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Cite this article: Belgrad BA, Griffen BD. 2016 Predator–prey interactions mediated by prey personality and predator hunting mode. *Proc. R. Soc. B* **283**: 20160408.
http://dx.doi.org/10.1098/rspb.2016.0408

Received: 23 February 2016
Accepted: 21 March 2016

Subject Areas:
behaviour, ecology, environmental science

Keywords:
individual variation, predation risk, hunting mode, predator avoidance response

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Predator–prey interactions mediated by prey personality and predator hunting mode

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Predator–prey interactions are important drivers in structuring ecological communities. However, des[illegible]idespread acknowledgement that individual behaviours and predator species regulate ecological processes, studies have yet to incorporate individual behavioural variations in a multipredator system. We quantified a prevalent predator avoidance behaviour to examine the simultaneous roles of prey personality and predator hunting mode in governing predator–prey interactions. Mud crabs, *Panopeus herbstii*, reduce their activity levels and increase their refuge use in the presence of predator cues. We measured mud crab mortality and consistent individual variations in the strength of this predato[illegible]dance behaviour in the presence of predatory blue crabs, *Callinectes sapidus*, and toadfish, *Opsanus tau*. We found that prey personality and predator species significantly interacted to affect mortality with blue crabs primarily consuming bold mud crabs and toadfish preferentially selecting shy crabs. Add[illegible]ly, the strength of the predator avoidance behaviour depended upon [illegible]redation risk from the predator species. Consequently, the personality composition of populations and predator hunting mode may be valuable predictors of both direct and indirect predator–prey interaction strength. These findings support theories postulating mechanisms for maintaining intraspecies diversity and have broad implications for community dynamics.

1. Introduction

The role of predation is critical in shaping ecosystem structure and function [1,2]. Predator–prey interactions can alter community composition [3], mediate trophic cascades [4], increase biodiversity [5] and affect species invasions [6]. Furthermore, predators can control the dynamics of prey populations by influencing such aspects as survival [7], growth [8], behaviour [9], size structure [10] and distribution [11]; while prey can likewise regulate predator populations [12,13]. One of the primary components of predator–prey interactions is the behaviour and subsequent survival of prey in the presence of predators.

For decades, scientists have studied the behavioural response of prey to predators. Numerous studies have directly linked prey activity levels (e.g. [7,14]) and refuge use (e.g. [15,16]) to predation risk, while other investigations have determined that predator avoidance behaviours (e.g. migration, reduced foraging) can limit prey growth [9], development [17] and fecundity [8]. These behavioural changes also have an enormous impact on the natural community. Shifts in the distribution of prey to avoid predators can alter competitive interactions between different prey species [18], whereas reduced foraging by prey in response to predation risk can reverberate across trophic levels [19,20].

Owing to the importance of predator avoidance behaviours in structuring ecological communities, ecologists seek to uncover the factors that determine the strength, variation and effectiveness of these behaviours in order to predict community and population dynamics. Towards this end, studies have concentrated on identifying the respective roles that biological and environmental variables play in shaping these behavioural changes. For instance, studies

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have documented predator avoidance behaviours varying by such factors as parasitic infection [16], environmental contamination [21], predator species [22] and even predator diet [23]. Nevertheless, despite advances in our ability to qualitatively predict the response of prey to predators [24], our knowledge remains limited on the effectiveness of predator avoidance behaviours in promoting survival because of the wide range of responses prey may exhibit and the myriad ways predators can respond to these behaviours.

Recently, there has been growing recognition of the importance of animal personality in mediating predator–prey interactions [20,25,26]. Animal personalities are a widespread phenomenon across the animal kingdom where individuals consistently exhibit different behaviour types [27–29]. While prey often seek refuge or reduce their activity in the presence of predators, every member in a population does not produce the same magnitude of a response. Instead, some individuals can be bold and spend the majority of their time active in risky, energetically advantageous locations, while other individuals may be shy and stay in habitats which provide refuge, but not opportunities to forage. These differences in personalities not only probably affect their chances of overall survival, but may also alter the species of predator from which they are at risk, as different predators use different habitats and hunting modes (e.g. larval fish which migrate to shallow water to avoid aquatic predators may expose themselves to terrestrial predators; [30]). Despite the frequency with which prey encounter multiple predators in the natural environment [31,32], only one study to our knowledge has examined the interactive effects of prey personality and predator species on predation risk [33].

