

## LETTER

## Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*)

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### Abstract

A perplexing new question that has emerged from the recent surge of interest in behavioural syndromes or animal personalities is – why do individual animals behave consistently when behavioural flexibility is advantageous? If individuals have a tendency to be generally aggressive, then a relatively aggressive individual might be overly aggressive towards offspring, mates or even predators. Despite these costs, studies in several taxa have shown that individuals that are more aggressive are also relatively bold. However, the behavioural correlation is not universal; even within a species, population comparisons have shown that boldness and aggressiveness are correlated in populations of sticklebacks that are under strong predation pressure, but not in low predation populations. Here, we provide the first demonstration that an environmental factor can induce a correlation between boldness and aggressiveness. Boldness under predation risk and aggressiveness towards a conspecific were measured before and after sticklebacks were exposed to predation by trout, which preyed on half the sticklebacks. Exposure to predation generated the boldness–aggressiveness behavioural correlation. The behavioural correlation was produced by both selection by predators and behavioural plasticity. These results support the hypothesis that certain correlations between behaviours might be adaptive in some environments.

### Keywords

Aggression, behavioural syndrome, coping style, personality, plasticity, predation, stickleback.

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### INTRODUCTION

Behavioural correlations are difficult to explain because behavioural flexibility is advantageous (Sih *et al.* 2004a). For example, if individuals have a tendency to be generally aggressive, then a relatively aggressive individual might be overly aggressive towards offspring (Wingfield *et al.* 1990; Ketterson & Nolan 1999), mates (Johnson & Sih 2005) or even predators (Sih *et al.* 2004a). Despite these costs, studies in several taxa have shown that individuals that are more aggressive are also relatively bold (Huntingford 1976; Hedrick & Riechert 1989; Riechert & Hedrick 1990; Bell 2005; Johnson & Sih 2005). However, the behavioural correlation is not universal, even within a species: population comparisons (Bell 2005; Dingemanse *et al.* in press) have shown that sticklebacks from populations that are under strong predation pressure behave consistently

towards predators and conspecific competitors, but their counterparts from safe environments do not.

One possible reason why there is a behavioural correlation in high but not low predation populations could be that predators favour the correlation between boldness and aggressiveness via correlational selection. Correlational selection occurs when certain combinations of traits are favoured over others, such that the fitness of one trait depends on the value of other traits (Lande & Arnold 1983; Brodie *et al.* 1995; Svensson *et al.* 2001). For example, correlational selection favours certain combinations of colour patterns and escape behaviours in garter snakes (Brodie 1992). As both behavioural reactions to predators (Tulley & Huntingford 1987; Huntingford *et al.* 1994) and conspecifics (Bakker 1986) are partly heritable in sticklebacks, a response to natural selection by predators might have produced the correlation in high predation popula-

tions. However, it is worth keeping in mind that both of these behaviours are also sensitive to the environment (Huntingford & Wright 1992; Bell 2005).

In this experiment, we subjected sticklebacks from a population that did not exhibit a boldness–aggressiveness behavioural correlation to real predation in order to test the hypothesis that predators induce the behavioural correlation. Boldness and aggressiveness were measured on individually marked sticklebacks prior to exposure to real predation and after half of them had been consumed by rainbow trout (*Oncorhynchus mykiss*). To our knowledge, this is the first experiment to test whether behavioural correlations are favoured in certain environments.

## MATERIALS AND METHODS

Subadult sticklebacks were collected in February–March 2006 from Putah Creek, California and were brought to the Center for Aquatic Biology and Aquaculture, University of California, Davis. Historically, sticklebacks in Putah Creek have not been subjected to strong predatory selection by fish and boldness and aggressiveness are not correlated with each other in this population (Bell 2005). The sticklebacks were maintained in groups in 379-L flow-through fiberglass tanks on a natural (Davis) photoperiod at 17–18 °C. Sticklebacks were fed *c.* 10% of their body weight in frozen brine shrimp, live tubifex worms or frozen blood worms once a day.

