



Prey behavioural reaction norms: Response to threat predicts susceptibility to predation



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Behavioural syndromes (i.e. population-level behavioural correlations) arise when individuals, on average, maintain the same behavioural expression across different ecological contexts. Population-level syndromes can appear maladaptive, such as when prey remain active across the absence and presence of a sit-and-wait predator. Yet in nature, individuals often vary in syndrome adherence, exhibiting individual-level differences in behavioural plasticity. Here, I use an experiment to show that individual behavioural plasticity (a reduction in activity level in the presence of predation threat) increases a prey's likelihood of surviving predator exposure, and further predicts survival better than single-context activity level measures. In an additional experiment, I identify conditioning (nonlethal predator exposure) as a process that reduces prey activity level. This work demonstrates that although population-level behavioural syndromes can appear maladaptive, behavioural plasticity and conditioning could potentially ameliorate negative effects at the individual level.

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Animal personality describes among-individual variation in behaviour that persists over time (i.e. behavioural types; Bell, Hankison, & Laskowski, 2009) and across ecological contexts (i.e. behavioural syndromes; Sih, Bell, & Johnson, 2004). The occurrence of personality across diverse taxa (Bell et al., 2009; Gosling, 2001) suggests that within-individual behavioural variation is often limited. This raises questions regarding the existence and maintenance of personality in nature, because an individual's failure to modify behaviour across environmental contexts (i.e. behavioural spillover) can entail significant costs. In fishing spiders (*Dolomedes triton*) for example, aggression towards conspecifics is correlated with precopulatory sexual cannibalism (i.e. mate consumption prior to copulation; a maladaptive behaviour), forming part of a population-level behavioural syndrome between foraging, predator avoidance and mating (Johnson & Sih, 2005). Interestingly, a number of recent studies show that even when behavioural syndromes are present at the population level, individuals may still differ in the amount of behavioural plasticity they exhibit in response to changing environmental context (Dingemanse & Wolf, 2013; Dingemanse, Kazem, Réale, & Wright, 2010; Mathot et al., 2011; Mathot, Wright, Kempnaers, & Dingemanse, 2012).

Individual plasticity could potentially alleviate the negative effects of behavioural spillover and is further predicted to have important consequences for a number of ecological processes such as population stability, persistence and species interactions (Dingemanse & Wolf, 2013; Mathot et al., 2011). Nevertheless, few studies have tested the effects of individual behavioural plasticity on ecological dynamics.

Examining the fitness consequences of animal personality and individual plasticity is essential to understanding the ecological and evolutionary significance of individual-level behavioural differences (Smith & Blumstein, 2008; Wolf, Van Doorn, Leimar, & Weissing, 2007; Wolf, Van Doorn, & Weissing, 2008). Fluctuating selection, or trade-offs across environmental contexts or time, is a frequently cited process maintaining behavioural syndromes within natural populations despite the potentially negative consequences of behavioural spillover (Ballew, Mittelbach, & Scribner, 2017; Boon, Réale, & Boutin, 2007; Dingemanse, Both, Drent, & Tinbergen, 2004; Le Cœur et al., 2015). For example, in a consumer population that varies along a boldness–shyness (i.e. risk-taking) continuum, bold individuals may forage at a higher rate (Carter, Goldizen, & Tromp, 2010; Griffen, Toscano, & Gatto, 2012; Toscano & Griffen, 2014; Toscano, Gownaris, Heerhartz, & Monaco, 2016) but suffer reduced survival due to increased predation risk (Biro, Abrahams, Post, & Parkinson, 2006, 2004; Carter et al., 2010; Smith & Blumstein, 2008). In such a scenario, spatial or temporal variation in predation intensity ensures that neither

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behavioural type performs consistently better across contexts, thereby homogenizing fitness (Dingemans & Réale, 2005; Réale & Festa-Bianchet, 2003).

Still, behavioural plasticity should be relatively advantageous if individuals optimize their behaviour according to ecological context (Wolf & Weissing, 2010), although plasticity itself can entail costs (DeWitt, Sih, & Wilson, 1998; Snell-Rood, 2013). While a number of studies have tested how behavioural types and behavioural syndromes affect survival (Bremner-Harrison, Prodohl, & Elwood, 2004; Carlson & Langkilde, 2014; Carter et al., 2010; Le Cœur et al., 2015; Réale & Festa-Bianchet, 2003; Yli-Renko, Vesakoski, & Pettay, 2015), relatively few have examined the fitness consequences of individual behavioural plasticity per se (but see Blake & Gabor, 2014). Behavioural reaction norms decompose individual behaviour into relatively stable (animal personality) and labile (plasticity) components (Dingemans et al., 2010), and thus can be used to quantify individual behavioural plasticity and its effects on aspects of individual fitness. Behavioural reaction norms can be measured whenever a single behavioural trait is assayed across two or more ecological contexts. Within this reaction norm framework, the intercept of the reaction norm is closely related to animal personality (Mathot et al., 2012): if individuals maintain a similar rank order across environmental contexts, this will produce a population-level behavioural syndrome. However, even when rank order is maintained, individuals may differ in the slope of their reaction norm (Dingemans & Wolf, 2013), providing a measure of individual behavioural plasticity (Favreau et al., 2014). Behavioural plasticity could allow individuals to avoid the costs of behavioural spillover even when a behavioural syndrome is present at the population level.

