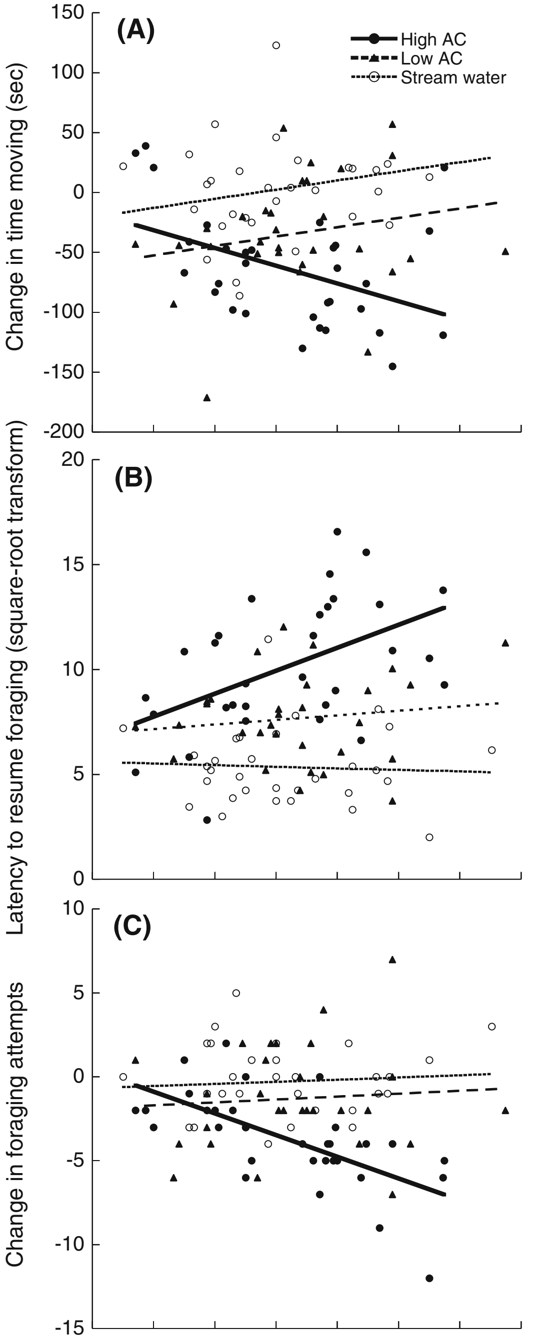

Fig. 1 Change in time moving (seconds) (**a**), latency to resume foraging (seconds, square-root transform) (**b**) and change in foraging attempts (**c**) for guppies exposed to high concentrations of alarm cue (*solid circles*, *heavy bold line*), low concentration of alarm cue (*solid triangles*, *long dashed line*) or stream water control (*open circles*, *short dashed line*) plotted as a function of latency to escape a start chamber (seconds, square-root-transformed). $N = 30$ per stimulus type