Studies which attempt to predict prey responses to m e predator species have theorized that predator avoidanc viours should be the strongest in the presence of cues from sit-and-wait (ambush) predators, as detection should be more indicative of impending predation, than cues from active hunters which are dispersed widely and encountered frequently [34–36]. However, to date there have been few studies that have explored the relationship between predator hunting mode/domain and prey mortality (e.g. [36–38]), and none that have incorporated prey personality. Here, w mine the interactive roles of prey personality and preda nting mode in governing predation risk within a simple food web.

2. Material and methods

(a) Study system

We studied a food web which is prevalent within intertidal salt marsh ecosystems along the Atlantic and Gulf coasts of North America. This system consists of blue crabs, *Callinectes sapidus*, and toadfish, *Opsanus tau*, as top predators, the mud crab *Panopeus herbstii* as an intermediate predator, and the scorched mussel *Brachidontes exustus* as prey. Blue crabs and toadfish are abundant predators that commonly inhabit oyster reefs along the Atlantic coast [39,40]. While blue crabs are opportunistic foragers which actively search for prey (approx. 34% of diet consists of other crabs; [41]), toadfish are ambush predators which feed predominantly on mud crabs (77% of diet in South Carolina; [42]). In turn, mud crabs strongly reduce their activity levels and increase their time in refuge in response to different predators [43], and exhibit a bold–shy continuum of personality types [20,44]. Thus, ecological theory predicts that mud crabs should have an elevated predator avoidance response and higher predation risk in the presence of toadfish than blue crabs [34,35]. This theory was tested by using cohorts of animals that were sequentially moved through two experiments. The first experiment measured the personality of individual mud c hen assessed together as naturally occurring cohorts in th ence of a specific type of predator. The second experiment measured the mortality risk of that same predator on each of these same mud crabs as a consequence of their individual personality type.

(b) Refuge use in the presence of different predator odour cues

We performed an experiment to assess the proportion of time individual mud crabs spend active versus hiding in refuge in the presence of predator odour cues from either a single toadfish, a single blue crab or control conditions with no predator cue. Previous work in our laboratory determined that differences in this behaviour between individuals persist over months [44], are consistent across a range of conditions (i.e. predator present/absent [20]; changes in conspecific density (B. A. Belgrad 2015, unpublished data); starvation level (B. A. Belgrad 2015, unpublished data)), and are correlated with individual energetic strategies [45]. We collected 300 mature mud crabs that were not missing any limbs (mean ± s.d. carapace width = 24.1 ± 2.2 mm) by hand from intertidal oyster reefs within the North Inlet National Estuarine Research Reserve (33°20′ N, 79°10′ W, Georgetown, SC, USA). Crabs were collected in three cohorts of 10 individuals during each of 10 blocked sampling periods (i.e. each blocked trial consisted of 30 crabs total). Individuals were randomly selected from 1 m^2 plots to ensure that natural cohorts of 10 crabs were measured. Crab gender was identified by examination of the telson (167 males and 133 females). Crabs were starved for 24 h and the carapace of each was marked with a unique nail polish (Sonia Kashuk) design to identify individuals. Preliminary work determined that these markings did not alter crab behaviour. Cohorts were randomly assigned a predator cue treatment and placed into one of three separate flow-through mesocosms (circular with diameter 1 m; water height 15 cm). Each mesocosm contained approximately 2 cm sediment under an approximate 8 cm matrix of cleaned oyster shells covering the entire tank bottom. This composition mimicked the natural structure of reefs and ensured that crabs had ample refuge to hide completely. Thirty scorched mussels were distributed in three mesh containers within each mesocosm outside the reach of crabs to continuously stimulate foraging behaviour [20]. Flow-through mesocosms were supplied with water from the estuary which was first pumped through a head tank. The head tank for each mesocosm contained either a mature toadfish (caudal length ± s.d. = 28.4 ± 2.8 cm), blue crab (carapace width ± s.d. = 14.8 ± 0.6 cm), or no predator depending on the predator odour cue treatment. Predators were caught from the estuary by dip net no more than one week prior to the experiment and fed mud crabs each day to ensure kairomones were produced. We conducted all experimental trials at night under red light following the observational procedures of [20,44] to ensure mud crabs were at their most active and were undisturbed by the observer.