The main goal of the present study was to examine how prey behavioural types measured in single contexts and individual behavioural plasticity measured across contexts affect prey survival in the presence of a predator. I accomplished this using a well-studied predator–prey interaction between oyster toadfish, *Opsanus tau*, and the common mud crab, *Panopeus herbstii* (Grabowski & Kimbro, 2005; Grabowski, 2004; Grabowski, Hughes, & Kimbro, 2008; Griffen et al., 2012; Kimbro, Byers, Grabowski, Hughes, & Piehler, 2014; Toscano & Griffen, 2014; Toscano, Fodrie, Madsen, & Powers, 2010). To avoid being eaten, mud crabs reduce activity in the presence of waterborne chemical cues from ambush (i.e. sit-and-wait)-foraging toadfish (Belgrad & Griffen, 2016; Grabowski, 2004; Griffen et al., 2012; Gudger, 1910; Toscano & Monaco, 2015). This behavioural response reduces the foraging rate of crabs on their main prey, juvenile bivalves (Toscano & Griffen, 2012), driving a strong behaviourally mediated trophic cascade (Grabowski & Kimbro, 2005; Grabowski, 2004) that is geographically widespread (Kimbro et al., 2014).

Previous work shows that mud crabs exhibit consistent individual differences in activity level measured both in the absence and presence of toadfish predation threat (i.e. behavioural types; Toscano, Gatto, & Griffen, 2014; Toscano & Monaco, 2015), and these differences are stable (i.e. repeatable) over both short (48 h: Toscano & Monaco, 2015) and relatively long time spans (up to 81 days: Toscano et al., 2014). Furthermore, the effects of among-individual variation in crab activity cascade to lower trophic levels: crabs that exhibit high activity consume more mussels (*Brachidontes exustus*) than less active crabs (Griffen et al., 2012; Toscano & Griffen, 2014). Thus increased activity can benefit crabs by increasing their energetic intake. These aforementioned feeding experiments, however, were conducted in the absence of toadfish per se. Heightened activity in the presence of threat could increase vulnerability to toadfish predation as a consequence of behavioural spillover across ecological contexts.

Here, I measured individual crab activity level in the absence and presence of toadfish predation threat and then exposed crabs

to toadfish predation and tracked crab survival. Measuring activity level across ecological contexts allowed me to quantify behavioural plasticity (i.e. the activity response to predation threat) and its effect on crab survival. I hypothesized that crabs that reduce their activity to a greater degree in the presence of predation threat would be more likely to survive predator exposure. In an additional experiment, I tested whether crab activity level was a relatively stable trait or could be modified with continuous exposure to waterborne chemical cues from toadfish (i.e. conditioning). I hypothesized that crabs exposed to toadfish chemical cues would reduce activity level over time relative to control crabs. Such a finding would suggest conditioning as a process generating behavioural variation among individual crabs. In theory, behavioural plasticity across contexts and conditioning to predator presence could allow individual prey to adjust, respectively, to short- and long-term variation in predation risk, thus enhancing survival across gradients in predation intensity.

METHODS

Experiments were conducted from May through August 2013 in a screened-in, outdoor wet laboratory at the Baruch Marine Field Laboratory (Georgetown, SC, U.S.A.). The Baruch Marine Field Laboratory is adjacent to North Inlet estuary (33°20'N, 79°10'W) and situated within the North Inlet-Winyah Bay National Estuarine Research Reserve (NERR). Mud crabs and toadfish inhabit biogenic reefs formed by oysters (*Crassostrea virginica*) along the eastern coast of the U.S. and Gulf of Mexico (Dame, 1979; Kimbro et al., 2014; Wells, 1961). Within North Inlet, intertidal oyster (*Crassostrea virginica*) reefs provide the only hard-bottom habitat, supporting a diverse, multitrophic food web (Dame & Patten, 1981; Dame, 1979). Mud crabs were collected by hand from reefs in North Inlet for use in this study. Toadfish, which inhabit burrows within reefs, are a major predator of mud crabs in coastal South Carolina where mud crabs are present in up to 65% of toadfish stomachs (Wilson, Dean, & Radtke, 1982). Toadfish were collected either by excavating their burrows or using baited fish traps set on the edges of reefs and left overnight. Animals used in this study were collected under Scientific Permit No. 2999 from the South Carolina Department of Natural Resources.

