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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.

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, Kempenaers, & 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 (Dingemanse & 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 (Dingemanse et al., 2010), and thus can be used to quantify individual behavioural plasticity and its effects on aspects of individual fitness. Behavioural reactions 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 (Dingemanse & 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, & Dingemanse, 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) $\pm$ 1 SD: 29.35 $\pm$ 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