Exploratory behaviour and novel predator recognition: behavioural correlations across contexts

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It was hypothesized that the exploratory behaviour of an individual measured in a novel environment could predict its behaviour in response to a novel predator. This study examined novel predator recognition in the western mosquitofish *Gambusia affinis*, a species with individual differences in risk-taking, activity and exploration in novel environments. Prey responded with characteristic shoaling and avoidance in response to native predators, but did not show characteristic antipredator behaviour towards novel predators. Furthermore, *G. affinis* exhibited individual-level behavioural correlations across contexts but only when prey were tested with native predators. This could be the result of native predatory selection on behavioural correlations in the prey species.

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Key words: antipredator behaviour; behavioural syndromes; boldness; introduced predators; invasive species.

INTRODUCTION

As human activities lead to the introduction of predator species into new habitats, the ability of prey to recognize and respond to novel predators becomes increasingly important for the survival of prey species. Native species can suffer indirect damage from invasive species that alter habitats and ecosystem processes, or direct effects from interactions with introduced predators (Cox & Lima, 2006; Sih *et al.*, 2010; Strayer, 2010). Prey species that do not respond with effective antipredator behaviour towards novel predators may suffer lethal effects that can put native species at risk (Nannini & Belk, 2006; Banks & Dickman, 2007; Salo *et al.*, 2007).

The effects of a novel predator can be mitigated if the prey species can recognize it as a threat, through innate or learned responses. For aquatic organisms, chemical cues, or kairmones, given off by predators are often important for prey to identify and respond to potential predator threats (Chivers & Smith, 1998; Kelley & Magurran, 2003). Fishes can sometimes use associative learning to respond to novel predator cues that are paired with alarm cues of attacked or consumed conspecifics (Kelley & Magurran, 2003; Wisenden, 2003; Aizaki & Yusa, 2010; Mitchell *et al.*, 2011). In contrast, innate recognition can allow an immediate response to a novel predator that does not require multiple experiences. Innate recognition of non-native visual or chemical

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predator cues without prior exposure is possible when prey species are able to generalize from a native predator to recognize and perform antipredator behaviour towards a similar, non-native predator (Ferrari *et al.*, 2007; Davis *et al.*, 2012; Mitchell *et al.*, 2013). Generalization, however, is less likely in situations where the introduced predator is phylogenetically distant and dissimilar from native predators in morphology and behaviour (Blake *et al.*, 2014).

In addition to understanding how prey species react to introduced predators, it is important to consider how prey may differ in their response to novel predators at the individual level. Individual variation in behavioural traits within a species, termed behavioural syndromes or personalities, has been shown to affect many aspects of ecology (Sih *et al.*, 2012), and appears to be particularly important in predator–prey relationships (Biro *et al.*, 2004; Bell, 2005; Bell & Sih, 2007; Dingemanse *et al.*, 2007). In addition to observed population-level effects, prey personalities can affect direct behavioural interactions among predator and prey individuals (Dugatkin & Alfieri, 2003; Smith & Blumstein, 2010; Pruitt *et al.*, 2012; Blake & Gabor, 2014).

Research on behavioural syndromes in animals has often examined risk-taking behaviour, *e.g.* latency to remerge after a simulated predator attack (Webster *et al.*, 2007; Burns, 2008; Carter *et al.*, 2013). Studies on behavioural syndromes also often test response to novelty, such as willingness to enter a novel environment or approach a novel object (Brown *et al.*, 2007; Dingemanse *et al.*, 2007; Carter *et al.*, 2013). Additional research has shown that some individuals respond with less caution to novelty, but may also be slower in responding to changes in their environment (de Lourdes Ruiz-Gomez *et al.*, 2011). As facing an introduced predator combines elements of both risk-taking and novelty, individual prey may differ in their reaction, and these individual differences could have important consequences for their recognition and response to novel predators, and ultimately their survival when faced with novel predators. Furthermore, there may be correlations between risk-taking and reaction to novelty in the context of novel predator recognition to these same behavioural characteristics measured in other contexts, such as emerging from an enclosed structure into a novel environment. For example, individual prey that are more likely to take risks such as emerging quickly from shelter into an unfamiliar environment may be less likely to recognize a novel predator as threatening.