Crabs were tested in trials consisting of one cohort per treatment (toadfish, blue crab, no predator) with 6 days separating the commencement of each trial. All trials began between the hours 20.00 and 21.00, and once cohorts were placed in the mesocosms, crabs were given 10 min to acclimate. After acclimating, we recorded whether crabs were actively exposed on the surface of the shell layer or were taking refuge underneath the shells at 6 min intervals for the next 3 h. The proportion of these 30 observations in which crabs hid in refuge and were not visible to the observer was used as our response variable. We examined the effect of predator presence on crab behaviour using a mixed-effects generalized linear model (GLM) with a binomial distribution (R package: lme4). We treated predator treatment, gender and the covariate carapace width as fixed effects, and trial as well as individual crab identification as random effects to control for non-independence of crabs within the same trial and for repeated measures of each individual crab. This and all other analyses were conducted using R v3.0.3 (R Development Core Team, 2015).

(c) Effect of mud crab personality on predation risk

Immediately after observing crab behaviour (described in the last subsection), we used the same crab cohorts to assess whether crab predation risk was influenced by the proportion of time individual crabs spend in refuge within oyster shells and by predator species. We assigned crabs the same predator treatment they experienced previously to keep cohorts intact throughout the entire study. Crabs were fed a satiating amount of fish (*Fundulus heteroclitus*), marked with individually numbered bee tags (queen marking kit: the Bee Works, Orillia, Ontario, Canada), and starved for 24 h. After the starvation period, the cohorts were placed into one of three large flow-through mesocosms (diameter 2 m; water height 90 cm). Each mesocosm contained approximately 2 cm of sediment underneath four clusters of live oysters (length approx. 38 cm, width approx. 31 cm and height approx. 28 cm) which were standardized by weight (15 000 kg within less than 0.1%). Oysters were collected from the estuary and cleaned of any inhabiting crabs. Scorched mussels naturally attached to these collected oysters were standardized by number of individuals (within 8.3%) and served as the mud crabs' food source to mimic natural conditions.

During each blocked trial ($n = 10$), a single toadfish, blue crab or no predator (to serve as a control for cannibalism) was placed in each mesocosm depending on the experimental treatment. Each trial used new predators, but we used the same individual predators which provided odour cues in the previous behaviour experiment as predators within the large mesocosms to ensure prey behaviour remained consistent. Predators were starved 24 h to standardize hunger levels and placed in the mesocosms 10 min prior to the mud crabs to ensure kairomones were distributed throughout the tank (no crabs were lost to predation during introduction into the tanks). Mud crab survival was checked daily for seven consecutive days to determine which individuals were consumed. This was done by removing all the oyster clumps and thoroughly raking the sediment. No additional crabs were consumed until at least 10 min after the sediment had been raked (length of observation). Any missing crabs were presumed dead as there was no way for crabs to escape and remnants of missing animals were often found. We assessed whether crab mortality was influenced by the fixed effects of predator species, and the covariates crab refuge use (measured in the first experiment), and crab size using a mixed-effects Cox proportional hazards model (i.e. a survival analysis) with trial as a random effect (R package: frailtyHL). This model allowed us to right censor the data to account for crabs that were not consumed by the end of the trial. A Cox proportional hazards analysis is a statistical model which recognizes that the highest values in a study may simply be the maximum possible value, because a result did not occur by the end of the observation period, so the model weighs the data points accordingly (i.e. the data are right censored). We also conducted a two-sample Kolmogorov–Smirnov test to compare the distribution of mud crab personality types consumed by blue crabs and toadfish.

