

Trait-mediated functional responses: predator behavioural type mediates prey consumption

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Summary

1. The predator functional response (i.e. per capita consumption rate as a function of prey density) is central to our understanding of predator–prey population dynamics. This response is behavioural, depending on the rate of attack and time it takes to handle prey.
2. Consistent behavioural differences among conspecific individuals, termed behavioural types, are a widespread feature of predator and prey populations but the effects of behavioural types on the functional response remain unexplored.
3. We tested the effects of crab (*Panopeus herbstii*) behavioural type, specifically individual activity level, on the crab functional response to mussel (*Brachidontes exustus*) prey. We further tested whether the effects of activity level on the response are mediated by the presence of toadfish (*Opsanus tau*) predation threat in the form of waterborne chemical cues known to reduce crab activity level.
4. The effects of crab activity level on the functional response were dependent on crab body size. Individual activity level increased the magnitude (i.e. slope and asymptote) of the type II functional response of small crabs, potentially through an increase in time spent foraging, but had no effect on the functional response of large crabs. Predation threat did not interact with activity level to influence mussel consumption, but independently reduced the slope of the type II functional response.
5. Overall, this study demonstrates size-specific effects of a behavioural type on a predator–prey interaction, as well as a general pathway (modification of the functional response) by which the effects of individual behavioural types can scale up to influence predator–prey population dynamics.

Key-words: animal personality, behavioural syndrome, boldness, *Crassostrea virginica*, food web, interaction strength, oyster reef

Introduction

Predator–prey interactions have traditionally been described, measured and modelled at the population or species levels. For example, classic food webs are depicted with species as nodes and feeding links determined with mean trophic data from species or solely from adults (Cohen 1978; Polis 1991). Similarly, the functional response, i.e. per capita prey consumption dependent on prey density, is generally averaged across predator individuals for use in models that predict predator–prey population dynamics (Okuyama 2008; Bolnick *et al.* 2011) or the dynamics of multi-trophic systems (e.g. Rosenzweig 1973; Oksanen *et al.* 1981). This is a decidedly taxonomic

approach (sensu Rall *et al.* 2011) to studying predator–prey interactions that obscures individual-level variation and assumes interactions can be understood by mean values of populations or species (Bolnick *et al.* 2011).

Recent empirical work has illuminated extensive individual-level phenotypic variation in predator and prey populations with important ecological consequences (reviewed by Bolnick *et al.* 2003; Araujo, Bolnick & Layman 2011; Bolnick *et al.* 2011; Sih *et al.* 2012). For example, conspecific individuals often differ in their behavioural traits (e.g. activity, boldness or aggression) and these differences are consistent over time (termed behavioural types, BTs; Sih, Bell & Johnson 2004; Carter *et al.* 2013). Furthermore, behavioural syndromes describe correlations between different BTs (e.g. boldness and aggression; Bell & Sih 2007), or correlations of a single

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BT measured across ecological contexts (Sih, Bell & Johnson 2004; Carter *et al.* 2013). BTs can influence various aspects of predator–prey interactions including consumption rates (Pruitt & Krauel 2010), predator foraging tactics (Coleman & Wilson 1998; Kurvers *et al.* 2010), predator diet breadth (Riechert 1991) and predator–prey spatial distributions (Cote *et al.* 2010; Griffen, Toscano & Gatto 2012). Nevertheless, it remains unclear whether accounting for such individual-level behavioural variation in traditional models of predator–prey interactions could help explain patterns or alter predictions at the population and community levels (Okuyama 2008; Bolnick *et al.* 2011).

The functional response is central to our understanding of predator–prey population dynamics (Holling 1959; Murdoch & Oaten 1975) and co-evolutionary theory (Abrams 2000). This response is dependent on behavioural traits, including an individual predator's rate of attack, determined by its reactive distance, movement speed, capture success and the behaviour of its prey, as well as its handling time, i.e. the time it takes to capture, subdue and consume an individual prey (Jeschke, Kopp & Tollrian 2002; Tully, Cassey & Ferriere 2005); these model characteristics affect the long- and short-term stability of predator–prey dynamics (Murdoch & Oaten 1975; Abrams 2000). If predator or prey BTs can influence these emergent behavioural traits (attack rate and handling time), then BTs can alter the functional response and potentially scale up to influence population dynamics. Accounting for BTs in the functional response could be especially important if there is a spatial structure to behavioural types (e.g. Boon, Réale & Boutin 2008; Griffen, Toscano & Gatto 2012), or when combining different functional responses to make predictions at the population level (Jensen's inequality; for discussion see Okuyama 2008; Bolnick *et al.* 2011).

