Are fast explorers slow reactors? Linking personality type and anti-predator behaviour

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Response delays to predator attack may be adaptive, suggesting that latency to respond does not always reflect predator detection time, but can be a decision based on starvation–predation risk trade-offs. In birds, some anti-predator behaviours have been shown to be correlated with personality traits such as activity level and exploration. Here, we tested for a correlation between exploration behaviour and response latency time to a simulated fish predator attack in a fish species, juvenile convict cichlids (*Amatitlania nigrofasciata*). Individual focal fish were subjected to a standardized attack by a robotic fish predator while foraging, and separately given two repeated trials of exploration of a novel environment. We found a strong positive correlation between exploration and time taken to respond to the predator model. Fish that were fast to explore the novel environment were slower to respond to the predator. Our study therefore provides some of the first experimental evidence for a link between exploration behaviour and predator-escape behaviour. We suggest that different behavioural types may differ in how they partition their attention between foraging and anti-predator vigilance.

Keywords: personality; shy–bold continuum; anti-predator behaviour; adaptive-response delays; attention; convict cichlid

1. INTRODUCTION

Avoidance of predation is an important determinant of fitness in many animals (Godin 1997; Ruxton *et al.* 2004). Individuals must trade-off the risk of predation against the benefits of foraging (Lima & Dill 1990). This 'starvation–predation risk trade-off' is central to many foraging decisions individuals make, such as which patch to forage in (Gilliam & Fraser 1987; Butler *et al.* 2005), when to forage (Dall & Witter 1998; Macleod *et al.* 2005) and with whom to forage (Giraldeau & Caraco 2000; Krause & Ruxton 2002).

Recent work (e.g. Cresswell *et al.* 2000, 2009; Fernandez-Juricic *et al.* 2002; Quinn & Cresswell 2005) has suggested that delays in responding to a predatory attack can actually be adaptive. Individuals must trade-off an immediate response to a potential threat against potential lost-opportunity foraging costs of taking flight (economic hypothesis; Ydenberg & Dill 1986; Quinn & Cresswell 2005). Experiments quantifying the response time of visually guided animals to predator models have shown that there is significant interindividual variation in response times (Krause & Godin 1996; Stankowich & Coss 2006; Jones *et al.* 2009). However, the mechanisms underlying such variation are not fully understood.

Variation in response delays may result from differences in inherent ability to detect predators (perceptual limit hypothesis; Quinn & Cresswell 2005) or differences in vigilance, with animals that devote more time to vigilance (e.g. via more frequent and/or longer vigilance bouts) being faster to detect an approaching predator (Cresswell *et al.* 2003). Individuals can vary their

vigilance level by allocating their brain's 'attention' between searching for and handling food items and searching for predators (Godin & Smith 1988; Clark & Dukas 2003; Fernandez-Juricic *et al.* 2004).

When behavioural ecologists talk of attention, they refer to the devotion of the brain's computing power to completing a particular task (Dukas & Kamil 2000). Attention has been shown to be limited (Dukas & Kamil 2000, 2001). Therefore, it is hypothesized that the relative division of attention between foraging and anti-predator vigilance will vary both within and between individuals. Birds and fishes are less able to detect approaching predators when attending to a difficult foraging task, most probably owing to their attention being focused on obtaining food (Milinski 1984; Krause & Godin 1996; Kaby & Lind 2003), which can translate into a direct fitness cost owing to an increased chance of capture by a predator (Godin & Smith 1988; Krause & Godin 1996).

Between-individual differences in either inherent ability to detect predators or the relative division of attention towards foraging versus anti-predator vigilance may not be simply 'noise around a maximally adapted mean' (Bell 2007). Increasingly, behavioural ecologists are viewing differences in behaviour among individuals in a population as adaptive and representing different behavioural strategies (reviewed in Dall *et al.* 2004; Bell 2007; Réale *et al.* 2007; Smith & Blumstein 2008). Depending on environmental and social conditions, different strategies (each associated with different costs and benefits) will have different payoffs. For example, a recent experiment on rainbow trout (*Oncorhynchus mykiss*) showed that larger, bolder, fast-growing phenotypes were more likely to be captured by fishermen (Biro & Post 2008). Predation has also been proposed as one mechanism underlying the maintenance of behavioural syndromes by selecting against certain

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combinations of traits (e.g. being bold and non-exploratory, or shy and exploratory; Stamps 2007), which is supported by experimental evidence on three-spined sticklebacks, *Gasterosteus aculeatus* (Bell & Sih 2007).

Early work on personality in animals has focused on laboratory paradigms, such as exploration, neophobia and risk-taking (reviewed in Sih *et al.* 2004; Réale *et al.* 2007). There is thus a need to investigate how these paradigms translate to more natural contexts such as foraging (Wilson & McLaughlin 2007), mate choice (Godin & Dugatkin 1996) and parental care (Budaev *et al.* 1999). In particular, there are few studies investigating the relationship between personality traits and anti-predator behaviour (reviewed in Réale *et al.* 2007), most likely because predation events are infrequently observed in nature compared with other behavioural phenomena. In birds, van Oers *et al.* (2004) found that great tits (*Parus major*), which were more willing to explore more of a novel environment, were also more likely to return to forage quicker after being startled. Quinn & Cresswell (2005) is one of the few studies to consider the effects of prey animal personality at the moment of a predatory attack; they reported that chaffinches (*Fringilla coelebs*), which were less active at the beginning of a trial, were more likely to freeze than flee in response to a hawk attack and took longer to resume activity following the attack. However, this study did not quantify exploration in a non-predatory context; that is, their anti-predator behaviour and personality measurements were conducted in the same, non-independent trials.