Age 1+ trout (0.34–0.45 kg) were delivered to the laboratory from the Silverado Hatchery (California Fish and Game) on 8 March 2006. Three trout per pool were kept in four outdoor 379-L pools, which were supplied with well water at 16° and exposed to a natural (Davis) photoperiod. An identical pool adjacent to the experimental pools was used to hold animals in the ‘control’ group, which were not exposed to predation by trout. All of the pools were covered with mesh which prevented other predators (birds and mammals) from gaining access to the fish.

### Behavioural observations

Behavioural observations were carried out between 16 and 24 March 2006 (before) and between 3 and 7 April 2006 (after). The sticklebacks had been in the laboratory for 1–2 months. Throughout the experiment, we minimized the number of times each individual was netted to reduce a possible confounding effect of simulated predation. Twenty-four individuals were observed on each observation day. Individual sticklebacks were placed in 37.9 L aquaria where they were allowed to acclimate to the tank for one night before behavioural observations began. Each aquarium had a food cup attached at the surface near the front of the tank and a piece of 5 cm in diameter polyvinyl chloride

pipe which served as a refuge. Sticklebacks were deprived of food for 1 day prior to behavioural observations to standardize hunger levels. At least 10 min prior to behavioural observations, opaque dividers were inserted between the aquaria to prevent visual contact between the sticklebacks.

### Measuring aggressiveness towards conspecifics

Individual levels of aggressiveness were assessed by recording their behavioural response to a simulated intrusion by a competitor. During this assay, the focal fish typically behaves aggressively towards the unfamiliar conspecific probably due to a prior residence advantage. A conspecific of approximately the same size (within 5 mm standard length) as the focal fish was gently netted from a holding tank containing 20 individually marked sticklebacks which acted as intruders. Several intruders were used to prevent chronic stress caused by repeated fighting. The intruder was gently placed into a cup and lowered into the focal fish’s tank and the focal fish’s response to the simulated intrusion was recorded for 5 min after the focal fish first oriented to the intruder. We defined orienting as occurring when the focal fish turned its body head-first towards the intruder and visually tracked the intruder by orienting to it. Specifically, we measured the latency to bite the intruder, the total time spent orienting, the number of times the focal fish oriented to the intruder, the number of chases, the number of bites delivered to the intruder and the time spent within one body length of the intruder.

### Measuring boldness under predation risk

At least 2 h after a fish was observed for aggressiveness, we measured its willingness to forage under predation risk by a simulated bird predator (Jonsson *et al.* 1996; Krause *et al.* 1998; Bell 2005). We carefully secured a great egret skull directly over the focal fish’s tank and placed six live tubifex worms into a food cup located directly under the egret skull. After the fish took a bite of food from the food cup, the egret skull was quickly released, simulating a strike. It is important to note that this assay of willingness to forage under predation risk required an initial behavioural response to the threat.

At the end of each observation day, sticklebacks were marked with an elastomer tag (Northwest Marine Technologies, Shaw Island, WA, USA) under a low dose (5 mg L<sup>-1</sup>) of anaesthetic (MS-222). Each fish was injected in four different locations with one of three different colours (yellow, orange or red) with a fine syringe (29-gauge). The different colour combinations were randomly assigned. The elastomer was injected under the skin and is only visible under UV light. After marking, fish were allowed to recover

from the anaesthesia in a bucket with an airstone and refuge. Behavioural observations took place over the course of 8 days. Fish were measured for length with a measuring board to the nearest 1 mm and weight with an electronic balance to the nearest 0.01 g and were randomly assigned to one of the five pools. The fish were then transferred to holding tanks (one tank per pool).

After all of the fish were observed and marked, the sticklebacks were transferred to the system of outdoor pools. Each pool contained two refuges which consisted of a 20 × 35 cm piece of transparent grey plexiglass supported by four different screws at 5 cm height which allowed many sticklebacks at a time to hide under the plexiglass but did not allow trout to enter. Although this standardized, experimental set-up is simple relative to more complex natural environments, it includes refuges and sufficient space for prey to exhibit their natural antipredator behaviours. It should thus be suitable for determining whether exposure to predation induces the behavioural correlation.