Activity level is one of the most well-studied behavioural traits (Careau *et al.* 2008), and numerous studies have shown that activity level differs consistently between conspecifics (i.e. a BT; Sih, Bell & Johnson 2004). Activity level is typically measured by placing an individual animal in a familiar environment and measuring either the distance moved over a period of time (e.g. Harcourt *et al.* 2009; Pruitt, Stachowicz & Sih 2012) or the frequency or duration of movement (e.g. Wilson *et al.* 2010; Maffi, Wakamatsu & Roulin 2011; Beckmann & Biro 2013). In a foraging context, these measures of activity level should influence predator–prey encounters (although this also could depend on the activity of prey; Sweeney *et al.* 2013), particularly when prey are at low densities, thus modifying the attack rate (i.e. initial slope) in functional response models. Furthermore, while greater predator activity increases encounters with prey, it also heightens the risk of being eaten by higher order predators (Werner & Anholt 1993; Anholt, Werner & Skelly 2000). Therefore, intermediate predators often modify their activity level to balance foraging demands with the threat of being

eaten. While this trade-off is traditionally studied from an optimization perspective (i.e. activity level is modified to maximize fitness), it has been suggested that individual BTs impose limits on behavioural plasticity, thereby precluding perfect optimization (Sih, Bell & Johnson 2004). Thus, predation threat from a higher order predator could modify the effects of activity level on the intermediate predator functional response, depending on whether individuals respond behaviourally to predation threat, and the degree to which they respond.

In this study, we explored the hypothesis that individual predator activity level can modify the predator functional response and further examined how predation threat could mediate the effects of activity level on the response. This is an important first step in determining whether accounting for individual predator behaviour in the functional response could improve our predictive capacity regarding consumption rate and predator–prey interaction strength. We used a well-studied tri-trophic system consisting of toadfish (*Opsanus tau* Linnaeus) as a top predator, mud crabs (*Panopeus herbstii* Milne-Edwards) as an intermediate predator and scorched mussels (*Brachidontes exustus* Linnaeus) as prey of crabs (Grabowski & Kimbro 2005; Griffen, Toscano & Gatto 2012). Previous work in this system indicates that individual differences in crab activity level are consistent over time, validating activity level as a BT of mud crabs (see Methods: Study system for further discussion). Furthermore, smaller crabs generally have lower activity levels than large crabs (Griffen, Toscano & Gatto 2012; Toscano, Gatto & Griffen 2014), likely due to their greater susceptibility to toadfish predation (B.J. Toscano unpublished data). Therefore, due to the importance of crab body size in determining activity level as well as the outcome of predator–prey interactions more broadly (e.g. Aljetlawi, Sparre-veik & Leonardsson 2004; McCoy *et al.* 2011), we used a wide size range of crabs to test whether effects of activity level further depend on crab body size. In short, our study found that the effects of crab activity level on the crab functional response were indeed size-dependent, while toadfish predation threat had effects independent of crab activity level and body size on the crab functional response.

Methods

STUDY SYSTEM

Toadfish, mud crabs and scorched mussels are common inhabitants of oyster (*Crassostrea virginica* Gmelin) reefs along the Atlantic and Gulf coasts of the United States. Previous work has shown that individual mud crabs differ in their use of oyster shell refuge habitat (Griffen, Toscano & Gatto 2012), and that these behavioural differences are consistent over months in the field (Toscano, Gatto & Griffen 2014). Refuge use is negatively related to crab body size, but there is additional consistent variation in refuge use that is not explained by size (Griffen, Toscano & Gatto 2012; Toscano, Gatto & Griffen 2014). Furthermore, mud crabs increase refuge use in the presence of toadfish chemical cues

(Grabowski & Kimbro 2005), a widespread response to predation threat. This anti-predatory behaviour reduces the mussel consumption rate of crabs, thereby modifying the strength of the trait-mediated trophic cascade involving these species (Griffen, Toscano & Gatto 2012). This trophic cascade is a major determinant of community structure in oyster reefs (Grabowski & Kimbro 2005; Griffen, Toscano & Gatto 2012). Refuge use in these studies (Griffen, Toscano & Gatto 2012; Toscano, Gatto & Griffen 2014) was measured as the proportion of behavioural observations where an individual crab was under oyster shell and inactive. In this study, we use the inverse of this behavioural measurement (i.e. the proportion of observations where crabs are observed active), as measured in other studies of individual activity level as a BT (e.g. Wilson *et al.* 2010; Mafi, Wakamatsu & Roulin 2011; Beckmann & Biro 2013), to test the hypothesis that crab activity level influences the crab functional response to mussel prey density.