In the current study, we investigated experimentally whether individual juvenile convict cichlid fish (*Amatitlania nigrofasciata*) differ in their response latency time to an approaching predatory threat and whether such differences correlate with individual differences in behaviour in other contexts (i.e. exploration of a novel environment, and response to a novel object). We tested two plausible alternative hypotheses regarding the nature of this relationship: (i) that the relationship is a positive one; if risky behaviours such as exploration and foraging reduce (limited) available attention for other behaviours, then anti-predator vigilance might be compromised, such that good explorers would be expected to exhibit longer delays (latencies) in their responses to predatory threats than poorer explorers or (ii) that the relationship is a negative one: if exploratory behaviour is risky, then more exploratory individuals might be selected to compensate with increased anti-predator vigilance, such that good explorers would be expected to exhibit shorter delays in their responses to predatory threats than poorer explorers. Our study thus aimed to characterize the relationship between individual behavioural types or 'personalities' and anti-predation behaviour at the moment of a predatory attack. In doing so, we provide further explanation for the variation in response times to predatory attack observed in several species and a potential mechanism for the observed differential survival of personality types (Bell & Sih 2007; Smith & Blumstein 2008).

2. MATERIAL AND METHODS

(a) *Subjects*
We used two- to three-month-old juvenile convict cichlids (mean ± s.d. = 19.5 ± 3.0 mm, standard body length)

Table 1. Experimental time schedule. Fish were put through these tests in batches of five (total fish tested = 45) between January and May 2008. Individual fish were exposed to the predator-attack test only once, either before (Day 0) or after (Day 11) the two sets of 'personality' tests.

day from first test	test type
0	predator-attack test
1 and 2	no tests
3	first novel-object test
4	first novel-environment test
5–8	no tests
9	second novel-object test
10	second novel-environment test
11	predator-attack test

originating from a laboratory stock population derived from wild Costa-Rican adults as experimental subjects. Broods were maintained in 80 l stock aquaria containing aged filtered tap water (24–25°C), a gravel substratum and a plastic plant refuge.

Each individual test fish ($n = 45$) was exposed to a predator-attack test, two novel-object tests, and two novel-environment tests over an 11-day period (table 1). We used the novel-object and novel-environment tests to assess individual personality. To control for order of presentation, individual fish were exposed to the predator-attack test either before ($n = 29$) or after ($n = 16$) the aforementioned two sets of personality tests (table 1). Because the results were not dependent on the order of presentation of the predator-attack test (§3), we pooled the before–after data for statistical analyses.

(b) *Predator-attack trials*
Following Krause & Godin (1996), we standardized the threat of predation presented to individual test cichlids using a model (19 cm length, constructed to scale and painted realistically) of an approaching wolf cichlid (*Parachromis dovii*), a major predator of juvenile convict cichlids in nature (J.-G. J. Godin 2008, personal observations). The model was suspended in the water column (5 cm above the gravel substratum) at one end of the experimental tank (110 cm × 40 cm × 34 cm, $L \times W \times H$; water depth = 15 cm; figure 1a) by two pieces of monofilament nylon line attached to an overhead clear Plexiglas track. When not moving, the model was hidden from the test fish in a simulated refuge constructed of a piece of opaque plastic overhead, rocks and plastic plants.