(d) Predator behaviour

We monitored predator behaviour during five of the 10 experimental trials described in the previous section to determine the hunting strategies of blue crabs and toadfish, and to assess whether hunting strategy could potentially explain the preferential consumption of bold or shy crabs. We examined two aspects of predator hunting behaviour: predator location and movement within the mesocosms. These were each recorded every hour between 7.00 and 22.00 (20 observations) during the second and fifth day of the trial, and then data from these two time periods were combined for analyses. We analysed proportion of time within versus outside of oysters and proportion of time moving versus stationary using two separate mixed-effects GLMs with a binomial distribution, using predator species as a fixed effect and trial block treated as a random effect.

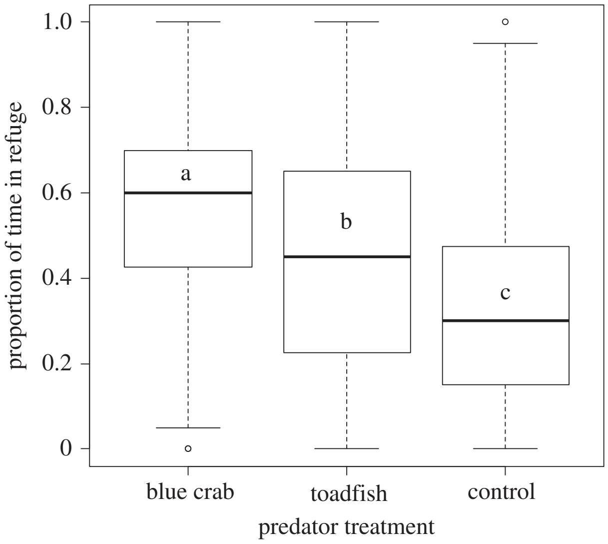

Figure 1. Proportion of time mud crabs, *Panopeus herbstii*, spent in refuge when exposed to different predator odour cues (blue crab *Callinectes sapidus*, toadfish *Opsanus tau*, and control of no cue; $n = 100$). Boxes indicate the 25th and 75th percentiles, whiskers denote 1.5 × interquartile range and the median is shown by the horizontal line within each box. Data were grouped from 10 trials.

3. Results

(a) Refuge use in the presence of different predator odour cues

The presence of a predator cue caused mud crabs to spend significantly more time in the refuge of oyster shells (predator absence, estimate ± s.e. $= 1.26 \pm 0.19$, $z = 6.74$, $p < 0.0001$; figure 1). In controls with no predator cue, crabs only spent, on average, 32% of their time under shells with crabs substantially altering their refuge use depending on the predator species so that crabs hid 47% of the time when exposed to toadfish cues and 57% of the time in the presence of blue crab cues (comparison between predators: toadfish versus blue crab presence, estimate ± s.e. $= 0.47 \pm 0.19$, $z = 2.50$, $p = 0.0125$; figure 1). There was a large amount of individual variation (i.e. differences in personality) across all predator treatments in the proportion of time crabs spent hiding rather than actively foraging, with some individuals spending 100% of their time in refuge while others hid for 0% of the time (variance in time by treatment: blue crab = 5%, toadfish = 7%, control = 6%). Conversely, crab behaviour did not vary greatly with experimental trial (variance < 0.001). Both carapace width and gender also had negligible effects on crab behaviour (estimate ± s.e. $= -0.03 \pm 0.03$, $z = -1.04$, $p = 0.2988$; estimate ± s.e. $= -0.10 \pm 0.15$, $z = -0.64$, $p = 0.5197$, respectively).