EXPERIMENTAL SET-UP

The experiment was run from May to August 2012 in a screened-in wet laboratory at the Baruch Marine Field Laboratory in Georgetown, South Carolina, USA. Organisms used in the experiment were collected from the adjacent Oyster Landing intertidal oyster reef in North Inlet estuary (33°20'N, 79°10'W).

To examine the effects of individual crab activity level on the functional response, we measured both the activity level and mussel consumption rate of individual crabs. Activity level was measured prior to consumption rate trials. We manipulated the presence of chemical cues from toadfish during measurements of both activity level and consumption rate to test how the presence of predation threat directly affects the functional response, and how threat could mediate the effects of activity level on the functional response. Specifically, both the activity level and consumption rate of individual crabs were measured under one of two predation threat treatments: toadfish chemical cue absent ($n = 240$ crabs) or toadfish chemical cue present ($n = 207$ crabs). Activity level measured under predation threat is a measure of boldness as defined in the animal personality literature (Carter *et al.* 2013). The consumption rate of individual crabs was measured at a single prey density rather than a range of prey densities to minimize the duration crabs were held in the laboratory, which could modify individual behaviour through conditioning (Butler *et al.* 2006). We ran the experiment in a complete block design and the following methods pertain to a single block of 4 day duration.

On the first day, 16 crabs (20–30 mm carapace width, CW) were collected from the high intertidal portion of the Oyster Landing reef. Mud crabs become important predators of adult bivalves in oyster reefs in North Inlet estuary when they reach *c.* 20 mm CW (Toscano & Griffen 2012), and attain a maximum size of 55 mm CW at this site (McDonald 1982). All crabs were fed with mussels *ad libitum* as soon as they were brought into the laboratory. Eight of these 16 crabs were then randomly assigned to the toadfish cue absent treatment while the other eight were assigned to the toadfish cue present treatment, and these treatments were maintained for both activity level and consumption rate trials (methods for activity level and consumption rate trials are detailed below). To create the toadfish cue present treatment, we pumped seawater through a holding chamber that contained a single adult toadfish (*c.* 30 cm total length) fed *ad libitum* with

mud crabs in between experimental trials. This seawater was then divided equally among mesocosms containing crabs to keep the amount of chemical cue consistent within blocks. Crabs assigned to the cue absent treatment received seawater that did not first pass by a toadfish, but was otherwise distributed using the same seawater system. Mesocosms receiving the toadfish cue absent and cue present treatments were always alternated spatially.

On the second day, four crabs receiving the toadfish cue absent treatment and four crabs receiving the cue present treatment (eight of the 16 crabs) were observed to measure their activity level, and on the third day, the other eight crabs were observed in the same manner. This second group of eight crabs was fed again on the second day to keep their starvation time before activity level measurement (24 h) consistent with the first group of eight crabs, and on the third day, all crabs were fed to maintain starvation consistency before consumption rate trials. On the fourth day, the consumption rate of all 16 crabs was measured in a 24-h feeding trial. All crabs were held in the laboratory for an additional 2 days after consumption rate trials to ensure that crabs were not approaching a molt cycle or female crabs were not becoming reproductive. This procedure for a single experimental block was repeated 33 times over the course of the summer (May through August). Any crabs molting, carrying eggs or dying during their time in the laboratory were removed from the final data set. Additionally, the toadfish chemical cue treatment failed during the measurement of crab consumption rate for five blocks and these crabs were therefore removed from the final data set. However, complete removal of these blocks (i.e. both cue absent and present treatments) from the final data set did not alter our results.

MEASUREMENT OF CRAB ACTIVITY LEVEL

The activity level of individual crabs was measured using a similar behavioural assay to that used in previous studies of mud crab BTs (Griffen, Toscano & Gatto 2012; Toscano, Gatto & Griffen 2014). Each crab was observed in a glass mesocosm (50 × 28 × 30 cm) containing a 3 cm layer of sand/mud substrate and 5 L of oyster shell that had been dried and cleaned to remove epifauna. This experimental crab density (one crab per 0.14 m²) is within the range of densities previously reported in North Inlet (McDonald 1982, B.J. Toscano unpublished data). Oyster shell was placed on top of the substrate to mimic natural reef habitat. This amount of shell ensured that crabs had ample space to hide completely. In each tank, eight large mussels (*c.* 25 mm shell length, SL) were suspended in a mesh bag near the surface of the water to release chemical cues and induce crab foraging behaviour while remaining out of reach of crabs.