At the opposite end of the experimental tank, we placed a small glass aquarium (30 cm × 12.5 cm × 20 cm, $L \times W \times H$; water depth = 15 cm) to house the test fish (figure 1a). One-half of the small tank was covered overhead and on the sides with opaque plastic and contained a plastic plant, providing a 'refuge' for the test fish. The open half of the housing tank contained a food 'patch' (figure 1a), which consisted of a glass microscope slide that was thinly coated with a 2 × 2 cm layer of gelatin, onto which crushed TetraMin cichlid pellets (Tetra Werke, Melle, Germany) were evenly sprinkled, to provide an excess of food, simulating foraging on algae-covered rocks in nature (J.-G. J. Godin 2008, personal observations). The slide was placed at an angle against the end wall of the tank facing the refuge. When feeding on this food patch, test fish were typically oriented horizontally
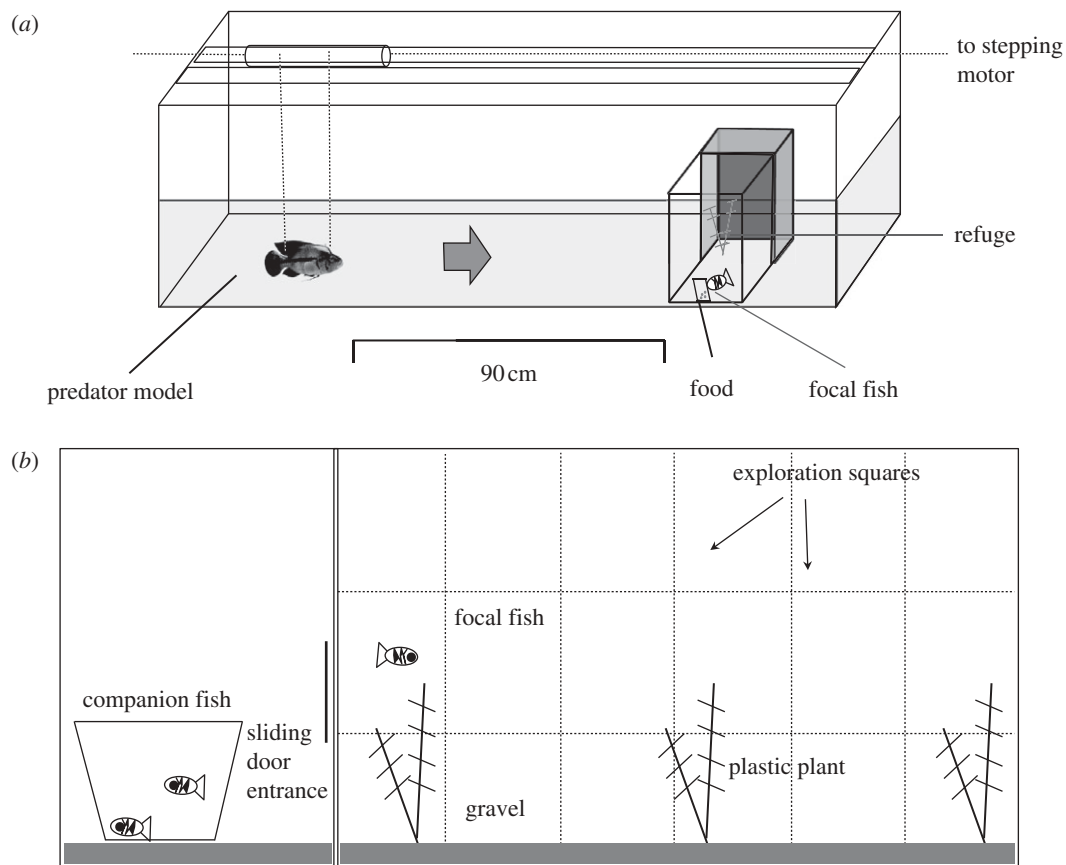
Figure 1. (*a*) Experimental apparatus for quantifying the anti-predator response of test fish to an approaching predator model. The fish predator model was hidden prior to its 'attack' in a dimly lit refuge of rocks and a plastic plant at one end of the experimental aquarium (for simplicity, not shown in the figure). The arrow denotes the direction of movement of the fish predator model during the 'attack' phase of the protocol. (*b*) Experimental apparatus for quantifying the exploratory behaviour of test fish in a novel environment.

or slightly obliquely downward and with their right side facing the direction of the predator model. Fish were given prior experience feeding on such glass slides in their home aquaria prior to testing. Test fish were deprived of food for 24 h prior to experimentation to standardize their hunger level.

For each predator-attack trial, we haphazardly dip-netted a test fish from a brood and placed it in the small housing tank within the experimental apparatus and allowed it 30 min to acclimatize. To control for capture bias, for a given trial, we captured five fish from a brood and then used a random number between 1 and 5 to determine which one of the individuals captured would be used as the test fish in the trial. Following the acclimatization period, the food patch (described above) was gently lowered into the housing tank (see figure 1*a* for position). Once the test fish had been foraging on the food patch for 30 s, the model was moved remotely towards the test fish at 15 cm s^{-1} (simulating an 'attacking' wolf cichlid) by activating a stepping motor with a computerized controller. Once activated, the predator model travelled forwards towards the test fish for 6 s (covering a distance of 90 cm), then waited at the end of its 'attack' just in front of the test fish housing tank for 5 s before slowly moving backwards over 45 s into its refuge. Test fish typically responded to the approaching predator model by stopping foraging and either freezing near the substratum, fleeing from the patch and freezing within the open zone of the housing tank or fleeing into the nearby refuge.

The behaviour of test fish was filmed with a digital HD video camcorder (Sony model HDR-HC7) mounted overhead. From the video tapes, we recorded (i) the time when the predator model first started moving and (ii) the time when the test fish first visibly reacted to the approaching model, as indicated by an abrupt change in behaviour (e.g. interruption of foraging, fleeing). We calculated the test fish's response latency time to the approaching predator model by subtracting (i) from (ii).