This study investigated recognition of a novel predator, and how other behavioural characteristics of prey individuals are connected to responses to predators. In this experiment, responses of western mosquitofish *Gambusia affinis* (Baird & Girard 1853) were examined to native predatory, novel predatory and novel non-predatory stimuli fishes. The first prediction was that on average prey would not respond as strongly to the novel predators as native predators because the novel species was dissimilar from native predators phylogenetically, morphologically and behaviourally. The novel predator in this study, the cyprinid Gulf killifish *Fundulus grandis* Baird & Girard 1853, is contrasted with a native predator stimulus, the centrarchid green sunfish *Lepomis cyanellus* Rafinesque 1819. In addition to being taxonomically distant, these two predators contrast in their hunting styles, with *F. grandis* being more active in searching for prey. *Fundulus grandis* has been introduced into several freshwater drainages sympatric with *G. affinis* in central Texas; thus, a lack of recognition of this predator implies detrimental impacts of this introduction for wild *G. affinis* populations.

Secondly, this experiment explored whether the behaviour of an individual towards native predatory, novel predatory and novel non-predatory stimuli correlated with

behaviour of these same prey individuals during novel environment emergence tests. Previous studies have found that bold or risk-taking behaviours occur with consistent individual differences in several species of mosquitofishes (Cote *et al.*, 2010, 2011; Blake & Gabor, 2014). It was hypothesized that individual risk-taking behaviour in a novel environment could predict the behaviour of these same prey individuals in response to a novel predator. If some behavioural types were better able to recognize or respond to novel predators, this could modify the effects of introduction on the prey species and could also lead to new selection pressures on behavioural syndromes in the prey population.

MATERIALS AND METHODS

STUDY SPECIES

Gambusia affinis is a widespread species, its native range stretching from Alabama to some parts of New Mexico and as far north as Illinois, and has also become invasive in other introduced habitats. *Gambusia affinis* is common in fresh water throughout Texas, and is small (<65 mm), mostly insectivorous, and live-bearing. *Lepomis cyanellus* is a common native piscivorous predator in central Texas, and thus is currently and historically sympatric with *G. affinis* (Hubbs *et al.*, 1991). *Fundulus grandis* is native to fresh and brackish waters along the coasts of north-eastern Florida and the Gulf of Mexico, and consumes an omnivorous diet including invertebrates and small fishes (Rozas & Lasalle, 1990; Hubbs *et al.*, 1991). *Fundulus grandis* can tolerate a range of salinity and has been introduced into many freshwater environments in Texas and New Mexico through bait-bucket releases (Hillis *et al.*, 1980). In its current distribution, *F. grandis* co-occur with *G. affinis* in some areas of Texas, but are novel to the *G. affinis* population used in this study (Hillis *et al.*, 1980; Thomas *et al.*, 2007; Perkin & Bonner, 2014). Guppies *Poecilia reticulata* Peters 1859 from a laboratory stock population roughly equivalent in size to the focal *G. affinis*, were used as an allopatric, non-predatory control. For the predator treatments juvenile individuals [60–100 mm standard length (L_S)] were used to allow for ease of maintenance in laboratory tanks, but all individuals were large enough to potentially consume focal *G. affinis* individuals (20–35 mm L_S). Mean L_S was similar between the two predator species (*F. grandis* 82 mm and *L. cyanellus* 86 mm).

COLLECTION AND LABORATORY MAINTENANCE

Wild-caught *G. affinis* were collected from the Comal River, Comal County, TX (29° 42′ 15″ N; 98° 7′ 49″ W) in February 2014. *Poecilia reticulata* were selected haphazardly from a stock laboratory population of several hundred fish. Before and between trials *G. affinis* and *P. reticulata* resided in 38 l aquaria (50 cm × 25 cm × 30 cm) on a 14L:10D cycle at 25–27° C and were fed flake food (Ocean Star International; www.oceanstarinternational.com) *ad libitum* once a day at 1630 hours. *Lepomis cyanellus* were collected from Spring Lake, Hays County, TX (29° 53′ 40″ N; 97° 55′ 49″ W), and *F. grandis* were collected from the Brazos River, Hill County, TX (31° 52′ 23″ N; 97° 21′ 53″ W). *Lepomis cyanellus* and *F. grandis* were maintained in single-species 150 l aquaria (91 cm × 46 cm × 41 cm) on a 14L:10D cycle at 25–27° C, and fed pellet food (Purina Aqua Max 200; www.purinamills.com) *ad libitum* once a day at 1630 hours.