Crabs were observed at night (from *c.* 2000 to 2300 h) under dim red light and from behind a blind to minimize disturbance. Over a period of 3 h, we observed whether crabs were exposed and active (vs. hiding and remaining motionless) every 6 min (30 observations per crab in total). Activity level was measured as the proportion of 30 observations that crabs were visible to the observer and moving. In addition to activity level, we recorded the carapace width, major claw width and sex of each crab.

MEASUREMENT OF CRAB CONSUMPTION RATE

Eight mussel (12–16 mm SL) prey densities (2, 4, 6, 8, 12, 16, 24 and 36 mussels per mesocosm) were randomly assigned to the eight crabs receiving the toadfish cue absent treatment as well as the eight crabs receiving the cue present treatment for each block. These mussel densities fall within the range of recorded mussel densities within a single large oyster cluster from the study site (Toscano & Griffen 2012). This created a total of 16 unique treatment combinations in each block. These trials were conducted in glass mesocosms of the same dimensions that we used to observe crab activity level. Mesocosms contained a 3 cm layer of sand/mud substrate and 10 large oyster shells, and were enclosed in black plastic to mimic the low-light conditions of North Inlet estuary during summer months (Dame *et al.* 1986; Toscano & Griffen 2013). Mussels were scattered evenly on oyster shells throughout each mesocosm and allowed to attach to oyster shells for 6 h prior to the start of trials. Crabs were allowed to forage for 24 h (starting and ending at *c.* 1500 h) and the number of mussels remaining as well as the water temperature was recorded at the end of trials.

ANALYSIS

We first tested the factors influencing individual mussel consumption by crabs with a generalized linear mixed model (GLMM) using the complete data set ($n = 447$ crabs). After establishing the importance of these factors, we then fit functional response models to subsets of the data set and compared the parameter estimates of functional response model fits to test for the effects of specific factors of interest (notably toadfish predation threat and crab activity level) on the crab functional response. All analyses were conducted using the statistical software R (R Core Team 2012).

We used a GLMM (lme4 package) with a binomial error distribution to examine the effects of crab activity level, crab claw width, experimental treatments (toadfish cue absence/presence, mussel prey density) and temperature, as well as all potential two-way interactions between these factors on the proportional mussel consumption of individual crabs. Claw width, which was strongly related to crab carapace width (linear regression: $R^2 = 0.855$), was used in this model because it is mechanistically tied to mussel consumption in oyster shell habitat (Toscano & Griffen 2013). To correct for overdispersion in this model, we included an observation-level random effect (Browne *et al.* 2005). Experimental block was also included as a random effect to control for pseudoreplication. Our original GLMM included all main factors, as well as all potential two-way interactions. This original model was simplified by dropping non-significant interaction terms.

We then fit functional response models to subsets of the complete data set to test the effects of specific factors of interest (toadfish predation threat and crab activity level) on the shape and parameter estimates of the func-

tional response. To test how toadfish predation threat affected the functional response, we fit models separately to crabs with consumption measured in the absence vs. presence of the toadfish chemical cue (two separate functional response models). To test how crab activity level affected the functional response, models were fit to the consumption rates of small crabs (<24 mm CW; activity level had no effect on the mussel consumption of large crabs, see Fig. 1) with low activity (≤ 0.22) vs. high activity (> 0.22) (two separate functional response models). Based on visual inspection of the data, this threshold adequately demonstrated the effect of activity level on the functional response of small crabs, though using other threshold values (0.15–0.3 activity level) did not qualitatively alter our results. We included both small crabs receiving the toadfish cue absent and present treatments because there was no interaction between the toadfish chemical cue and crab activity level on mussel consumption (Table 1). Thus, we fit a total of four functional response models in total to subsets of the data.

Our approach to fitting each functional response model was as follows. First, to determine the proper type (i.e. type I, type II or type III) of functional response, we plotted proportional mussel consumption as a function of prey density and analysed these data using a polynomial logistic regression (Juliano 2001). In all cases, these plots showed decreasing proportional consumption with prey density and a significantly negative first-order term, indicative of type II functional responses (Juliano 2001). Because prey were depleted over the 24 h that crabs foraged and not replaced, a Rogers type II functional response model that accounts for prey depletion was used (Rogers 1972; Kalinkat, Brose & Rall 2013):

$$N_e = N_0(1 - \exp(\alpha(N_e T_h - PT))) \quad (\text{eqn 1})$$

where N_e is the number of prey eaten, N_0 is the initial prey density, α is attack rate, T_h is handling time, P is the number of predator individuals (set to 1 in all models) and T is the experimental duration (24 h). This functional response model was fit using maximum likelihood estimation (bbmle package) in the statistical software R.