Testing for a Behavioural Syndrome

I first tested for the presence of a behavioural syndrome, or more specifically, for a population-level correlation between individual crab activity level measured in the absence versus presence of toadfish predation threat. Activity level represents one of five major personality axes (activity, exploration, boldness, aggressiveness and sociability: Réale, Reader, Sol, McDougall, & Dingemans, 2007), and is frequently measured as the spatial or temporal amount of individual movement in an environment familiar to the test animal. In contrast, activity level measured in the presence of threat is often taken as boldness, defined as an individual's reaction to a risky, but not novel, situation (Réale et al., 2007).

I used adult crabs ($N = 64$) from a narrow size range (mean carapace width (CW) ± 1 SD: 29.35 ± 1.31 mm) to test for this behavioural syndrome. Crab size variation was minimized throughout this study because activity level increases with crab size (Griffen et al., 2012; Toscano et al., 2014) and my focus here was on activity as a personality trait that varies independently of other phenotypic traits. Even within a narrow size range, crab activity level measured in the absence of threat varies substantially among individuals and is repeatable over time (Toscano & Monaco, 2015).

Individual crab activity level was measured both in the absence and presence of toadfish predation threat in a temporally blocked

design ($N = 4$ blocks total; a fifth block was conducted but removed due to toadfish mortality). For each block, I first collected 16 crabs and marked these crabs using individually numbered bee tags (queen marking kit: the Bee Works®, Orillia, ON, Canada) fixed to the centre of crab carapaces with superglue. Crabs were marked to keep track of individuals over the duration of the study. To standardize hunger levels, I then fed these crabs crushed hard clams (*Mercenaria mercenaria*) and starved them for ~24 h in the laboratory before the first behavioural measurement. Crabs were held in individual tackle box container compartments (3 length \times 3 cm width) during this starvation period and tackle boxes (with holes drilled for water exchange) were submerged in flow-through, unfiltered sea water pumped in from North Inlet. On the first night after this initial starvation period, I measured the activity level of eight crabs in the absence of predation threat and simultaneously measured the activity level of the other eight crabs in the presence of predation threat. Treatment order was varied within blocks to control for a potential effect of treatment order on crab behaviour due to prior experience (Williams, 1949). Crabs were then fed immediately following this first behavioural measurement and again starved for 24 h before their activity level was measured under the alternative treatment on the second night.

I measured individual crab activity level following similar methods to those used in previous studies of *P. herbstii* individual behaviour (Griffen et al., 2012; Toscano & Monaco, 2015; Toscano et al., 2014). The activity level of each crab was measured in a plastic mesocosm (43 \times 31 cm and 18 cm tall) that received continuous flow-through unfiltered sea water. Mesocosms were set up to mimic natural oyster reef habitat. Each mesocosm received sand substrate (1 cm deep) and a matrix of loose oyster shell (6 cm deep) that had been scrubbed clean and dried to remove epifauna. Mesocosms additionally received a mesh bag containing five scorched mussels (*B. exustus*) hung just below the water surface. Scorched mussels are a main prey for mud crabs (Toscano & Griffen, 2012, 2014) and while these mussels were never consumed by crabs, they released chemical cues through filter-feeding, which presumably induced crab foraging. The measurement of activity level began at 2000–2300 hours and lasted for 3 h. Observations were made under red light and behind a blind to minimize observer disturbance of crabs.

To measure activity level, I placed crabs in mesocosms and allowed them to acclimate for 15 min. After this acclimation period, I observed crab behaviour once every 9 min over 3 h, yielding 20 total behavioural observations per crab. During each observation, I recorded whether crabs were active (usually walking on top of the oyster shell matrix) or inactive (usually hiding beneath shells). Crab activity level was calculated as the proportion of observations where crabs were active out of 20 total observations. Thus activity level measurement followed a standard scan-sampling procedure (Martin, Bateson, & Bateson, 1993). To measure activity level in the presence of predation threat from toadfish, sea water was first passed through a holding chamber that contained a single adult toadfish (38 mm total length (TL)) that was fed mud crabs daily between trials. Following behavioural measurements, these same 64 crabs of known behaviour were used in a predation experiment that examined the effects of crab activity level on susceptibility to toadfish predation (see [Predation Experiment](#)).