NOVEL ENVIRONMENT TRIALS

Several weeks before testing, focal *G. affinis* were injected immediately anterior to the pectoral fin with an individualized tag, using up to two colours of elastomer (Northwest Marine Technology; www.nmt.us). Mortality from elastomer was <1·0% and generally occurred within the first 24 h after injections. Novel environment trials were conducted in a shallow, opaque plastic tank (52 cm × 35 cm) with video cameras mounted above the tank to record trials. Tanks

contained 8 cm of water, so that movement was primarily horizontal, and water temperature ranged from 25 to 27° C. *Gambusia affinis* were placed individually in an opaque container (9 cm × 9 cm × 18 cm) and allowed to acclimate for 5 min before opening the door (5 cm × 5 cm) of the container remotely using a pull string. Latency to emerge was calculated as the log of the maximum time allowed to exit (10 min) minus the log of the time until the *G. affinis* exited the container into the novel tank environment. Thus, a higher value for latency to emerge indicates that the *G. affinis* entered the novel tank environment sooner. Time spent moving was calculated as the proportion of the 5 min observation period the individual spent moving, and area used as the proportion of the tank area explored, each calculated from videos of the trials using Image (http://imagej.nih.gov/ij/; Blake & Gabor, 2014). During the novel environment assays, most *G. affinis* exited the chamber within the time allotted, and only these *G. affinis* with complete novel environment data were included in analysis of behavioural correlations across contexts ($n = 42$ per treatment). These trials were performed in between 0800 and 1300 hours, during March to April 2014.

PREDATOR RECOGNITION TRIALS

Predator recognition trials were conducted using the same marked individuals, 4–6 weeks following the novel environment trials. Each *G. affinis* was exposed to all three treatments in random order: (1) native *L. cyanellus* predator, (2) novel *F. grandis* predator and (3) novel non-predatory *P. reticulata*. Before predator recognition trials, *G. affinis* were also photographed for another study, measured for L_S from tip of the snout to the end of the last vertebra and weighed for body mass. Predator recognition trials used 76 l testing tanks (76 cm × 30 cm × 30 cm) filled with 15 cm of dechlorinated tap water. Tanks were covered on three sides with opaque barriers and window tinting was put on the front of the tank to reduce visual disturbance. The tank was divided into two unequal sections by a clear, water-permeable plastic barrier, one 56 cm section containing the focal individual and shoalmates, and the other 20 cm section for the stimulus fish. The focal fish section was marked with lines on the outside of the glass to indicate three (5 cm) vertical zones and 14 (4 cm) horizontal zones. Thus, a *G. affinis* in horizontal zone one was within 4 cm of the barrier to the stimulus fish section, whereas a *G. affinis* in zone 14 was 52–56 cm from the stimulus fish area.

To initiate the predator recognition trial, a marked focal individual was placed into the testing tank with two unmarked conspecifics collected at the same site and location as the focal fish. These conspecific shoalmates were haphazardly selected for each trial from another tank in the laboratory. After a 5 min acclimation period, vertical position of the focal *G. affinis*, horizontal position and shoaling behaviour were recorded every 30 s for 5 min. The focal *G. affinis* was considered to be exhibiting shoaling behaviour if they were within two body lengths of a conspecific by visual estimation of the observer. After the 5 min pre-stimulus observation period, the stimulus fish was introduced with a net into the separated section of the experimental tank. Multiple individuals of each stimulus species were used and rotated between trials so that no one stimulus fish became too stressed (*F. grandis* = 9, *L. cyanellus* = 5 and *P. reticulata* = 15). Following the introduction of the stimulus fish, vertical and horizontal positions and shoaling of the focal *G. affinis* were recorded every 30 s for 5 min. After the trial, all fishes were moved back to their home tanks. This process was repeated on subsequent days (24 h later) for all three treatments, using a repeated measures design so that each focal *G. affinis* received each treatment ($n = 51$ per treatment).