Prior to actual predation, the density of sticklebacks was  $n = 34\text{--}36$  per experimental pool and  $n = 20$  in the control pool. We monitored the pools via visual inspection to determine when approximately half of the sticklebacks had been consumed by the trout (24 h after the sticklebacks were added to the pools), at which point we removed the trout. The survivors' boldness and aggressiveness were re-assayed within 1 week after the trout were removed following the same procedures described above ('after').

### Data analysis

To reduce the dimensionality of the data set for the selection analysis (Brodie *et al.* 1995), we identified one behaviour in each context (aggressiveness and willingness to forage under predation risk) that was variable across individuals and which summarized their overall behavioural response: number of orients to the conspecific and time spent eating under predation risk. We interpret orienting as a mild form of aggression because it was positively correlated with attacking a conspecific, and an attack was always preceded by orienting.

As some of the behavioural variables were not normally distributed, we tested for the effects of body size, pool, treatment (control/experimental) on behaviour using the appropriate nonparametric tests. Correlations between behaviours within (boldness before and after, aggressiveness before and after) and across (boldness and aggressiveness before, boldness and aggressiveness after) contexts were assessed by Spearman's rank nonparametric correlations. We tested for differences in correlation coefficients using Fisher's  $Z$  transformation (Zar 1999).

Of the 122 experimental individuals measured before exposure to predation, 65 individuals were consumed by the

trout and 57 individuals survived. The control group consisted of 20 individuals. We found no effect of either length or weight on behaviour or survivorship and therefore did not include those variables in the phenotypic selection analysis (see *Results*).

Phenotypic selection gradient analysis (Lande & Arnold 1983) was employed to identify the best behavioural predictors of fitness (survivorship) while accounting for both direct and indirect selection. First, we standardized the 'before' behavioural variables within the experimental group. Then, we used linear regression to regress the standardized values, their squared terms and the cross-products of the pairwise combination on relative fitness (whether an individual died or survived, divided by average fitness of the population) to estimate directional, stabilizing and correlational selection gradients, respectively. As we predicted *a priori* that boldness would be selected against (Dugatkin 1992; Biro *et al.* 2004), we used a one-tailed test for this variable. All other statistical tests were two-tailed.

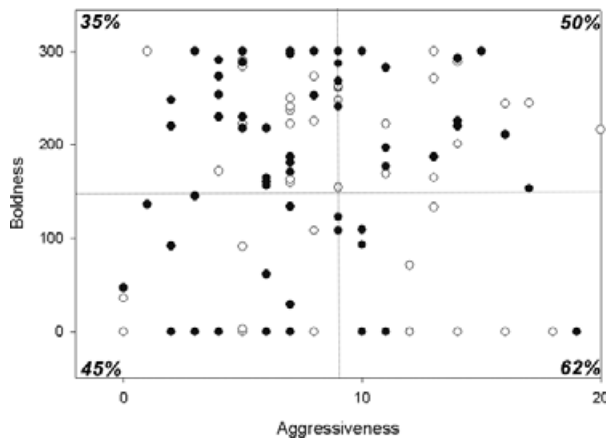
In addition to this measure of correlational selection, we divided individuals into four groups based on whether they were above or below the mean values for boldness and aggressiveness. We then used a chi-squared test to determine if certain combinations of behaviours (bold and aggressive, bold and non-aggressive, etc.) had higher survivorship than others. We compared behaviour 'before' and 'after' exposure to trout using paired (Wilcoxon signed rank test) analyses of the behaviour of the survivors.