To test for a behavioural syndrome, I examined the relationship between crab activity level measured in the absence versus presence of toadfish predation threat. I did this using a generalized linear mixed model (GLMM; glmer function, lme4 package in the statistical software; R Core Development Team, 2012) with activity level in the presence of threat as the response variable and activity level in the absence of threat as a fixed effect. Because crab activity level was quantified as a proportion, I used a binomial error

distribution and logit link. I also included treatment order (varied within blocks) and crab carapace width as fixed effects to test whether treatment order and crab size influenced crab behaviour. Experimental block was modelled as a random factor. I tested the significance of fixed effects by dropping fixed effects and comparing nested models using likelihood ratio tests. The random effect of block was retained in all model comparisons. I additionally tested for a simple correlation between crab activity level measured in the absence versus presence of threat using a nonparametric Spearman's rank correlation test.

I tested the overall effect of predation threat on crab activity level using a GLMM (binomial error distribution and logit link) with activity level as the response variable and predation threat (absent or present) as a fixed factor. I further included crab ID (two activity level measurements per crab) and experimental block as random effects to account for these sources of nonindependence. I tested the effect of predation threat by dropping this factor and comparing nested models (retaining random effects) using a likelihood ratio test.

Predation Experiment

Following behavioural measurement, I subjected these 64 crabs to toadfish predation. For each block ($N = 16$ crabs), I first ranked crabs based on their activity level in the presence of threat and then divided crabs into groups of four from low to high activity. One crab from each of these groups was haphazardly selected and assigned to an experimental unit to ensure substantial behavioural variation within each unit (four crabs per experimental unit). Thus each experimental block consisted of four experimental units. Individual crabs had been marked prior to activity level assays (see [Testing for a Behavioural Syndrome](#)) and this allowed me to track individual crab survival over the course of the predation experiment.

Predation trials were conducted in large cylindrical mesocosm tanks (0.97 m diameter \times 0.41 m height; 0.25 m water depth) that contained two rectangular reef patches (0.3 \times 0.16 m and 0.12 m tall) among a 1 cm deep sand substrate. These patches provided a structurally complex refuge for crabs from toadfish predation. To create patches, I drilled holes in clean oyster shells and assembled clusters of shells using zip-ties to mimic natural reef formations. These clusters were then fastened to a fibreglass base to make reef patches. Reef patches were standardized by shape, size, as well as volume (measured through water displacement) to ensure a consistent amount of refuge across experimental units. Furthermore, a single artificial toadfish shelter (0.4 \times 0.2 m and 0.15 m tall) was constructed from bricks in each mesocosm to provide a refuge for toadfish. Mesocosms additionally received a plastic sheet on which 20 scorched mussels (*B. exustus*) were glued, although these mussels were never consumed by crabs. Mesocosm tanks received flow-through sea water throughout the experimental duration.

Each mesocosm first received a single toadfish (mean TL \pm 1 SE: 31.88 \pm 5.56 cm) that had been fed mud crabs and then starved for 24 h. Toadfish were allowed to acclimate for 1 h, and after this acclimation period crabs were placed on reef patches within tanks (two crabs per patch) to ensure that crabs began trials in the safety of the refuge. Predation trials were generally started in the afternoon (~1500 hours) and toadfish were allowed to forage on crabs for 72 h. Once per day, each mesocosm tank was partially drained to find remaining crabs and the total number and ID of these crabs was recorded. The majority of predation happened during the first 24 h and this precluded testing the effect of crab activity level on the order in which crabs were consumed (i.e. survival analysis).

I tested the effects of behavioural plasticity (i.e. activity level under predation threat minus activity level in the absence of threat) as well as individual crab activity level measured in the absence and presence of threat on the probability of being eaten using two

separate GLMMs. In the first model, I included activity level in the absence of predation threat (i.e. baseline activity), individual behavioural plasticity and an interaction between these terms as fixed effects with crab mortality as the response variable. Including this interaction term allowed me to test whether the effect of behavioural plasticity (i.e. behavioural change in the presence of threat) depended on the baseline activity level. To test whether crab activity level measured in the presence of threat was alone sufficient to predict crab mortality, I constructed a second model with crab activity level in the presence of predation threat as a fixed effect with crab mortality as the response variable. In both these models, crab mortality (the probability of being eaten) was modelled using a binomial error distribution and logit link, and crab carapace width was included as an additional fixed effect to test whether crab size influenced predation. All fixed effects were standardized by transforming to z scores. I included experimental block and the experimental predation tank (four crabs per tank) as a random intercept and slope, respectively, in both models. I tested the significance of fixed factors by dropping fixed factors and comparing nested models using likelihood ratio tests. Random effects were retained in all model comparisons.