Behavioural responses of *G. affinis* were calculated by subtracting the focal *G. affinis*' average zone during the pre-stimulus from its average zone during post-stimulus observation. Thus, a positive value for change in distance from the stimulus represented a move away from the stimulus, while a positive value for change in water column use indicated a higher position in the water column post-stimulus. Similarly, shoaling response was calculated as the number of times the focal individual was observed shoaling in the pre-stimulus period subtracted from their shoaling in the post-stimulus period. Increased shoaling, moving upwards in the water column and moving away from predator cues were considered indications of antipredator behaviour (Magurran, 1990; Christensen, 1996; Kelley & Magurran, 2003; Zheng *et al.*, 2005). Thus, positive values for all three behavioural responses were associated with an increase in antipredator behaviour. Predator recognition trials were performed between

0800 and 1300 hours at 25–27° C in May 2014. The experimental methods described above were approved under IACUC protocol 0515_0612_13, and follow guidelines for ethical use of experimental animals, and fishes specifically (Metcalfe & Craig, 2011; ASB/ABS, 2012).

ANALYSES

Preliminary analyses showed testing order and L_S of the focal individual did not have significant effects and these factors were not included in the final analyses. Latency to emerge was calculated on a log scale to improve normality. Following this, Shapiro–Wilk tests and diagnostic plots showed that all variables were normal or near-normal in distribution. To assess effects of treatment on behavioural responses to the stimuli fish, a repeated-measure ANOVA was used, followed by Tukey's *post hoc* test to compare means of behavioural responses among treatment groups. Pearson correlations were used to examine relationships among behaviours across contexts. Analyses were conducted in R 2.15.0 (www.r-project.org).

RESULTS

Changes in distance of the focal *G. affinis* from the stimulus differed among treatments (ANOVA, $F_{2,100} = 6\cdot21$, $P = 0\cdot001$). Focal *G. affinis* also varied in their shoaling response to the stimulus among the different treatments (ANOVA, $F_{2,100} = 6\cdot36$, $P = 0\cdot001$) and in their water column use (ANOVA, $F_{2,100} = 3\cdot12$, $P = 0\cdot05$). Focal *G. affinis* responded to native predatory *L. cyanellus* by moving away from the stimulus and shoaling more closely (Figs 1 and 2). In contrast, focal *G. affinis* moved towards novel predatory *F. grandis* and did not change their shoaling behaviour following stimulus introduction (Figs 1 and 2). Focal *G. affinis* also responded to *F. grandis* by moving downwards in the water column, but did not change their water column usage following introduction of native *L. cyanellus* (Fig. 3). Responses to *P. reticulata* stimuli were near zero for all three behaviours, indicating little change in focal *G. affinis* behaviour following stimulus introduction.

Behaviour in the novel environment assays and in the predator recognition trials showed several significant relationships among the behaviours measured in these two contexts. There were only significant correlations across contexts, however, when focal *G. affinis* were tested with the native *L. cyanellus* treatment (Table I). The amount of time an individual spent moving in the novel environment was positively correlated with their change in distance from *L. cyanellus* stimulus (*i.e.* more active individuals moved further from *L. cyanellus* than less active individuals). The area used by an individual in the novel environment assay was negatively correlated with their change in shoaling tendency, and change in water column use in response to the *L. cyanellus* stimulus. The most exploratory individuals showed a decrease in shoaling and moved lower in the water column in response to *L. cyanellus*. There were no significant correlations across the two testing contexts when individuals were exposed to the *P. reticulata* or *F. grandis* treatments (Table I).