We used bootstrapping to test whether toadfish predation threat and crab activity level influenced functional response parameters (α and T_h). Specifically, we randomly subdivided the data into two subsets of the same size as the actual treatment groups (e.g. absence of predation threat: $n = 240$, presence of threat: $n = 207$). We then fit the functional response model (eqn 1) to each of these random subsets and calculated the difference in parameter estimates between random subsets. We repeated this procedure 10 000 times to generate a distribution of random differences in parameter estimates. We then compared the actual differences in parameter estimates (i.e. between predation threat absence vs. presence and small crabs with low vs. high activity) to these bootstrapped null

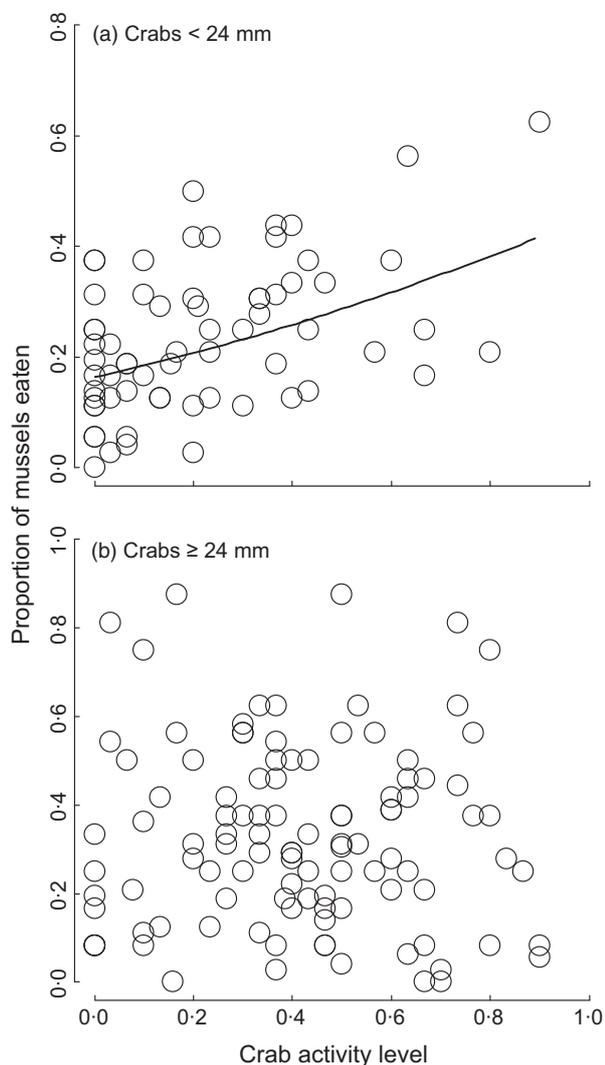


Fig. 1. Effects of individual crab activity level on proportional mussel consumption by small [<24 mm carapace width, CW; panel (a)] and large [≥ 24 mm CW; panel (b)] crabs at the three highest levels of mussel prey density (i.e. where crab consumption was not limited by prey density; 16, 24 and 36 mussels per tank). Line in panel (a) depicts significant relationship between crab activity level and proportional mussel consumption from binomial model fit to mussel consumption of small crabs at the three high mussel prey densities. Removal of the data point in the top-right corner of panel (a) had no effect on model coefficient estimates or significance of estimates presented in Table 1.

distributions of differences to test whether the actual differences fell outside of 95% of null distributions.

Results

Crab activity level and crab claw width interacted to influence proportional mussel consumption (Table 1); small crabs that exhibited a higher activity level during behavioural observation ate more mussels during consumption rate trials (Fig. 1a), while crab activity level had no effect on the mussel consumption of large crabs (Fig. 1b). Due to the interaction between crab activity

Table 1. Generalized linear mixed model (GLMM) testing the effects of fixed factors on the proportional mussel consumption of mud crabs ($n = 447$). Experimental block and an observation-level factor were included as random effects. Consumption was measured over 24 h in glass mesocosms set up to mimic oyster reef habitat. Eight levels of mussel prey density (2, 4, 6, 8, 12, 16, 24 and 36 mussels per tank) were offered to crabs

| Model factors | Estimate | SE | <i>t</i> | <i>P</i> |
|--|----------|-------|----------|----------|
| Response: proportion of mussels consumed | | | | |
| Mussel prey density | -0.075 | 0.004 | -16.148 | <0.001 |
| Crab activity level | 3.914 | 1.249 | 3.133 | 0.002 |
| Crab claw width | 0.482 | 0.091 | 5.314 | <0.001 |
| Toadfish cue | -0.314 | 0.113 | -2.786 | 0.005 |
| Temperature | 0.083 | 0.033 | 2.503 | 0.012 |
| Crab activity level \times Crab claw width | -0.619 | 0.203 | -3.048 | 0.002 |

and claw width, we could only interpret the conditional effect of crab claw width (i.e. the effect of claw width when activity level was zero) (Brambor, Clark & Golder 2006). At zero activity level, crab claw width increased mussel consumption (Table 1). Temperature, which varied between 23 and 33 °C over the course of the study, also increased mussel consumption by crabs (Table 1). In contrast, the presence of chemical cues from toadfish reduced the mussel consumption of crabs (Table 1). Mussel prey density also reduced proportional mussel consumption by crabs (Table 1), resulting in saturating functional responses (Figs 2 and 3).