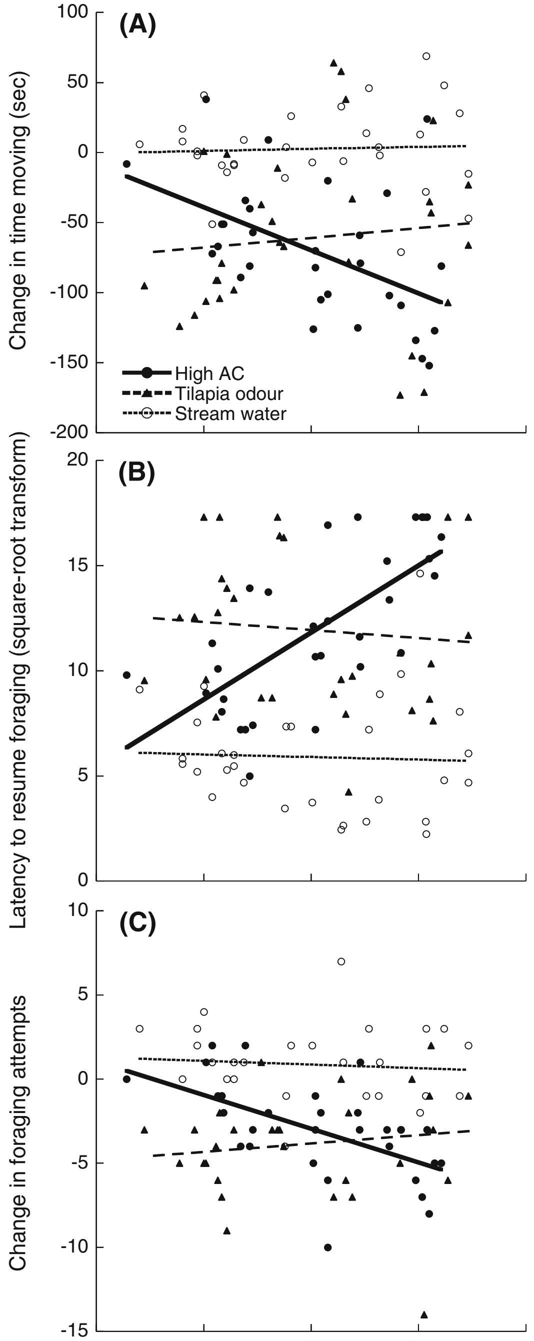

Fig. 2 Change in time moving (seconds) (**a**), latency to resume foraging (seconds, square-root transform) (**b**) and change in foraging attempts (**c**) for guppies exposed to high concentrations of alarm cue (*solid circles*, *heavy bold line*), tilapia odour, a novel chemosensory cue (*solid triangles*, *long dashed line*) or stream water control (*open circles*, *short dashed line*) plotted as a function of latency to escape a start chamber (seconds, square-root-transformed). $N = 30$ per stimulus type

of local risk. For example, prey responding to chemosensory cues may initiate an increased predator avoidance response (e.g., reduced foraging), but in the absence of complementary visual information (i.e. they do not see a predator), they may judge the situation sufficiently safe to return to baseline activity levels. Given that bolder prey are more likely to inspect potential predators (Harris et al. 2010; Jones and Godin 2010; Pellegrini et al. 2010), it is possible that personality impacts the complementary use of multiple sensory modalities during predation threat assessment. Here, bolder guppies may judge the lack of secondary information (e.g. visual cues) as indicating a lower level of risk, resulting in weaker responses compared to shyer guppies. Such relatively risk-prone strategies may allow bolder individuals to better meet their immediate energy needs compared to shyer ones (Brown et al. 2005). Recent studies by Bell and Sih (2007) and Adriaenssens and Johnsson (2013) suggest that exposure to increased predation risk may rapidly select for behavioural syndromes in which bolder individuals may also be more aggressive towards both competitors and predators. Such positive correlations between boldness and aggression may further allow bolder (risk-prone) prey to maintain sufficient energy intake and reduce mortality risk under high levels of predation threats.

Our second experiment further extends these findings, demonstrating that the reliability of information associated with publically available cues also shapes the effects of individual risk-taking tactics. As in Experiment 1, guppies exposed to a known cue (high concentration of conspecific alarm cue) exhibited a strong interaction with individual risk-taking. However, guppies exposed to an unknown novel cue exhibited strong responses regardless of individual personality. We have recently demonstrated that guppies from high-predation risk sites exhibit avoidance of novel chemosensory cues in both laboratory and field trials (Brown et al. 2013). Such a neophobic response can be induced by exposure to elevated levels of risk and may function as a phenotypically plastic response to high and/or variable predation threats (Brown et al. 2013). Recent data suggest that while the response to conspecific alarm cues by juvenile convict cichlids is proportional to the concentration detected (Brown et al. 2006), the response to novel chemosensory cues is independent of concentration (i.e. elicits a response if detected). Rather, the strength of convict cichlid neophobic responses matches the level of background predation risk (Brown et al. 2014). Thus, while guppies exposed to the known high-risk cue are able to adjust the intensity of response according to individual risk-taking tactics, those exposed to the unknown cue may overestimate the acute threat and exhibit a high intensity regardless of personality. Intuitively, this makes sense as the cost of lost foraging opportunities would likely be much less than the risk of mortality for prey failing to respond to a novel cue (i.e. Csanyi 1985).

Within the context of foraging decisions, Mathot et al. (2012) argue that variable and unpredictable foraging opportunities lead to ecological uncertainty and that as uncertainty increases, the costs associated with an inappropriate decision also increase. Bolder individuals would potentially suffer higher relative costs under uncertain conditions than would shyer individuals. Our current results are consistent with this prediction, as novel cues appear to be less reliable indicators of local risk (i.e. uncertain indicators of risk) compared to conserved conspecific alarm cues. While bold guppies may be able to compensate for high levels of a known risk (Experiment 1), the costs of failing to respond to a novel cue may be too high. As a result, bolder guppies show a similar response to the novel cue as seen for shyer guppies (Experiment 2).

Recent studies have highlighted the context-dependent nature of personality within prey populations (Adriaenssens and Johnsson 2011b; David et al. 2012; Quinn et al. 2012). The latency to forage of captive zebra finches (*Taeniopygia guttata*) is dependent upon the additive effects of personality and body condition, with bolder finches and/or finches in poorer body condition exhibiting shorter latencies than shyer and/or better condition ones (David et al. 2011). Likewise, under conditions of unpredictable foraging opportunities, for example, guppies engage in riskier foraging tactics and are more likely to explore novel foraging opportunities than those exposed to predictable foraging conditions (Chapman et al. 2010b). While we did not measure repeatability of risk-taking tactics, our results further demonstrate that there is considerable intrapopulation variability in individual risk-taking tactics. Moreover, our findings suggest that the expression of these tactics is dependent on the nature of public information detected (i.e. is context-dependent) and provide further support for the context-dependent nature of personality within prey populations.

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