(c) Personality trials: novel-object test

Prior to a novel-object trial, the test fish was measured (standard body length) and transferred with two size-matched 'companion' conspecific fish (each marked with a small elastomer tag, Northwest Marine Technology Inc., Shaw Island, WA, USA) into a holding tank (40 cm × 20 cm × 25 cm, $L \times W \times H$). Companion fish were used to minimize stress to the focal fish (Barlow 1968), which commonly occur in social groups as juveniles. Fish were given two days to acclimatize to their new home tank before the first novel-object trial was conducted. The novel object consisted of a block of small green or brown Lego (no. 6162; LEGO Canada Inc., Richmond Hill, Canada) attached to a small metal sinker. The test fish was presented with the brown Lego in one trial and the green Lego in the other (repeated) trial, with the order of presentation and trial time randomized. A test fish was given 10 min to settle after setting up a video camcorder in front of the tank, following which the novel object was placed in the center of the tank using long

forceps and fish behaviour recorded for 10 min. The novel object was removed at the end of the observation trial. From our analysis of the video tapes, we quantified the test fish's (i) latency to first approach the object, (ii) total number of approaches (to within 1 cm), and (iii) number of bites on the object. Aggressive interactions between the companion fish and the focal test fish were also recorded. One week after the first novel-object test trial (table 1), a second novel-object trial was conducted using the same protocol to ascertain repeatability of behaviour.

(d) Personality trials: exploration of novel-environment test

The day after the first and second novel-object test trials, we conducted novel-environment tests (table 1). The novel environment consisted of a tank (75 cm × 30 cm × 28 cm, $L \times W \times H$; water depth = 25 cm) divided into two compartments (a small holding compartment and a larger novel compartment/environment) with an opaque partition, equipped with a sliding door, and illuminated from above (figure 1b). The novel environment contained a gravel substratum and three plastic plants, which were either red or green (plant colour was alternated between the two repeated trials on each test fish, with the order of presentation randomized, to mitigate potential habituation to the environment between trials). The holding compartment contained the two tagged companion fish, in a weighted clear container, for the test fish to socially associate with. Test fish were individually transferred using a dip-net to the holding compartment of the tank and left undisturbed to acclimatize for 1 h. Following this period, the opaque sliding door of the compartment was raised remotely (using a string and pulley system) and the test fish was allowed up to 20 min to enter and swim freely in the open novel compartment. Once the test fish entered the novel environment, its behaviour was filmed for 10 min with a video camcorder 1 m from the front of the tank. A grid of 18 equal-sized squares (three rows of six) was taped to the back wall of the tank (figure 1b) to facilitate the recording of area explored by the test fish.

From our analysis of the video tapes, we quantified (i) latency of the test fish to leave the holding refuge area, (ii) proportion of trial time it spent in the refuge area, (iii) number of squares on the grid it traversed, and (iv) its activity level (number of darts forward and turns).

(e) Statistical analyses

All statistics were performed in R v. 2.6.2 (The R foundation for statistical computing, http://www.r-project.org/).

(i) Personality measures

Behavioural measures from the two tests of personality were analysed separately as some of the variables were binary, therefore making it difficult to robustly apply a principal components analysis (Quinn & Keough 2002). We only used behavioural measures that were repeatable across trials and therefore represented a robust measure of individual exploration of a novel environment and response to novelty in a familiar environment.

To ascertain whether individual test fish were consistent in their behaviour (and therefore to ensure that our behavioural measures could be used reliably to classify individuals into different behavioural types), we calculated the repeatability of each behavioural measure across the two repeated novel-object and novel-environment trials. Only variables which

were significantly repeatable (table 2) were used in subsequent analyses for comparison with fish response latency time to the approaching predator model.

Repeatability (R) was calculated by performing a general linear mixed model with individual fish identification (ID) inserted as a random factor in the model. From the resulting ANOVA results, the ratio of variance explained by fish ID to total variance represents a measure of repeatability of behaviour (following Nakagawa *et al.* 2007; Minderman *et al.* 2009). Confidence intervals around each repeatability estimate were calculated using a Fisher r-to-z transformation (Cohen *et al.* 2003), and z values were then divided by the standard error and compared against the z distribution. By way of comparison, our calculated R values were very similar to ones we alternatively obtained using the intraclass correlation coefficient method described in Lessells & Boag (1987).

(ii) Correlation between personality measures and response time to a fish predator model

The relationship between each repeatable personality measure and response latency time to the fish predator model was determined using the Pearson correlation test if both variables were continuous, Fisher's exact test if both were binary and linear models if one variable was continuous and the other binary. For linear models, we arbitrarily used the continuous variable as the dependent variable, but verified that the results were similar if the binary variable had been specified as the dependent variable (using a general linear model with a binomial link function); we therefore did not infer *a priori* the direction of the relationship. To control for potential confounding effects of brood, fish body size and order of predator-model presentation, we also constructed two mixed models (using the lmer function in *lme4* v. 0.999375-31 package (Bates & Maechler 2009) in R v. 2.6.2) with brood specified as a random effect, standard length and personality measure specified as fixed effects and response time as the dependent variable. Separate models were constructed for each of the three personality measures because small samples sizes and missing data meant a very reduced sample size with a full model. *p*-values were calculated using the pvals.fnc function in the languageR package v. 0.955 (Baayen 2009).