Conditioning Experiment

I used an additional experiment to test whether crab activity level could be modified by continuous exposure to chemical cues from toadfish (i.e. conditioning). I ran this experiment in a complete block design ($N = 3$ blocks) with eight crabs per block ($N = 24$ total crabs; mean CW \pm 1 SD: 30.08 \pm 1.64 mm). For each block, crabs were collected from the field, fed and starved using the same procedure as described previously (see [Testing for a Behavioural Syndrome](#)). After starvation, I measured the activity level of these eight crabs in the absence of toadfish predation threat (for activity level measurement methods, see [Testing for a Behavioural Syndrome](#)), and fed crabs immediately following this behavioural measurement. I then haphazardly assigned crabs to two conditioning treatments: half the crabs were held in a tackle box (one crab per compartment) submerged in a large cylindrical tank that received flow-through sea water while the other half were held the same way but submerged in a tank with a single adult toadfish in flow-through sea water. Small holes were drilled in tackle boxes to allow the exchange of water and chemical cues from toadfish but keep crabs protected from toadfish. These treatments were maintained for 3 days and crabs were fed daily during this period. The toadfish was also fed with mud crabs daily. In nature, toadfish excavate and inhabit burrows in reefs from which they exude a persistence source of chemical cues. Thus this conditioning treatment is relevant to natural situations. After the conclusion of treatments, the activity level of individual crabs was measured for a second time (on the following day) in the absence of predation threat (the same context as the first behavioural measurement). Crabs used in the two treatments did not differ in carapace width (t test: $P = 0.877$).

I tested for the effect of conditioning on crab activity level using a binomial GLMM. Crab activity level served as the response variable in this model while the conditioning treatment (toadfish absence or presence) and the behavioural measurement number (first or second measurement) were modelled as fixed factors. I also included an interaction between the conditioning treatment and behavioural measurement number in this model to test the hypothesis that conditioned crabs would decrease their activity level in response to heightened predation risk while control crabs would not. Experimental block was modelled as a random factor and I added an additional observation-level random effect to correct for overdispersion (Browne, Subramanian, Jones, & Goldstein, 2005). I

tested for the significance of the interaction between the conditioning treatment and behavioural measurement number by dropping this interaction from the full model and comparing nested models using a likelihood ratio test.

Ethical Note

This work was conducted under the University of South Carolina IACUC No. 100696 in accordance with institutional laws regarding the ethical treatments of animals. Animals were returned to the wild at end of the study in their location of collection.

RESULTS

Testing for a Behavioural Syndrome

The activity level of individual crabs in the absence of threat was related to activity in the presence of threat (effect of activity \pm 1 SE: 5.281 \pm 0.308; likelihood ratio test: $P < 0.001$; Spearman rank correlation: $r_s = 0.448$, $P < 0.001$; Fig. 1), providing evidence of a population-level behavioural syndrome.

The treatment order that crabs received in activity level assays and crab carapace width had no effect on crab activity measured in the presence of threat (likelihood ratio tests: $P \geq 0.825$). Predation threat reduced crab activity level on average (effect of threat \pm 1 SE: -0.569 ± 0.092 ; likelihood ratio test: $P < 0.001$; Fig. 2).

Despite the presence of the overall behavioural syndrome and mean reduction in activity under threat, however, individual crabs exhibited substantial variation in their response to threat or behavioural plasticity (Fig. 3). While the majority of crabs decreased activity level in the presence of threat, some actually increased activity or exhibited little if any behavioural change in response to threat (Fig. 3).

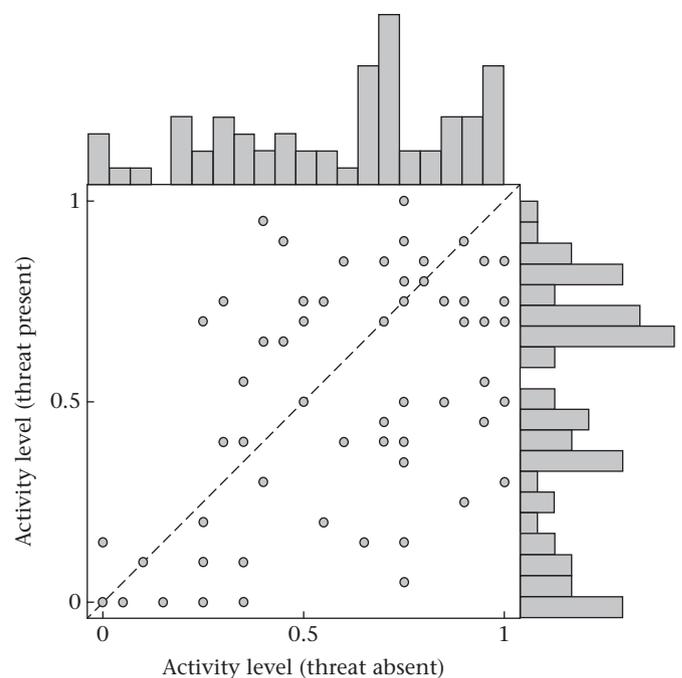


Figure 1. Relationship between individual crab (*Panopeus herbstii*) activity level measured in the absence and presence of toadfish (*Opsanus tau*) predation threat. Histograms depict the distribution of activity level values in the absence (across from X axis) and presence of threat (across from Y axis). Activity level measurements were separated by 24 h and predation threat was manipulated through waterborne chemical cues from toadfish. Dashed line indicates a 1:1 relationship (i.e. perfect consistency) for comparison to the distribution of data points.