### RESULTS

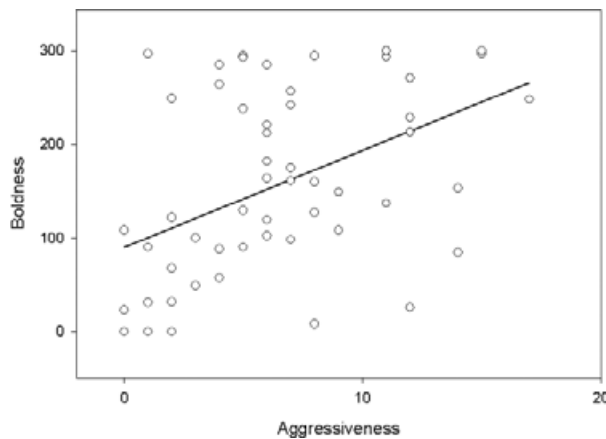
Neither length nor weight was related to behaviour (weight: aggression  $r = 0.124$ ,  $P = 0.177$ , boldness  $r = 0.010$ ,  $P = 0.913$ ; length: aggression  $r = 0.104$ ,  $P = 0.258$ , boldness  $r = 0.027$ ,  $P = 0.766$ ) or survival (regression length  $\beta = -0.408$ ,  $P = 0.067$ , weight  $\beta = 0.333$ ,  $P = 0.134$ ). The average length of the experimental animals was  $42 \pm 4.1$  mm SD and weight was  $1.02 \pm 0.34$  g SD. We did not detect an effect of experimental pool on behaviour or the correlation using ANCOVA (after aggression: pool  $F_{3,56} = 1.274$ ,  $P = 0.294$ , pool \* boldness  $F_{3,56} = 2.251$ ,  $P = 0.094$ ).

Prior to exposure to actual predation by trout, aggressiveness (orients towards a conspecific) was not correlated with boldness (time eating under predation risk; Fig. 1,  $r = 0.143$ ,  $P = 0.117$ ). This result is in agreement with other studies which have found that this population of sticklebacks does not have the boldness–aggressiveness behavioural syndrome (Bell & Stamps 2004; Bell 2005).

However, the behaviours became significantly positively correlated after exposure to real predation by live trout (Fig. 2,  $r = 0.459$ ,  $P < 0.001$ ). The before and after exposure to predation correlation coefficients between



**Figure 1** The behaviours were not correlated prior to exposure with real predation. Individual differences in aggressiveness (number of orients to an unfamiliar intruder) were not correlated with boldness under predation risk (time spent eating following a simulated attack by an egret). Survivors are represented by open circles, individuals that were consumed by the trout are represented by closed circles. Some circles represent more than one individual. Rates of survivorship in each quartile are marked.



**Figure 2** The behavioural correlation appeared among the survivors.

boldness and aggressiveness are significantly different from each other ( $Z = 2.43$ ,  $P = 0.008$ ).

The failure to detect a correlation before predation was not due to lack of variance or lack of statistical power (see Fig. 1). Indeed, it is important to note that the sample size after predation was less than half of what it was before exposure to predation. In addition, events other than exposure to the trout were not sufficient to generate the correlation: the behaviours were not correlated in the control group either before ( $r = 0.366$ ,  $P = 0.113$ ) or after the control animals were placed in a pool which did not contain trout ( $r = -0.175$ ,  $P = 0.460$ ). Finally, differences

between pools did not affect the correlation (partial correlation coefficient, controlling for the effect of pool = 0.446,  $P < 0.001$ ).

One possible mechanism that could have generated the correlation after exposure to predation is natural selection favouring individuals that behaved in a consistent way towards both predators and conspecifics. That is, perhaps individuals that were either bold or aggressive, shy and non-aggressive or showed intermediate levels of both behaviour survived better than individuals that were mismatched. Another process that could have produced the behavioural correlation after exposure to real predation by trout is behavioural plasticity. That is, perhaps individuals changed their behaviour to generate the correlation after exposure to predation.

We found that both selection and plasticity contributed to the induced correlation between boldness and aggressiveness. With respect to selection, as predicted (Dugatkin 1992; Biro *et al.* 2004), bold individuals were more likely to be consumed by the trout (Table 1). In addition, there was directional selection favouring aggressiveness: sticklebacks that were more aggressive and more likely to survive exposure to predators (Table 1).