3. RESULTS
(a) Personality measures

For the novel-object test, two behavioural measures were repeatable (table 2); whether an individual bit the novel object or not (a response to novelty) and whether an individual chased either of the companion fish or not (a measure of aggression). For the novel-environment test, the number of grid squares explored (i.e. the amount of the environment explored in 10 min) was repeatable. Consequently, all subsequent analyses use the following personality measures: (i) biting/inspecting a novel object (binary two-level factor), (ii) chasing companion fish (binary two-level factor), and (iii) and number of grid squares explored (continuous covariate).

(b) Correlation between personality measures and response time to a fish predator model

There was no significant association between aggression (chase or not chase) and tendency to inspect a novel

Table 2. Repeatability estimates (and 95% confidence intervals) of fish behavioural measures obtained from novel-object and novel-environment tests. Estimates that are statistically significant are indicated in boldface. The actual p-values for the number of squares explored and chasing companion measures were 0.039 and 0.023, respectively.

type of test	behavioural measure	repeatability (R)	95% confidence interval
novel object	inspect or not	0.19	$-0.14, 0.53$
	bite object or not	**0.55****	0.31, 0.91
	chase companion fish or not	**0.40***	0.06, 0.79
	chased by companion fish or not	0.07	$-0.27, 0.42$
novel environment	leave refuge or not	0	$-0.30, 0.30$
	number of squares explored	**0.41***	0.02, 0.89
	activity level	0.15	$-0.32, 0.61$
	proportion of time in refuge	0	$-0.42, 0.42$

*$p < 0.05$.
**$p < 0.001$.

object (Fisher exact test, $p = 0.72$) nor between inspection of a novel object and exploration of a novel environment ($F_{1,34} = 0.89$, $p = 0.35$). However, there was a significant relationship between aggression and exploration of a novel environment ($F_{1,31} = 9.61$, $p = 0.004$). Fish that chased companion fish in the novel-object trial explored less of the novel environment (coefficient chase versus not chase $= -4.64$ squares).

There was a significant positive correlation between exploration of a novel environment during the first trial, where an individual fish entered the novel tank compartment (when this environment was most 'novel'), and the response latency time to the simulated predator attack while foraging (Pearson's correlation, $r_{22} = 0.52$, $p = 0.010$, figure 2). Controlling for the potential confounding influences of brood origin (variance close to zero), size of individual test fish ($p = 0.70$) and order of predator-model presentation ($p = 0.35$) did not remove the significant positive relationship between exploration of the novel environment and response latency time to a predator attack while foraging ($p = 0.0035$, estimate of slope $= 0.286$). To remove aggression as a potential confound, we repeated the analysis on chasing fish only (i.e. removing the five non-chasing fish, and five fish for which there were no aggression data, from the dataset). A positive relationship of similar magnitude remained, although marginally non-significant, between exploration and response latency time to the fish predator model ($r_{12} = 0.47$, $p = 0.089$) using this reduced dataset, which seems reasonable given the smaller sample size ($n = 14$).

There was no significant relationship between whether an individual bit the novel object or chased the companion fish in the novel-object trial and response latency time to the fish predator model (coefficient bite versus not bite $= -0.92$ s, $p = 0.28$, $n = 26$; coefficient chase versus not chase $= -0.60$ s, $p = 0.59$, $n = 21$, both models controlling for brood, order of presentation and fish standard length).

4. DISCUSSION

The major novel finding of our study is that juvenile convict cichlids that were more exploratory in a novel environment were slower to react to a simulated fish predator attack. This salient result supports the first of our two alternative hypotheses under test, namely, that the level of exploratory behaviour of an individual is negatively

correlated with its response time to an immediate predatory threat (in other words, fast explorers are slow reactors).

This observed relationship could be driven by two possible mechanisms. Firstly, consistent with the economic hypothesis of fleeing from predators (Ydenberg & Dill 1986; Fernandez-Juricic *et al.* 2002; Quinn & Cresswell 2005), bolder, more exploratory fish could devote more attention to foraging than to anti-predator vigilance, thereby delaying their response to a detected predator threat and reducing potential lost-opportunity foraging costs (Lima & Dill 1990). Devoting less attention to anti-predator vigilance may allow for more efficient foraging, but at the potential cost of increased risk of mortality to predation (Godin & Smith 1988; Krause & Godin 1996). Secondly, consistent with the perceptual limits hypothesis (Quinn & Cresswell 2005), fish differing in personality may be 'hard-wired' differently, having a different neurological capacity to detect predator attacks. In another study on convict cichlids (on adults rather than juveniles), Reddon & Hurd (2008) found that the extent of cerebral lateralization differed between aggressive and non-aggressive fish. Neurological architecture, such as cerebral lateralization, may also differ along other behavioural dimensions and has already been shown that it can influence vigilance behaviour in dark-eyed, juncos *Junco hyemalis* (Franklin & Lima 2001). Further research is required to elucidate potential relationships between predator detection, personality and brain structure.

Contrary to previous studies reporting that aggressive animals also tend to be more exploratory (Dingemanse & de Goede 2004; Bell & Sih 2007), we found the opposite in juvenile convict cichlids. Fish that chased conspecifics were less, not more, exploratory. However, this does not detract from our main result that fish that are more willing to leave a companion shoal and explore a novel environment are slower to respond to a predator attack, as the magnitude of this positive correlation remained relatively unchanged for those fish showing aggression in the novel-object trial.