DISCUSSION

The results indicate that *G. affinis* used in this study did not recognize and respond to a novel predator stimulus. *Gambusia affinis* behaviour towards native predatory *L. cyanellus* was characterized by increased shoaling and moving away from the
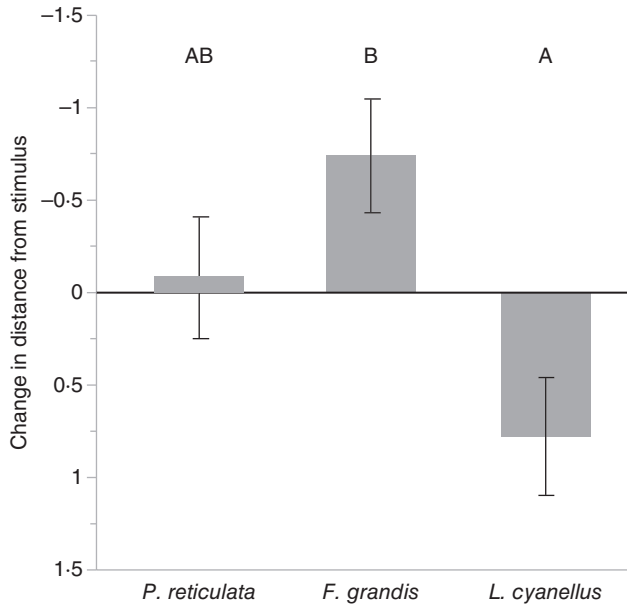
Fig. 1. Mean ± s.e. change in distance from stimulus fish by treatment for *Gambusia affinis*, calculated as post-stimulus minus pre-stimulus zone such that a positive value indicates moving further from the stimulus. One zone represents 4 cm of the tank. *Fundulus grandis* is a novel predator, *Lepomis cyanellus* is a native predator of *G. affinis* and *Poecilia reticulata* is a novel non-predator. Responses varied by treatment and uppercase letters distinguish significant difference from Tukey's *post hoc* test.

stimulus, with no significant change in water column use. Increased shoaling and moving away coincide with previous descriptions of antipredator behaviour in *G. affinis* (Magurran, 1990; Kelley & Magurran, 2003). In contrast, behavioural responses to novel *F. grandis* stimuli were characterized by moving towards the bottom and towards the stimulus fish, without significantly changing shoaling behaviour. Overall, behavioural responses to the *F. grandis* were more similar to responses towards non-predatory *P. reticulata* than to native predator responses. These results contrast with other research showing that native species can sometimes respond in a threat-sensitive way to novel predators (Brown & Morgan, 2015). The results of this study, however, coincide with a previous study on the closely related largespring mosquitofish *Gambusia geiseri* Hubbs & Hubbs 1957, which also showed a lack of antipredator response to *F. grandis* (Blake *et al.*, 2014).

Changes in water column use can be important in antipredator responses, especially for fishes that use jumping behaviour as an escape mechanism. Moving upwards in the water column is a response to acute predation risk, as this allows fishes to perform antipredator behaviour by jumping out of the water (Christensen, 1996; Blake & Gabor, 2014). Previous research, however, suggests that the vertical movement of prey can also depend on water column use and hunting strategy of the particular predator species (Staudinger *et al.*, 2013). It is possible that prey *G. affinis* in this study did not change water column use in response to native *L. cyanellus* because they were responding to the way predator individuals were moving in the water column. Similarly, moving towards the bottom in response to novel *F. grandis* could be related to the water column usage
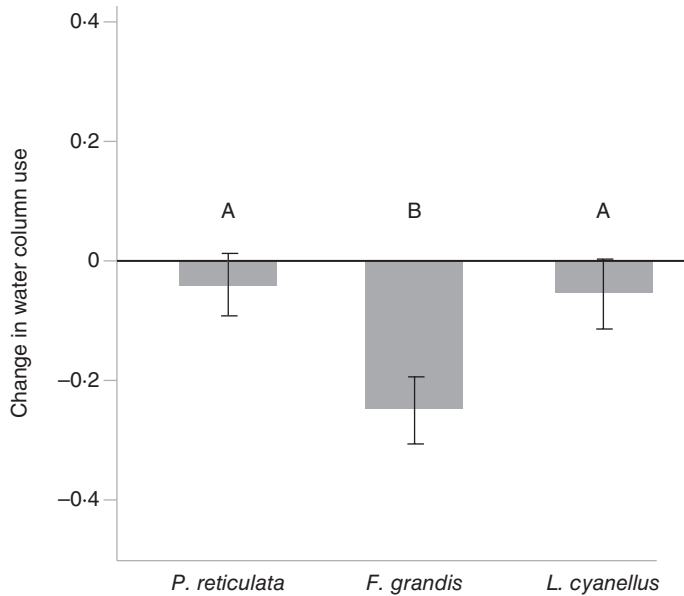
Fig. 2. Mean ± s.e. change in shoaling tendency (post-stimulus minus pre-stimulus) by treatment for *Gambusia affinis*. Units are number of times shoaling out of 10 observations over 5 min. *Fundulus grandis* is a novel predator, *Lepomis cyanellus* is a native predator of *G. affinis* and *Poecilia reticulata* is a novel non-predator. Responses varied by treatment and uppercase letters distinguish significant difference from Tukey's *post hoc* test.