Crabs exhibited type II functional responses (Figs 2 and 3), identified by uniformly decreasing proportional mussel consumption with mussel density. The presence of the toadfish chemical cue reduced the initial slope of the crab functional response (Fig. 2). Specifically, the presence of the cue decreased the attack rate parameter (observed difference between cue and no cue $\alpha = -0.029$, <97.8% of the bootstrapped parameter differences in α), but had little effect on the handling time parameter (observed difference in $T_h = 0.273$, >78.2% of the bootstrapped parameter differences) in type II functional response models (Fig. 2). In contrast, activity level increased the overall magnitude of the functional response of small crabs (Fig. 3), specifically increasing the attack rate parameter (observed difference between high activity and low activity $\alpha = 0.029$, >97% of the bootstrapped parameter differences) and reducing the handling time parameter (observed difference in $T_h = -1.096$, <99.9% of the bootstrapped parameter differences).

Discussion

In this study, we found that crab predator activity level increased both the initial slope and asymptote of the functional response of small crabs to mussel prey density. In contrast, activity level had no effect on the mussel consumption of large crabs. This shows that the effects of

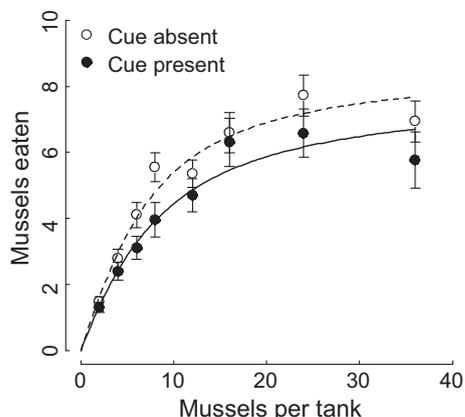


Fig. 2. Mean number of mussels eaten ± 1 standard error by crabs in the absence (white dots; $n = 240$) and presence (black dots; $n = 207$) of a toadfish predator chemical cue. Sample sizes for the eight prey density treatments (2, 4, 6, 8, 12, 16, 24 and 36 mussels per mesocosm) in the absence of the chemical cue were: $n = 27, 32, 28, 29, 30, 30, 32$ and 32 respectively. Sample sizes for the eight prey density treatments in the presence of the chemical cue were: $n = 26, 27, 26, 25, 27, 26, 24$ and 26 respectively. Lines depict functional response model (eqn 1) fits to the two groups of data (dotted line: model fit to consumption data in the absence of toadfish cue; black line: model fit to consumption data in the presence of toadfish cue).

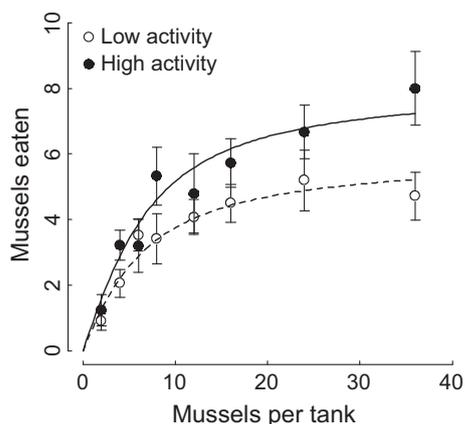


Fig. 3. Mean number of mussels eaten ± 1 standard error by small crabs (< 24 mm carapace width) that exhibited low activity (≤ 0.22 activity, white dots; $n = 104$) vs. high activity (> 0.22 activity, black dots; $n = 59$). Sample sizes for the eight prey density treatments (2, 4, 6, 8, 12, 16, 24 and 36 mussels per mesocosm) for crabs with low activity were: $n = 11, 16, 15, 12, 12, 10, 10$ and 18 respectively. Sample sizes for the eight prey density treatments for crabs with high activity were: $n = 4, 9, 5, 9, 5, 11, 9$ and 7 respectively. Crab activity level was observed prior to measurement of consumption rate. Lines depict functional response model (eqn 1) fits to the two groups of data (dotted line: consumption by small crabs with low activity; black line: consumption by small crabs with high activity).

individual behaviour on ecological dynamics can further vary within species depending on individual body size or population size structure. Similarly, sex dependence of the ecological effects of BTs has been observed in great tits (*Parus major*), where individual exploratory behaviour

had opposite effects on the survival of males and female birds depending on year-to-year variation in resource levels (Dingemanse *et al.* 2004; Dingemanse & Réale 2005).