More intriguingly, an individual's combination of behaviours was also important for fitness, but selection was not correlational. Among the individuals that survived predation, boldness and aggressiveness before exposure to predation were not correlated ( $r = 0.177$ ,  $P = 0.188$ ). This result is in agreement with the phenotypic selection analysis, which did not detect significant correlational selection favouring the correlation ( $\beta = 0.095$ ,  $P > 0.05$ ). Instead, individuals that were both bold and unaggressive suffered the highest mortality (Fig. 1,  $\chi^2 = 7.875$ , d.f. = 3,  $P = 0.049$ ). That is, there were antagonistic selection pressures on two positively correlated traits: selection favoured aggressive individuals and shy individuals.

**Table 1** Directional, stabilizing and correlational standardized selection gradients ( $\beta$ ) from linear regression

	$\beta$	$P$ -value	Selection differential
Number of orients	0.207	0.043	$8 \pm 0.4 - 6 \pm 0.6$
Time eating	-0.155	0.051	$151 \pm 10.5 - 153 \pm 13.4$
Number of orients * time eating	0.043	0.640	
Number of orients <sup>2</sup>	-0.067	0.502	
Time eating <sup>2</sup>	0.084	0.760	

Model  $F_{5,121} = 1.471$ ,  $P = 0.205$ . All  $P$ -values are two-tailed except time eating. The selection differentials show the difference between the population means before and after selection. There is a statistically significant difference between mean orients before and after (see text).

But selection is not the whole story because individuals changed how they behaved after they were exposed to trout which ate half of their conspecifics: they became less aggressive (survivors only: paired Wilcoxon signed ranks test  $Z = -2.444$ ,  $n = 57$ ,  $P = 0.015$ ). Behavioural plasticity was not observed in the control group, which showed no difference in aggressiveness before and after exposure to trout (paired Wilcoxon signed ranks test  $Z = -1.474$ ,  $P = 0.140$ ).

Moreover, exposure to predators shuffled the rank order differences between individuals in aggressiveness: the fish that were relatively aggressive before exposure to real predation risk were not necessarily the most aggressive individuals afterwards ( $r = -0.014$ ,  $P = 0.921$ ).

Surprisingly, individuals did not tend to change their boldness under predation risk after exposure to predators (Mann–Whitney  $Z = -0.176$ ,  $P = 0.861$ ) and boldness was stable across individuals: time spent eating before exposure to the trout was correlated with time spent eating afterwards ( $r = 0.29$ ,  $P = 0.029$ ).

## DISCUSSION

Population comparisons (Bell 2005; Dingemanse *et al.* in press) have shown that boldness and aggressiveness tend to covary in 'high predation' populations. This study provides experimental evidence that predation favours the correlation between boldness towards predators and aggressiveness towards conspecifics.

We found that there were both selected and plastic responses to predation. As predicted, individuals that were more willing to forage under predation risk were less likely to survive in the face of real predation. In addition, sticklebacks that were more aggressive were more likely to survive exposure to predators. This result is consistent with the field pattern showing that levels of aggression are higher in high predation populations (Giles & Huntingford 1984; Bell 2005). Because aggressiveness was measured in the absence of predation risk, this result implies that more aggressive individuals have some other attribute that is related to performance during predation. We suspect that more aggressive individuals are more attentive to the behaviour of either a conspecific or heterospecific, which might contribute to their ability to survive during a predatory challenge.

It is interesting to note that even though selection favoured more aggressive individuals, levels of aggressiveness actually decreased after predation risk was removed. One possible explanation for this pattern is that after being stressed by the predator (Bell *et al.* 2007) sticklebacks became acclimated to stress generally and became less reactive to other challenges. Another possibility is that perhaps the dampening effects of predation risk on

behaviour persisted after risk was removed because information about predation risk was still uncertain (Sih 1992).