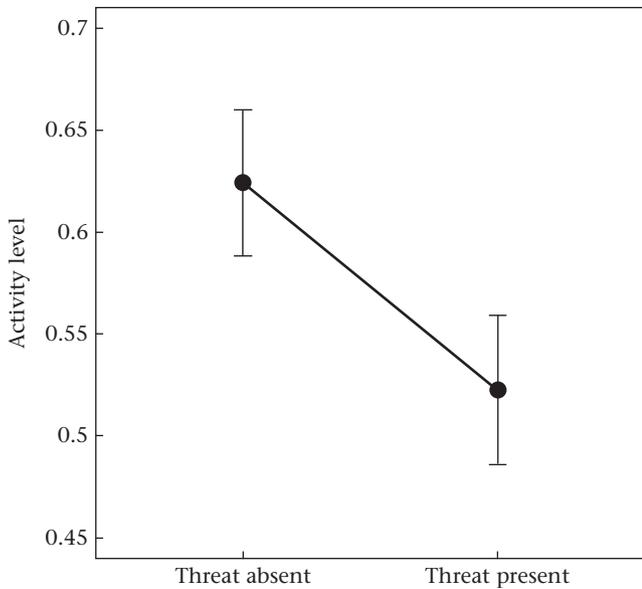


Figure 2. Effect of toadfish predation threat (i.e. waterborne chemical cues) on mean crab activity level (± 1 SE).

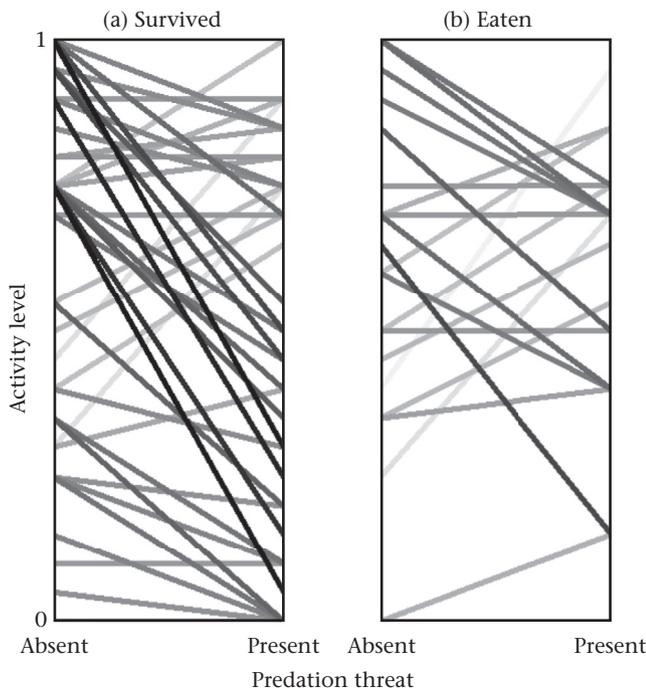


Figure 3. Behavioural reaction norms (i.e. change in activity across the absence and presence of predation threat) for (a) crabs that survived and (b) crabs that were consumed by toadfish in a 3-day predation experiment. Line colour scales from grey to black with darker reaction norm lines indicating a relatively lower reaction norm slope (i.e. reduced activity in response to threat).

Predation Experiment

Forty-four crabs survived over the duration of the predation experiment while 20 crabs were eaten by toadfish. The effect of crab behavioural plasticity on crab mortality did not depend on the baseline level of crab activity (i.e. the interaction between these factors; likelihood ratio test: $P = 0.240$). Rather, plasticity alone was a significant predictor of crab survival: crabs that reduced activity level in the presence of threat (during behavioural assays) were

more likely to survive the predation trial (effect of plasticity ± 1 SE: -0.752 ± 0.363 ; likelihood ratio test: $P = 0.028$; Fig. 4).

Specifically, surviving crabs showed a strong behavioural response to predation threat, decreasing their activity by 23% on average in prior behavioural assays (Fig. 4), with 64% of surviving crabs showing a reduction in activity with threat (Fig. 3a). Crabs that were eaten, in contrast, barely decreased their activity (Fig. 4), with 40% of consumed crabs showing a reduction in activity with threat (Fig. 3b). Crab activity level measured in the absence of threat (i.e. baseline activity) had no effect on crab survival (likelihood ratio test: $P = 0.287$), while the effect of crab activity level in the presence of threat on survival was marginal (likelihood ratio test: $P = 0.059$) (Fig. 4). Crab body size had no effect on crab survival (likelihood ratio tests: $P > 0.058$).