The functional response is a major determinant of predator-prey population dynamics and stability (Murdoch & Oaten 1975), and therefore changes in the response driven by individual crab activity level could scale up to influence the crab-mussel interaction at the population level. Individual-level variation in activity level is taxonomically widespread (Careau *et al.* 2008), and activity level is common mechanism mediating species interactions (Anholt, Werner & Skelly 2000). Models of size-dependent functional responses are typically built upon mechanistic or phenomenological links between predator-prey body sizes and attack rate and handling time parameters (e.g. Aljetlawi, Sparrevik & Leonardsson 2004; McCoy *et al.* 2011; Rall *et al.* 2011). Our work shows that functional response models for actively foraging predators could be modified to include the influences of additional size-dependent behavioural variation and predation threat to more accurately predict predation rates in heterogeneous populations.

Our observations of crab activity level in a foraging situation allowed us to indirectly examine the mechanisms by which crab activity level increased the functional response of small, but not large crabs. Despite the presence of mussel prey chemical cues in observational tanks, small crabs were often observed inactive and remaining in the same location over the entire 3 h behavioural observation period (Fig. 1a; see also Toscano, Gatto & Griffen 2014). Large crabs exhibited relatively higher levels of activity in comparison (Fig. 1b). This increase in activity level with crab size is likely driven by a size refuge reached by large crabs from predators in the field (Shervette *et al.* 2004; Hill & Weissburg 2013; B.J. Toscano unpublished data), where large crabs have little reason to remain inactive and forgo foraging opportunities (see also Krause *et al.* 1998). If we assume that crabs can only find and consume mussel prey when they are active, then it is possible that a certain level of activity is needed to reach the maximum possible consumption rate over 24 h. Further increases in activity beyond this level should have little effect on mussel consumption. This level of activity was likely reached by most large crabs but very few small crabs, thus limiting their mussel consumption rate.

This suggests that an overall increase in time spent foraging is the mechanism behind the positive effect of activity level on the mussel consumption of small crabs, and this is supported by functional response modelling. We investigated whether an increase in time spent foraging could explain the positive effect of activity level by varying the experimental duration factor (T) in the type II functional response model (eqn 1) fit to the consumption data of small crabs with low activity (activity level ≤ 0.22). Specifically, we fit a functional response model to consumption data from these crabs in which the attack rate (α) and handling time parameters (T_h) were set to values

from the functional response model fit to small crabs with a *high* activity level (activity level >0.22 ; $\alpha = 0.083$, $T_h = 2.943$). We then estimated T by fitting this model to the data. The experimental duration, T , in this model was reduced from 24 (as set in our original model) to 16.818 h, and this model provided an equally good fit to the consumption data of small crabs with low activity when compared to the model in which experimental duration was set to 24 h, and attack rate and handling time were allowed to vary ($\Delta AIC = 1.729$). This indicates that a simple reduction in the time parameter in the functional response model effectively captures the effect of activity level on the response.

Though we hypothesized that activity level would primarily influence prey consumption at low prey densities and thus the attack rate parameter, our results suggest that activity level does not change the nature of crab foraging behaviour (i.e. a shift in the type of response or relative changes in parameter estimates). It is worth noting, however, that the reduction in activity between small crabs exhibiting high vs. low activity (*c.* 80% reduction in mean activity level), was much greater than the magnitude of reduction in the time parameter, T , in the functional response model (30% reduction). This indicates that our behavioural observations of activity level underestimated actual activity level in consumption rate trials. This is made clear when considering that small crabs with zero activity during behavioural observation still consumed a substantial proportion of mussel prey (Fig. 1a), which could happen if crabs observed inactive during the 3 h behavioural observation eventually became active over the course of 24 h consumption rate trials. The underestimation of activity level in consumption rate trials is even more apparent when considering that large crabs with a low level of activity (<0.2) measured in behavioural observations consumed up to 90% of prey (Fig. 1b). This further suggests that individual crabs could have a different timing of activity over consumption rate trials that were not fully captured in the 3 h behavioural observation.