Exploration of a novel environment by our experimental subjects was repeatable, although the large confidence intervals around the repeatability estimate suggest significant individual variation in behaviour, perhaps owing to plasticity in the amount of habituation to the experimental apparatus (Martin & Réale 2008). In repeated trials, an environment becomes less novel, and individuals
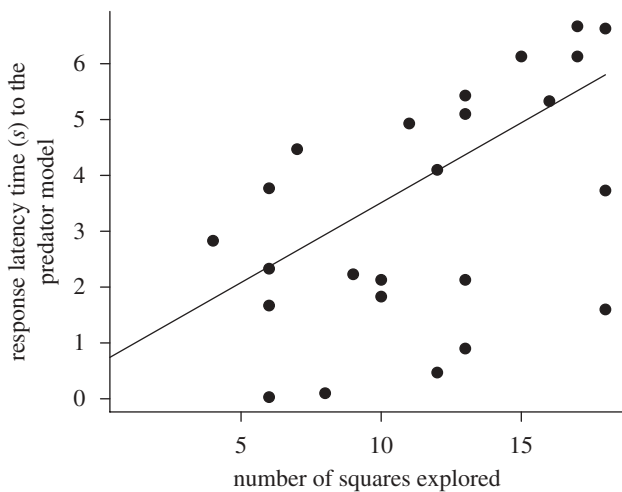
Figure 2. Relationship between the exploratory behaviour of individual test fish in the novel-environment test and their response latency time to an approaching fish predator model while foraging. Data presented are raw values. The regression line was obtained from our statistical model, which controlled for order of presentation and brood.

may even habituate to novelty itself (Réale *et al.* 2007). Here, we attempted to mitigate habituation by altering the colour of landmarks (plastic plants) in the environment between repeated trials. Given our sample size and significant repeatability estimate for exploration, we are confident that the number of grid squares explored by the test fish is a reliable measure of an individual's exploratory behaviour. The observed positive correlation between exploration and response latency time to a predator attack suggests that individuals consistently differ in their propensity to take risks across two different ecological contexts (i.e. exploration of novel habitats and response to a predation threat).

One limitation of our study is that we were unable to measure repeatability of response-delay behaviour. Very few studies have demonstrated repeatability of response delays (notably Fuiman & Cowan 2003). This is most likely not due to behaviour being unrepeatable (as animal behaviour is commonly repeatable; Bell *et al.* 2009), but rather owing to behavioural habituation effects (described above) being particularly strong when associated with negative stimuli such as a predator attack (thus making true repeatability of the behaviour difficult to quantify). As we were interested in how animals may partition their attention between foraging and anti-predator vigilance, our experimental set-up required individuals to forage in order to be subjected to an attack. However, with larger sample sizes (subject to ethical considerations) and for certain behaviours (cf. Bell *et al.* 2009), we believe measurement of repeatability of response delays to be a fruitful area for future research.

Our study does not demonstrate cause and effect. A behavioural syndrome is by definition a 'suite of correlated behaviors reflecting between-individual consistency in behavior across multiple (two or more) situations' (Sih *et al.* 2004). Therefore, it can be difficult to ascertain whether observed correlations are due to direct linkage of traits or due to so-called 'third variable effects'. A more robust test of the linkage between exploratory and predator-escape behavioural traits would be to selectively

breed fish lines based on their exploratory behaviour as juveniles and, after several generations, test whether fast and slow explorer groups differ in their response times to a predator attack. Speed of exploration here is taken to represent amount of a novel environment explored in a standardized time period, and not speed of movement *per se*, following van Oers *et al.* (2004). Working with the great tit, the latter researchers selectively bred lines of fast and slow explorers and then tested for differences in other unselected traits. They found that selectively bred fast explorers were more willing to take risks (such as returning to forage after being 'startled') than slow explorers. Nonetheless, our study does provide unique and novel evidence for a link between exploratory behaviour and predator-escape behaviour, which ultimately could have fitness consequences.

Recent work in behavioural ecology has shown a shift of emphasis from 'optimality' models to understanding why individuals within populations consistently behave differently and what maintains this variance in behaviour (reviewed in Dall *et al.* 2004; Bell 2007; Réale *et al.* 2007). Although we have a relatively good understanding of the various trade-offs between foraging and predation an individual animal can face, we are yet to fully explain why different individuals and different species adopt different anti-predator strategies. We suggest that being slow to flee from a predator is not always maladaptive but may simply represent an alternative behavioural strategy, operating much like alternative reproductive strategies and tactics (Gross 1996). In particular, the proximate mechanisms underlying variance in responses to predator attack (such as hormonal pathways and neurological pathways) need greater understanding. Further work on the fitness consequences of fleeing from predators is required to test whether the benefits of faster exploration outweigh the costs of being a slow reactor.

REFERENCES

Baayen, R. H. 2009 languageR: data sets and functions with "analyzing linguistic data: a practical introduction to statistics". R package version 0.955. See http://CRAN.R-project.org/package=languageR.

Barlow, G. W. 1968 Dither—a way to reduce undesirable fright behavior in ethological studies. *Z. Tierpsychol.* **25**, 315–318.