Conditioning Experiment

Crabs that were held in the presence of toadfish over 3 days decreased their activity level by 34% while control crabs held without toadfish barely altered activity (effect of interaction between conditioning treatment and behavioural measurement number ± 1 SE: 1.695 ± 0.852 ; likelihood ratio test: $P = 0.049$; Fig. 5).

DISCUSSION

Individual-level variation in behavioural plasticity is a ubiquitous aspect of animal behaviour (Dingemans & Wolf, 2013), yet the ecological effects of plasticity have rarely been quantified. This work demonstrates that plasticity is an important determinant of prey survival in the presence of a predator. Despite the presence of a population-level behavioural syndrome, crabs still exhibited substantial variation in their response to predation threat. Furthermore, crabs that reduced activity level under threat in behavioural assays were more likely to survive predator exposure than crabs that failed to adjust their activity. This indicates that individual plasticity can act to mitigate the negative effects of behavioural spillover across ecological contexts (Johnson & Sih,

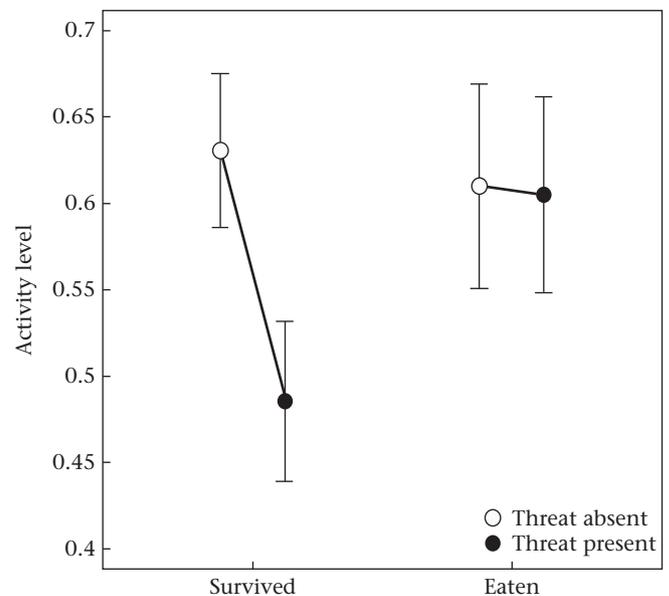


Figure 4. Mean crab activity level (± 1 SE) measured in the absence (empty circles) and presence of toadfish predation threat (black circles) of crabs that survived and were eaten during the 3-day predation experiment.

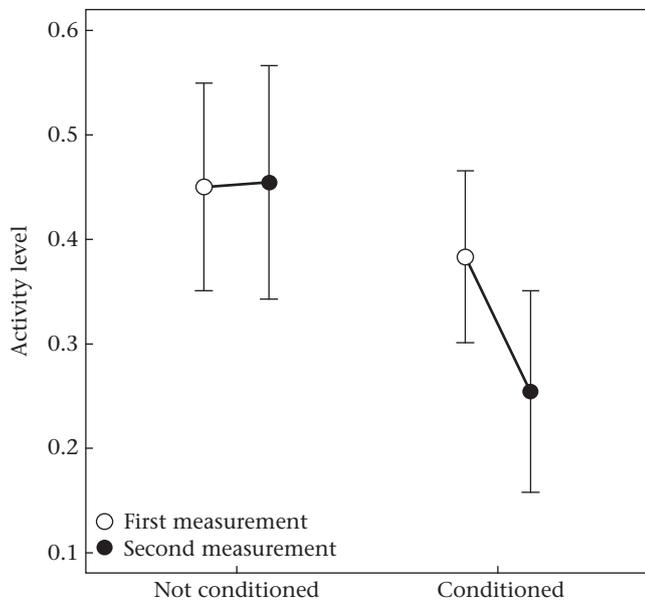


Figure 5. Mean crab activity level (± 1 SE) measured in the absence of predation threat for crabs that were held with toadfish for 3 days and control crabs that were held in the absence of toadfish for 3 days. White circles indicate initial activity level measured before the treatments began while black circles indicate activity level measured after the conclusion of treatments.

2005), and more broadly suggests that the outcome of predator–prey interactions may depend on individual prey behaviour (i.e. context dependence). Furthermore, crabs exposed to toadfish chemical cues over 3 days reduced their activity level compared to control crabs. This suggests that conditioning provides a means by which crabs can alter behaviour within a single context to reduce predation risk, and may further play a role in generating the substantial among-individual variation in activity level measured within mud crab populations (Belgrad & Griffen, 2016; Griffen et al., 2012; Toscano & Monaco, 2015; Toscano et al., 2014).