(b) Effect of mud crab personality on predation risk

Mud crab predation risk depended on predator treatment, as blue crabs consumed twice as many mud crabs as did toadfish, while only two crabs were cannibalized throughout all trials in

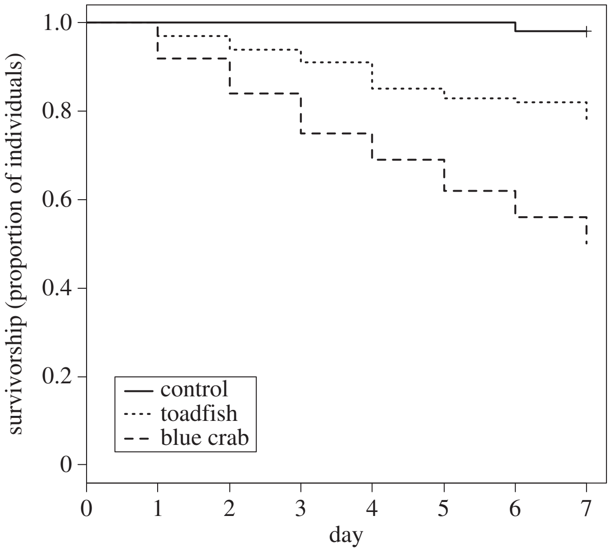

Figure 2. Survivorship curve of the proportion of individual mud crabs (*Panopeus herbstii*; $n = 100$) which survived each day as the experiment progressed. Lines denote mud crab exposure to different predators (blue crab *Callinectes sapidus*, toadfish *Opsanus tau*, and control of no predator).

the control mesocosms (figure 2). The amount of time mud crabs spent hiding in refuge during the previous experiment also had a significant effect on predation risk (refuge use, estimate ± s.e. $= -8.08 \pm 3.99$, $t = -2.02$, $p = 0.0430$) and strongly interacted with predator treatment (refuge use × predator treatment (blue crab versus toadfish), estimate ± s.e. $= 10.07 \pm 4.04$, $t = 2.50$, $p = 0.0126$; figure 3). Blue crabs preferentially consumed bold mud crabs with 87% of the crabs that exposed themselves ≥70% of the time lost to predation. By contrast, toadfish primarily selected shy crabs with only 9% of the crabs which exposed themselves ≥70% of the time consumed, and 0% of the crabs which exposed themselves ≥90% of the time (figure 3). Additionally, half of the crabs consumed by blue crabs spent 30–70% of their time hiding in refuge, while half the crabs consumed by toadfish hid for 50–80% of the time (figure 3). The distribution of mud crab personality types consumed by blue crabs and toadfish were thus considerably different ($D = 0.64$, $p = 0.0233$). Mud crab mortality was not significantly influenced by carapace width (size, estimate ± s.e. $= -0.09 \pm 0.06$, $t = -1.54$, $p = 0.1229$) and did not substantially differ across trials (mean variance in mortality across treatments = 1.40).

(c) Predator behaviour

Blue crabs and toadfish exhibited drastically different amounts of time inside versus outside refuge (location, estimate ± s.e. $= 1.52 \pm 0.30$, $z = 5.13$, $p < 0.0001$) and moving versus stationary (mobility, estimate ± s.e. $= 1.99 \pm 0.31$, $z = 6.34$, $p < 0.0001$). Whereas blue crabs actively searched for prey, toadfish remained hidden within oyster clumps three times longer than blue crabs on average (figure 4*a*). Observations of these predators also found that blue crabs were often mobile, spending five times longer than toadfish moving, whereas toadfish would remain still underneath the oysters (figure 4*b*).

4. Discussion

These findings support the conclusion that personality can help predict predation risk, and demonstrate that different personalities are best suited to distinct situations. Although mud crab refuge use and mortality were measured during two separate experiments, our previous research has determined that relative refuge use between individuals should remain consistent across these experiments ([20,44], B. A. Belgrad 2015, unpublished data). Crabs exhibited a wide range of behaviours along the continuum of bold versus shy personalities in the presence of both predators. However, the survival benefits of a particular personality varied as crabs displaying the same personality experienced different mortality rates depending on predator species encountered. Such results match conceptual predictions postulated by Sih *et al*. [46,47] and Wolf & Weissing [48] on the importance of personality for determining fitness and ecological processes.