Bates, D. & Maechler, M. 2009 lme4: linear mixed-effects models using S4 classes. R package version 0.999375-31. See http://CRAN.R-project.org/package=lme4.

Bell, A. M. 2007 Future directions in behavioural syndromes research. *Proc. R. Soc. B* **274**, 755–761. (doi:10.1098/rspb.2006.0199)

Bell, A. M. & Sih, A. 2007 Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecol. Lett.* **10**, 828–834. (doi:10.1111/j.1461-0248.2007.01081.x)

Bell, A. M., Hankison, S. J. & Laskowski, K. L. 2009 The repeatability of behaviour: a meta-analysis. *Anim. Behav.* **77**, 771–783. (doi:10.1016/j.anbehav.2008.12.022)

Biro, P. A. & Post, J. R. 2008 Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proc. Natl Acad. Sci. USA* **105**, 2919–2922. (doi:10.1073/pnas.0708159105)

Budaev, S. V., Zworykin, D. D. & Mochek, A. D. 1999 Individual differences in parental care and behaviour profile in the convict cichlid: a correlation study. *Anim. Behav.* **58**, 195–202. (doi:10.1006/anbe.1999.1124)

Butler, S. J., Whittingham, M. J., Quinn, J. L. & Cresswell, W. 2005 Quantifying the interaction between food density and habitat structure in determining patch selection. *Anim. Behav.* **69**, 337–343. (doi:10.1016/j.anbehav.2004.06.006)

Clark, C. W. & Dukas, R. 2003 The behavioural ecology of a cognitive constraint: limited attention. *Behav. Ecol.* **14**, 151–156. (doi:10.1093/beheco/14.2.151)

Cohen, J., Cohen, P., West, S. G. & Aiken, L. S. 2003 *Applied multiple regression/correlation analysis for the behavioral sciences*, 3rd edn. Mahwah, NJ: Lawrence Erlbaum.

Cresswell, W., Hilton, G. M. & Ruxton, G. D. 2000 Evidence for a rule governing the avoidance of superfluous escape flights. *Proc. R. Soc. Lond. B* **267**, 733–737. (doi:10.1098/rspb.2000.1064)

Cresswell, W., Quinn, J. L., Whittingham, M. J. & Butler, S. 2003 Good foragers can also be good at detecting predators. *Proc. R. Soc. Lond. B* **270**, 1069–1076. (doi:10.1098/rspb.2003.2353)

Cresswell, W., Butler, S., Whittingham, M. J. & Quinn, J. L. 2009 Very short delays prior to escape from potential predators may function efficiently as adaptive risk-assessment periods. *Behaviour* **146**, 795–813. (doi:10.1163/156853909X446217)

Dall, S. R. X. & Witter, M. S. 1998 Feeding interruptions, diurnal mass changes and daily routines of behaviour in the zebra finch. *Anim. Behav.* **55**, 715–725. (doi:10.1006/anbe.1997.0749)

Dall, S. R. X., Houston, A. I. & McNamara, J. M. 2004 The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* **7**, 734–739. (doi:10.1111/j.1461-0248.2004.00618.x)

Dingemanse, N. J. & de Goede, P. 2004 The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behav. Ecol.* **15**, 1023–1030. (doi:10.1093/beheco/arh115)

Dukas, R. & Kamil, A. C. 2000 The cost of limited attention in blue jays. *Behav. Ecol.* **11**, 502–506. (doi:10.1093/beheco/11.5.502)

Dukas, R. & Kamil, A. C. 2001 Limited attention: the constraint underlying search image. *Behav. Ecol.* **12**, 192–199. (doi:10.1093/beheco/12.2.192)

Fernandez-Juricic, E., Jimenez, M. D. & Lucas, E. 2002 Factors affecting intra and interspecific variations in the difference between alert distances and flight distances for birds in forested habitats. *Can. J. Zool.* **80**, 1212–1220. (doi:10.1139/z02-104)

Fernandez-Juricic, E., Erichsen, J. T. & Kacelnik, A. 2004 Visual perception and social foraging in birds. *Trends Ecol. Evol.* **19**, 25–31.

Franklin, W. E. & Lima, S. L. 2001 Laterality in avian vigilance: do sparrows have a favourite eye? *Anim. Behav.* **62**, 879–885. (doi:10.1006/anbe.2001.1826)

Fuiman, L. A. & Cowan Jr, J. H. 2003 Behavior and recruitment success in fish larvae: repeatability and covariation of survival skills. *Ecology* **84**, 53–67. (doi:10.1890/0012-9658(2003)084[0053:BARSIF]2.0.CO;2)

Gilliam, J. F. & Fraser, D. F. 1987 Habitat selection under predation hazard—test of a model with foraging minnows. *Ecology* **68**, 1856–1862. (doi:10.2307/1939877)

Giraldeau, L.-A. & Caraco, T. 2000 *Social foraging theory*. Princeton, NJ: Princeton University Press.

Godin, G. J. 1997 Evading predators. In *Behavioural ecology of teleost fishes* (ed. J.-G. J. Godin), pp. 191–236. Oxford, UK: Oxford University Press.