Aggressiveness appears to be generally more malleable than boldness. For example, individual differences in aggressiveness were not stable across individuals and the fish that frequently oriented before exposure to real predation were not necessarily the individuals that engaged in high levels of this behaviour afterwards. In contrast, willingness to forage under predation risk did not change after exposure to trout and was stable across individuals.

We infer that predation generated the boldness–aggressiveness behavioural correlation by removing individuals that were bold and unaggressive from the population, and by causing individuals to reduce their aggressiveness. We suspect that the contribution of plasticity to the correlation was driven primarily by changes in aggressiveness. A rough approximation of the change in the correlation due to plasticity is reflected in the difference between the correlation coefficients of the survivors 'before' ( $r = 0.177$ ) and 'after' predation ( $r = 0.459$ ). However, a strong test of the plasticity hypothesis needs to evaluate the effect of exposure to non-lethal risk on the correlation.

There is increasing evidence for covariance among behavioural responses [reviewed in Koolhaas *et al.* (1999), Gosling (2001), Sih *et al.* (2004b), Dingemanse & Reale (2005) and Bell (2007)]. Like other morphological or life history traits, many behaviours (including boldness and aggressiveness) that comprise behavioural syndromes are influenced by both inherited genetic and environmental factors. Therefore, both evolutionary and plastic responses to the environment could depend on the values of other, correlated behaviours (Stamps 2003). Future development of theory and a quantitative framework to explore the joint influence of correlational selection and correlational behavioural plasticity (e.g. Schlichting 1989; Stearns *et al.* 1991; DeWitt *et al.* 1999; Relyea 2002; Malusa *et al.* 2005; Parsons & Robinson 2006) should prove insightful.

An outstanding question that remains is – *why does predation favour the correlation?* That is, why are boldness and aggressiveness coupled together when predation is strong? One possibility is that stressful conditions impose a tradeoff (Van Noordwijk & de Jong 1986) and cause tighter correlations among traits (Waite & Levin 1993; Newman 1994; Badyaev & Foresman 2004). On a more behavioural level, another possibility is that there are different strategies for coping with predators, which is related to behaviours in other contexts. For example, in sticklebacks, schooling (Ward *et al.* 2002) and predator inspection (Walling *et al.* 2004) represent alternative antipredator tactics. Perhaps schooling individuals are fearful and rely on the safety of the school for protection against predators, whereas predator inspectors boldly approach predators to gain information about the threat of predation. If individuals vary in the

antipredator tactics that they employ, then that might also explain correlated individual differences in aggressiveness. High levels of aggression are incompatible with effective schooling (Magurran & Seghers 1994), so individuals relying on schooling for defence should be non-aggressive. In contrast, predator inspectors can afford to be generally aggressive.

The explanation proposed above could apply not just to sticklebacks, but also to other situations where prey individuals engage in alternative antipredator styles involving unaggressive group defence vs. aggressive individual defence (Fuiman & Cowan 2003). We suggest that a general mechanism that could generate and maintain alternative behavioural styles is if an individual's antipredator style is linked to some other stable, less plastic aspect of their state – e.g. their access to information or life history strategies. Bold individuals might have access to more information about risk or be on a particular life history trajectory (Stamps 2007; Wolf *et al.* 2007), and therefore be more likely to take risks in other situations.

Finally, in addition to the implications of these results for behavioural evolution in animals, this study is also relevant to studies of human personality. It is commonly observed that certain personalities tend to occur in certain environments (person–environment correlation; Plomin 2005). For instance, neurotic individuals are more likely to experience stressful life events. Such person–environment correlations might reflect active or passive situation choice. In the former case, certain personalities preferentially select certain environments. In the latter case, the environment favours certain personalities. Our results suggest that both types of mechanisms might be operating in sticklebacks: individuals plastically changed their behaviour in response to predators (active) but selection also favoured certain behavioural types over others (passive).

In conclusion, we found that exposure to predation generated a behavioural syndrome. The behavioural correlation was produced by both selection by predators and behavioural plasticity. These results support the hypothesis that certain combinations of behaviours might be adaptive in some environments (Dall *et al.* 2004; Bell 2005).

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