Our observations on predator behaviour confirm that blue crabs and toadfish use vastly different hunting strategies. Blue crab behaviour was characteristic of active hunters, with crabs spending most of their time exposed outside of oyster clumps, and frequently moving about the enclosure. In comparison, toadfish behaviour was representative of ambush predators, as the fish normally remained hidden and immobile underneath oysters. These behaviours are consistent with past observational studies which have investigated the foraging behaviour of these predators [49,50].

The consumption of specific personality types by predator species is probably a consequence of these differences in predator hunting mode. Bold mud crabs probably had higher mortality than shy crabs in the presence of blue crabs, because they spent a substantial portion of their time outside oyster clumps in the same locations blue crabs frequented. Conversely, shy mud crabs most probably had elevated mortality in the presence of toadfish, because they remained under oyster clumps whereas toadfish tend to lie hidden in wait. While we did not examine the simultaneous occurrence of both blue crabs and toadfish in the presence of mud crabs, such circumstances will be rare and brief given the relatively low densities of these predators and their mobility. Mud crabs respond to both predators by hiding, so there should not be synergistic impacts on mud crab survival in these instances. In fact, toadfish may actually reduce predation by blue crabs by causing mud crabs to hide more frequently, and thus the simultaneous occurrence of these predators could have an overall positive impact on mud crab survival. The only other known study to examine the effects of prey personality in a multipredator system found that the personality type with the most successful escapes depended on predator species, but did not find personality to have as large an impact on prey survival [33]. This may be because predators were not given a choice between prey personalities concurrently and had similar hunting strategies. The strong connection between predator and prey behaviour illustrated here highlights the necessity of examining both simultaneously (discussed by Lima [51]).

Interestingly, although blue crabs and toadfish selected specific personality types, the personality these predators consumed were the least common personalities mud crabs displayed in the presence of that particular predator species. The strength of the mud crab predator avoidance behaviour depended on predator species, with crabs increasing their refuge use in the presence of odour cues belonging to predators which cause the highest mortality (blue crabs). Other studies have described similar results with passerine birds and

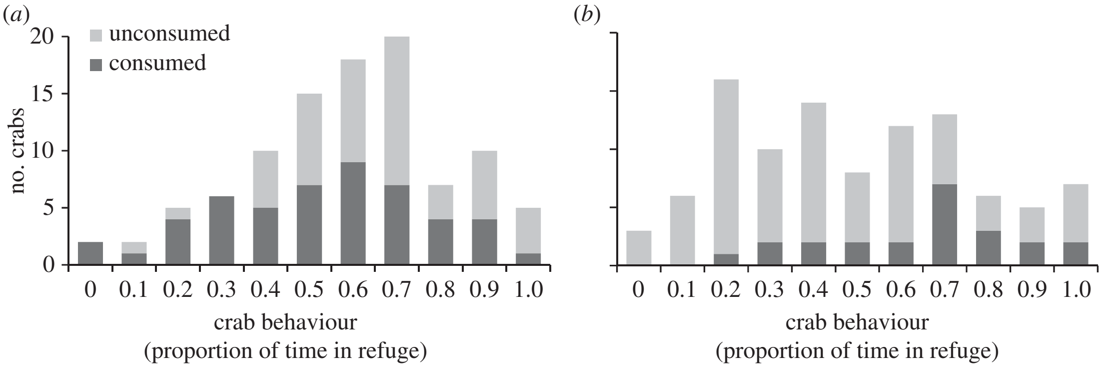

Figure 3. Histograms of the amount of mud crabs, *Panopeus herbstii*, consumed by predatory (*a*) blue crabs *Callinectes sapidus*, and (*b*) toadfish *Opsanus tau* for each behavioural class of mud crab. Crab behaviour was measured as the proportion of observations over 3 h in which a crab was observed taking refuge under oyster shells.