of the predator fish, especially as the observations made indicated that *F. grandis* spent a large amount of time near the surface compared with native *L. cyanellus* predators. Predator behaviour was not recorded during the trials so any behavioural differences there may have been between predators could not be quantified. In addition, future studies could further explore the effect of individual predator characteristics such as hunger level and body size on the strength of antipredator responses towards novel predators.

Increasing the average distance from the stimulus is consistent with an adaptive antipredator response to the native *L. cyanellus*. Focal *G. affinis* moving closer to the novel *F. grandis* predator, however, could have several explanations. Moving towards *F. grandis* after the stimulus was introduced could be the result of predator inspection behaviour, in which prey move closer to a potential threat to gain more information about the size and hunger level of the predator (Dugatkin & Godin, 1992). Inspection behaviour in response to the novel predator could indicate perception of a possible threat that requires more information gathering rather than immediate recognition of a predation threat. It is also possible that prey *G. affinis* simply did not recognize the novel *F. grandis* predator as threatening at all, and so were undeterred from going closer. The response to novel *F. grandis*, however, was distinct from the response to non-predatory *P. reticulata*, indicating that the focal *G. affinis* did distinguish between these two types of stimuli. Furthermore, in a previous study, *F. grandis* actually consumed *G. geiseri* more quickly than native *L. cyanellus* in one-on-one predation trials (Blake & Gabor, 2014). Thus, in a direct interaction, the lack of an immediate moving
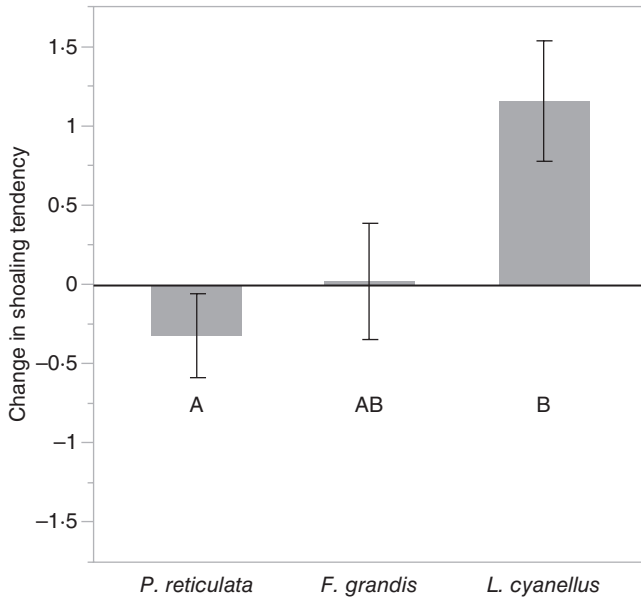
Fɪɢ. 3. Mean ± s.ᴇ. change in water column zone use (post-stimulus minus pre-stimulus) by treatment for *Gambusia affinis*. One zone represents 4 cm of the tank. *Fundulus grandis* is a novel predator, *Lepomis cyanellus* is a native predator of *G. affinis* and *Poecilia reticulata* is a novel non-predator. Responses varied by treatment and uppercase letters distinguish significant difference from Tukey's *post hoc* test.

away response with novel *F. grandis* predators would probably be detrimental to prey survival. These findings suggest that naïve *G. affinis* may not exhibit optimal behaviour when exposed to *F. grandis* in the wild, and could suffer high consumptive effects from these introduced predators.

Contrary to predictions, exploratory behaviour in a novel environment predicted antipredator behaviour when *G. affinis* were tested with native predators, but not novel predators. Behavioural correlations between the novel environment and predator recognition contexts were not significant for either novel predatory *F. grandis* or novel non-predatory *P. reticulata* stimuli. This finding was contrary to the prediction that individual responses to a novel environment and emergence tests would predict predator recognition responses. This finding is also contrary to previous studies in which proactive (bold) *v.* reactive (shy) individuals show unique responses to novel stimuli (de Lourdes Ruiz-Gomez *et al.*, 2011).