Griffen, Toscano & Gatto (2012) found that the presence of toadfish predation threat enhanced the effect of crab activity level (referred to as refuge use, the inverse of activity level, in this study) on mussel consumption, but detected no significant effect of activity level on mussel consumption in the presence of threat at an alpha level of 0.05. Griffen, Toscano & Gatto (2012) however used larger crabs (30–42 mm CW) than in this study, which may explain our different results (i.e. a significant effect of activity level on mussel consumption for small crabs only). Though we did not detect such an interaction between predation threat and activity level as hypothesized, our study provides some of the first empirical evidence of the effects of predation threat from a higher order predator on the functional response of an intermediate predator (see also Alexander, Dick & O'Connor 2013). The majority of studies on trait-mediated trophic cascades test for a significant effect of trait change on

intermediate predator consumption rate at a single prey density, rather than the range of prey densities needed to estimate the functional response (Bolker *et al.* 2003). As expected, the presence of the toadfish chemical cue reduced the crab functional response, but did not change the type of response (functional response remained type II). Similarly, Alexander, Dick & O'Connor (2013) found that a fish predator chemical cue reduced the magnitude of an amphipod's functional response to isopod prey, but did not change the type of response. Further study is needed before broad conclusions can be drawn on the general effects of predation threat from a higher order predator on the functional response of an intermediate predator.

In general, hyperbolic type II functional responses that predict declining proportional prey consumption destabilize predator–prey population dynamics, while sigmoidal type III responses, that predict initially increasing and then decreasing proportional prey consumption, stabilize predator–prey dynamics (Murdoch & Oaten 1975; Juliano 2001). Previous work with this study system showed that mud crabs exhibit type III functional responses when foraging in a more complex oyster shell habitat than used in this study (Toscano & Griffen 2013). Furthermore, Toscano & Griffen (2013) demonstrated that oyster shell habitat structure limits large crabs (>26 mm carapace width) from accessing mussel prey at low prey densities, thus driving differences in the attack rate parameter in the functional responses of small vs. large crabs. In this study, the direct effects of crab body size on mussel consumption were likely minimized by our use of a less complex oyster shell habitat, and these differences in mesocosm set-up can explain the difference in functional response type measured in this study compared to Toscano & Griffen (2013).

Several additional factors could influence predator activity level and functional responses that our laboratory experiment did not incorporate. First, interference between conspecific predators or other forms of predator dependence are important in determining functional responses (Abrams & Ginzburg 2000), and in particular the prey consumption rates of crabs (Grabowski & Powers 2004; Griffen & Delaney 2007). Furthermore, the presence of additional non-prey species has been shown to modify consumption rates (Kratina, Vos & Anholt 2007). Lastly, our experiment used a single predator (toadfish), and it is unclear how predator diversity might affect the functional responses of mesopredators. All these influences could modify individual activity levels. Thus, further work should test the importance of individual predator behaviour for the functional response under more natural conditions with additional ecological complexity.

Finally, while using a non-mobile prey (mussels) allowed us to isolate the effects of individual predator behaviour on the functional response, many predators are faced with the task of capturing mobile prey that exhibit their own individual behaviours (Sih & Christensen 2001).

Thus, the BTs of predators and prey can interact to determine prey consumption (Pruitt, Stachowicz & Sih 2012; McGhee, Pintor & Bell 2013; Sweeney *et al.* 2013). This has been demonstrated in a marine predator–prey system, where turban snails (*Chlorostoma funebris*) that exhibit greater predator avoidance behaviour have higher survivorship in the presence of active ocher sea stars (*Pisaster ochraceus*), while snails that exhibit reduced predator avoidance have higher survivorship in the presence of inactive seastars (Pruitt, Stachowicz & Sih 2012). Such interactions between predator and prey BTs are likely widespread in nature, and their effects on predator functional responses warrant research attention. Ultimately, measuring such BT-dependent functional responses and combining these measurements with ecological theory (e.g. individual-based models: Grimm & Railsback 2005; or state-dependent predator–prey models: e.g. Persson *et al.* 1998) offer a promising avenue whereby the long-term effects of individual behaviour on population and community dynamics can be explored (Bolnick *et al.* 2011).

Acknowledgements

Funding was provided by an NSF Graduate Research Fellowship under Grant No. DGE-0929297 and by NSF Grant No. OCE-1129166. We thank D.M. Allen, J.L. Dudycha, the editors and two anonymous reviewers for helpful suggestions that improved the manuscript.

Data accessibility

Data from this study are archived in the public archive Dryad (<http://datadryad.org>) at the DOI: 10.5061/dryad.vr14v (Toscano & Griffen 2014).

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Received 22 January 2014; accepted 11 April 2014

Handling Editor: Volker Rudolf