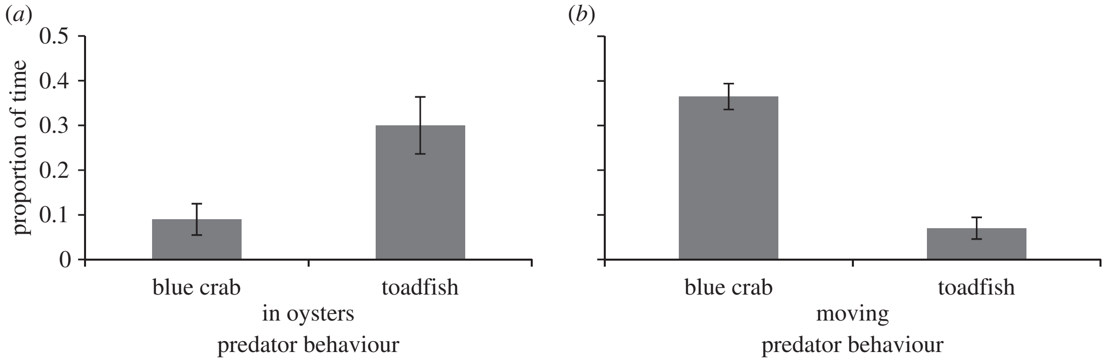

Figure 4. Mean ± s.e. proportion of time predatory blue crabs (*Callinectes sapidus*) and toadfish (*Opsanus tau*) (*a*) hid within oyster clumps and (*b*) were mobile. Behaviour was measured as the proportion of observations predators used cover within oysters and were moving over two 20 h periods which were measured on 2 separate days for a subset of the trials/individuals ($n = 5$).

grasshoppers responding most strongly to owl and spider species which present the greatest predation threat [36,52]. However, our findings demonstrate that the strength of predator avoidance behaviours not only relies on predator hunting mode as previously theorized [34,36], but also depends on prey personality. Here, personality comes into play when an individual has a disposition which naturally causes it to express the avoidance behaviour and the predator consumes the opposite prey personality. Thus, predator avoidance behaviours should be the strongest when both the avoidance behaviour and personality of the individual facilitate survival in the presence of a specific predator (e.g. prey will most often become inactive in the presence of predators which preferentially consume bolder individuals, and will be more active in the presence of predators which select shy individuals). Given the incredible variety of species which exhibit personalities and the numerous types of avoidance behaviours prey can exhibit in response to predators, these findings can be applied to a wide range of predator–prey interactions.

The link between personality type of prey and the suitability of that personality for the specific hunting mode of the predator could partially control the structure of communities. For example, the shift in mud crab refuge use in response to predator species reported here can govern trophic cascades. Previous research on *P. herbstii* established that the predator avoidance behaviour involves a substantial decrease in crab foraging effort which has positive benefits for mussel survival [19,20,53,54]. Consequently, the presence of either blue crabs or toadfish probably controls the strength of this indirect interaction on bivalve mortality. Numerous studies have suggested that such non-consumptive effects of predators may be equivalent or greater than the consumptive effects as they propagate across trophic levels [55–58]. Additionally, differences in the distribution of prey personalities within populations can have broad impacts on the community. Keiser *et al.* [59] determined that the personality composition of populations can be more important than population size in controlling overall foraging behaviour, and Cote *et al.* [60] found that personality composition affects offspring dispersal. Thus, by measuring the predation threat of different predators which is related to the strength of predator avoidance behaviours and their distribution within the population ([36,52]; this study), ecologists could potentially estimate the relative impact of these behaviours on the community. Knowledge on the distribution of personalities within prey populations and the relative frequency of predator species with different hunting modes are therefore powerful tools that could be combined to determine the strength of predator–prey interactions in field settings, where prey commonly exhibit a wide variety of personalities and encounter multiple predator types.