Godin, J.-G. J. & Dugatkin, L. A. 1996 Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proc. Natl Acad. Sci. USA* **93**, 10 262–10 267. (doi:10.1073/pnas.93.19.10262)

Godin, J.-G. J. & Smith, S. A. 1988 A fitness cost of foraging in the guppy. *Nature* **333**, 69–71. (doi:10.1038/333069a0)

Gross, M. R. 1996 Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* **11**, 92–98. (doi:10.1016/0169-5347(96)81050-0)

Jones, K. A., Krebs, J. R. & Whittingham, M. J. 2009 Heavier birds react faster to predators: individual differences in the detection of stalking and ambush predators. *Behav. Ecol. Sociobiol.* **63**, 1319–1329. (doi:10.1007/s00265-009-0778-6)

Kaby, U. & Lind, J. 2003 What limits predator detection in blue tits (*Parus caeruleus*): posture, task or orientation? *Behav. Ecol. Sociobiol.* **54**, 534–538. (doi:10.1007/s00265-003-0665-5)

Krause, J. & Godin, G. J. 1996 Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey. *Behav. Ecol.* **7**, 264–271. (doi:10.1093/beheco/7.3.264)

Krause, J. & Ruxton, G. D. 2002 *Living in groups*. Oxford, UK: Oxford University Press.

Lessells, C. M. & Boag, P. T. 1987 Unrepeatable repeatabilities—a common mistake. *Auk* **104**, 116–121.

Lima, S. L. & Dill, L. M. 1990 Behavioral decisions made under the risk of predation—a review and prospectus. *Can. J. Zool.* **68**, 619–640. (doi:10.1139/z90-092)

Macleod, R., Gosler, A. G. & Cresswell, W. 2005 Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. *J. Anim. Ecol.* **74**, 956–964. (doi:10.1111/j.1365-2656.2005.00993.x)

Martin, J. G. A. & Réale, D. 2008 Temperament, risk assessment and habituation to novelty in eastern chipmunks *Tamias striatus*. *Anim. Behav.* **75**, 309–318. (doi:10.1016/j.anbehav.2007.05.026)

Milinski, M. 1984 A predator's costs of overcoming the confusion-effect of swarming prey. *Anim. Behav.* **32**, 1157–1162. (doi:10.1016/S0003-3472(84)80232-8)

Minderman, J., Reid, J. M., Evans, P. G. H. & Whittingham, M. J. 2009 Personality traits in wild starlings: exploration behavior and environmental sensitivity. *Behav. Ecol.* **20**, 830–837.

Nakagawa, S., Gillespie, D. O. S., Hatchwell, B. J. & Burke, T. 2007 Predictable males and unpredictable females: sex difference in repeatability of parental care in a wild bird population. *J. Evol. Biol.* **20**, 1674–1681. (doi:10.1111/j.1420-9101.2007.01403.x)

Quinn, J. L. & Cresswell, W. 2005 Escape response delays in wintering redshank, *Tringa totanus*, flocks: perceptual limits and economic decisions. *Anim. Behav.* **69**, 1285–1292. (doi:10.1016/j.anbehav.2004.10.007)

Quinn, G. P. & Keough, M. J. 2002 *Experimental design and data analysis for biologists*. Cambridge, UK: Cambridge University Press.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007 Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318. (doi:10.1111/j.1469-185X.2007.00010.x)

Reddon, A. R. & Hurd, P. L. 2008 Aggression, sex and individual differences in cerebral lateralization in a cichlid fish. *Biol. Lett.* **4**, 338–340. (doi:10.1098/rsbl.2008.0206)

Ruxton, G. D., Sherratt, T. N. & Speed, M. P. 2004 *Avoiding attack: the evolutionary ecology of crypsis, warning signals, and mimicry.* Oxford, UK: Oxford University Press.

Sih, A., Bell, A. & Johnson, J. C. 2004 Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**, 372–378. (doi:10.1016/j.tree.2004.04.009)

Smith, B. R. & Blumstein, D. T. 2008 Fitness consequences of personality: a meta-analysis. *Behav. Ecol.* **19**, 448–455. (doi:10.1093/beheco/arm144)

Stamps, J. A. 2007 Growth–mortality tradeoffs and 'personality traits' in animals. *Ecol. Lett.* **10**, 355–363. (doi:10.1111/j.1461-0248.2007.01034.x)

Stankowich, T. & Coss, R. G. 2006 Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. *Behav. Ecol.* **17**, 246–254. (doi:10.1093/beheco/arj020)

van Oers, K., Drent, P. J., de Goede, P. & van Noordwijk, A. J. 2004 Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proc. R. Soc. Lond. B* **271**, 65–73. (doi:10.1098/rspb.2003.2518)

Wilson, A. D. M. & McLaughlin, R. L. 2007 Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Anim. Behav.* **74**, 689–698. (doi:10.1016/j.anbehav.2007.01.009)

Ydenberg, R. C. & Dill, L. M. 1986 The economics of fleeing from predators. *Adv. Stud. Behav.* **16**, 229–249. (doi:10.1016/S0065-3454(08)60192-8)