Instead, there were significant behavioural correlations across contexts when the focal *G. affinis* were exposed to a native *L. cyanellus* predator (Table I). Although the mean level responses to native *L. cyanellus* predators were characteristic of antipredator behaviour, the expression of these responses differed greatly among different prey individuals. Individuals that were more active in the novel environment moved further away than their less active conspecifics, possibly because they were simply moving around more. Exploratory individuals showed less characteristic antipredator behaviour in shoaling and water column use. The most exploratory individuals actually decreased their shoaling behaviour in response to *L. cyanellus*. This correlation could indicate a maladaptive behavioural carry-over in which individuals with a high ability

TABLE I. Correlations among behaviours measured in *Gambusia affinis* in a novel environment emergence test and in response to stimuli fishes. Significant Spearman correlation (ρ) is given in bold ($n = 42$)

	Latency to emerge	Time spent moving	Area used
Native *Lepomis cyanellus*			
Δ Distance from stimulus	0·03, $P > 0.05$	**0·38, $P = 0.01$**	0·01, $P > 0.05$
Δ Water column use	0·08, $P > 0.05$	−0·07, $P > 0.05$	**−0·35, $P = 0.01$**
Δ Shoaling tendency	−0·17, $P > 0.05$	−0·03, $P > 0.05$	**−0·36, $P = 0.01$**
Novel *Fundulus grandis*			
Δ Distance from stimulus	0·18, $P > 0.05$	0·26, $P > 0.05$	0·26, $P > 0.05$
Δ Water column use	0·002, $P > 0.05$	0·09, $P > 0.05$	−0·10, $P > 0.05$
Δ Shoaling tendency	0·06, $P > 0.05$	0·30, $P > 0.05$	0·17, $P > 0.05$
Novel non-predatory *Poecilia reticulata*			
Δ Distance from stimulus	−0·01, $P > 0.05$	−0·05, $P > 0.05$	0·04, $P > 0.05$
Δ Water column use	−0·06, $P > 0.05$	0·06, $P > 0.05$	0·02, $P > 0.05$
Δ Shoaling tendency	0·09, $P > 0.05$	0·02, $P > 0.05$	−0·18, $P > 0.05$

to explore and exploit novel environments continue highly exploratory behaviour in the context of a predation threat, when it is no longer advantageous (Johnson & Sih, 2005). Alternately, it is possible that there is more than one effective antipredator strategy, and individuals may employ distinct antipredator coping styles based on their individual characteristics. In other words, the negative correlation between exploration in a novel context and shoaling in response to predators could be adaptive (Dall *et al.*, 2004).

If the behavioural correlations across contexts are the result of adaptation, it would be unsurprising that behaviour correlated across contexts only when prey were exposed to native predators. Native predation pressure can affect prey behaviour over evolutionary time, and previous evidence suggests that predators may select for behavioural correlations across contexts (Bell, 2005; Bell & Sih, 2007). If this is the case for the prey species here, it would be less likely for behavioural correlations to occur across contexts when the situation includes a novel predator such as *F. grandis* or a novel non-predator such as *P. reticulata* that has not evolved in sympatry with the native prey. The lack of correlation between novel environment emergence tests and reactions to a novel predator found here are contrary to previous studies that have found correlations among proactive or bold behaviour and responses to novel stimuli (Dugatkin & Alfieri, 2003; de Lourdes Ruiz-Gomez *et al.*, 2011). Others have found that some behaviours that have been associated with boldness, such as responses to novel food, may not correlate to other measures associated with boldness, such as emergence tests (Carter *et al.*, 2013). Future studies could explore how individuals may differ upon repeated exposure to novel predators, because there may still be differences in speed of learned predator recognition among individuals with different coping styles (Dugatkin & Alfieri, 2003).

In summary, *G. affinis* did not show antipredator behaviour to a novel *F. grandis* predator. The introduction of *F. grandis* into central Texas could cause problems for native prey species unfamiliar with this type of predator. Furthermore, behavioural correlations across contexts were only significant when prey were exposed to a native predator stimulus. This suggests that individual behavioural traits cannot be

generalized to all contexts, especially when environmental conditions deriving from anthropogenic effects are unprecedented in the evolutionary history of a species.

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