Indeed, living in a multipredator system may explain why mud crabs generally increase their time underneath oysters to avoid predators. Numerous studies have documented mud crabs seeking refuge within oysters in response to toadfish ([19,20,44,54]; our behavioural data). Although the predator avoidance behaviour is not as strong as with blue crabs, our results on mud crab mortality indicate that crabs should exhibit the opposite behaviour when detecting toadfish (i.e. act boldly and leave oyster clumps). Crabs may therefore increase their time within refuge automatically when in the presence of a predator owing to the prevalence and heightened threat of predation from blue crabs. Mud crabs might also seek refuge in the presence of toadfish because of differences between crabs in experience or ability to distinguish predators. This further suggests that the maintenance of a variety of personalities in this system is driven by the simultaneous occurrence of different predator types. Our research demonstrates that the benefits of each personality type are context dependent where boldness is favoured in the presence of toadfish and shyness in the presence of blue crabs. These personalities are thus likely to be sustained within the same population as both predators can be encountered within the system, and the lack of one personality would be disadvantageous if the wrong predator became prevalent in the environment. Such findings corroborate conceptual ecological theories on context dependent trait-performance (for a discussion on this concept, see [46,48]).

Our results also reveal that different predators may shift the personality composition of prey populations to opposite extremes through two concurrent methods: by preferentially consuming specific personalities and by causing individuals to change their behaviour (e.g. blue crabs consume bold mud crabs and cause individuals to hide more frequently, causing the population to shift towards shyness). Such shifts promoting a particular personality type could occur under a number of circumstances. Habitat destruction and fishing pressure often remove key predators from the system [61,62], which can subsequently reduce the number of predators favouring a particular personality type (e.g. hypothetically, overfishing of blue crabs reduces the predation of bold mud crabs and need for individuals to act shyly, thus the population becomes bolder). Alternatively, the introduction of an invasive species could promote the supremacy of a particular prey personality if the introduced species displaces natural predators. In fact, invasive species are frequently associated with the decline of predator populations [63], and numerous studies already demonstrate that alien species can alter the behaviour of native species (for a brief list, see [64]). Therefore, shifts in the distribution of personalities within populations is likely to be a common phenomenon, but has been rarely explored. Future studies should thus strive to incorporate the range of behaviours exhibited when investigating predator–prey interactions and personality researchers should more frequently report the distribution of personalities rather than just documenting that mean differences exist, as our findings demonstrate that these behaviours can have strong impacts which will not be resolved if only the average is used.

In conclusion, variations in prey personality and multiple predator species are both the norm rather than the exception in natural systems [22,34,46–48,52]. The relationship between prey personality and predator hunting mode affects the survival and behaviour of prey which has a large potential to control trophic cascades and acts as a mechanism for maintaining intraspecific trait variation. Insights into the personality composition of prey populations and hunting mode of predators may guide predictions on the strength of predator–prey interactions as well as the response of ecosystems to such pervasive issues as habitat destruction, overfishing and species invasions Therefore, the results of this study should be generally applicable to a wide variety of situations, and underscore the importance of behavioural traits in mediating predator–prey interactions.

Ethics. All applicable institutional and national guidelines for the care and use of animals were followed and the experiment was approved by the Institutional Animal Care and Use Committee (Protocol Number: 2118-100696-050213). All blue crabs, toadfish, and surviving mud crabs were released near their point of capture upon the conclusion of this study.

Data accessibility. All relevant data files are available from the NSF online database URL: http://www.bco-dmo.org/project/562104.

Authors' contributions. B.A.B. performed the experiments. Both authors conceived and designed the experiments, analysed the data and drafted the manuscript and gave final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. This work was supported by NSF grant no. OCE-1129166 and by a Vernberg Fellowship from the Baruch Institute.

Acknowledgements. Thanks go to Jessica Karen and Eilea Knotts for help measuring crab mortality.

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