Surprisingly, many crabs not only failed to reduce their activity level in the presence of threat, but actually showed an increase in activity in the presence of threat. This counterintuitive finding could be explained by the concentration of toadfish chemical cues that crabs were exposed to in behavioural assays. It is possible that the cue concentration was low enough where bold crabs did not actually perceive a threat of predation and accordingly did not adjust their behaviour. In contrast, shy crabs, which are presumably more sensitive to predator chemical cues, reduced their behaviour despite the low cue concentration used. Regardless, behavioural responses during assays should reflect individual sensitivity to predation threat; using a higher cue concentration would presumably have shifted the overall magnitude but not the relative magnitude of behavioural responses.

Individual crabs in this study did not respond equally to predation threat, and a critical next step is examining whether crab behavioural plasticity is a repeatable or even heritable trait at the individual level. Thus far, no study in any system has demonstrated the repeatability of individual plasticity over time (Dingemans & Wolf, 2013; Dingemans et al., 2010), although a number of lines of evidence suggest that repeatability of plasticity should be common (Dingemans & Wolf, 2013). Among-individual variation in behavioural plasticity could be underpinned by genetic variation or could come about through past experiences (Dingemans & Wolf, 2013). In the present study, crabs that were conditioned to toadfish presence reduced their activity level, a response to increased

risk that presumably enhances survival. While this conditioning experiment did not examine whether behavioural plasticity was also modified by conditioning, work by Griffen et al. (2012) suggests that conditioning may play a role in generating individual variation in plasticity. Griffen et al. (2012) showed that crabs collected from subtidal oyster reef habitat, which experience greater exposure to fish predators, are less responsive to toadfish predation threat compared to crabs collected from intertidal reef habitat, which are presumably less exposed to fish predators (Griffen et al., 2012). This finding is counterintuitive; based on my results, plasticity has a clear benefit to survival, and thus one would expect that crabs exposed to greater predation risk would be more likely to reduce their activity in the presence of a predator.

My results demonstrate that the failure to reduce activity level in the presence of predation threat has a clear cost: crabs that maintained high activity level under threat were more likely to be consumed by toadfish. This finding is at face-value incongruous with a recent study by Belgrad and Griffen (2016), who report that toadfish preferentially select mud crabs with low activity/high refuge use, although this discrepancy could be the result of several key differences between the studies. First, in the study by Belgrad and Griffen (2016), individual crab behaviour was measured in the presence of nine other conspecifics (a different ecological context than in the present study) and the crabs used were significantly smaller than those used here. Most importantly, their analysis was designed to test whether individual crab behaviour interacted with predator species identity (toadfish or blue crabs, *Callinectes sapidus*) to influence predation risk, and it is unclear whether individual crab behaviour influenced predation risk in the presence of toadfish alone. Heightened predation risk with activity is expected because mud crabs take refuge within interstitial spaces between oyster shells that much larger toadfish (100 times the size of crabs) cannot access (Grabowski & Kimbro, 2005; Grabowski, 2004). Thus it seems that only during activity outside of interstitial spaces could mud crabs be vulnerable to toadfish predation.

Assuming a cost to activity, this leads to a key question stemming from my results: why do crabs maintain activity level across contexts (generating the population-level behavioural syndrome) if plasticity is apparently beneficial? Interestingly, previous work on mud crabs demonstrates a benefit to activity, that is, enhanced feeding rate on mussel prey (Griffen et al., 2012; Toscano et al., 2014). Furthermore, a number of studies indicate that the density-mediated trophic cascade involving toadfish, mud crabs and bivalves (i.e. toadfish consumption of mud crabs) is quite weak relative to the behaviourally mediated cascade: toadfish consume few crabs in experimental reefs, yet bivalves still benefit due to reduced foraging by crabs in the presence of toadfish predation threat (Grabowski, 2004; Kimbro et al., 2014). Thus, despite evidence that behavioural spillover is maladaptive in the presence of a predator, the positive effect of crab activity on energetic intake may very well outweigh the negative effect of reduced survival. Accordingly, it may benefit crabs to remain active and forage at a high rate across contexts, leading to the population-level behavioural syndrome observed here.

In summary, this work provides evidence that individual prey behavioural plasticity can enhance prey survival, circumventing the negative effects of behavioural spillover in the presence of a predator. Predation, however, is just one influence on crab survival and fitness. A more holistic view of the effects of individual behaviour on fitness could be gained from a long-term experiment that measures individual behaviour and tracks growth and survival in the field (e.g. Ballew et al., 2017). This type of research programme, combining detailed behavioural assays with laboratory and field experiments, is essential in teasing apart the multifaceted,

bidirectional effects of individual behaviour on ecological dynamics.

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