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Response to perceived predation threat in fiddler crabs: trust thy neighbor as thyself?

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Abstract Prey require information if they are to respond to predation threat in a risk-sensitive manner. One way that individuals can obtain this information is through the predator-mediated, threat-induced behavior of conspecifics. We examined such a possibility in a refuge-seeking species, the sand fiddler crab (*Uca pugilator*). Crabs were either exposed directly to a simulated predation threat (a moving cylinder) or the threat-induced response of a near neighbor. We found that fiddler crabs responded to the flight of their neighbors even when they, themselves, were not privy to the stimulus that induced their neighbor's response. However, the wider range of behaviors exhibited by these crabs—which included no reaction, freezing, running back to the burrow entrance, and burrow retreat—suggest that 'non-threatened' crabs either (1) perceived the gravity of the predation threat differently from their directly threatened neighbors and/or (2) engaged in behaviors that allowed them to acquire further information in the face of uncertainty. Conspecific behaviors also had an effect on the hiding duration of crabs, with individuals hiding longer if they saw both the predation threat and the flight of their neighbor. Our results suggest that cues provided by conspecifics can play an important role in guiding the antipredator response of refuge-seeking prey.

Keywords Antipredator behavior · Incomplete information · Public information · Refuge use · Social context · Vigilance

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Introduction

Despite obvious fitness benefits to prey, antipredator behaviors can also be costly. Avoidance of one predator may, for instance, increase the vulnerability of prey to another (Krupa and Sih 1998; Stapley 2004). Time and effort spent by individuals on predator detection and avoidance can also impinge on other activities, resulting in reduced feeding efficiency (Downes 2001; Stapley and Keogh 2004) and/or missed mating opportunities (Koga et al. 2001; Cooper 1999). In order to balance these conflicting demands, prey should adjust their responses to reflect the gravity of the predatory threat (Helfman 1989). Information necessary to effect an appropriate response can either be obtained by an individual directly or, under some situations, by relying on others to alert them to the threat (Danchin et al. 2004; Rainey et al. 2004). Examples of the latter are especially well documented in group-living species (Elgar 1989; Lima 1990). Glowlight tetras (*Hemigrammus erythrozonus*), for instance, are visually sensitive to the alarm-induced, fin-flicking display of shoal mates and respond accordingly even when they, themselves, are not privy to the actual threat that provoked the display (Brown et al. 1999). Such studies underscore the important role that social transfer of information can play in predator detection and avoidance.

Reliance on others, however, can be fraught with ambiguity. Emberizid sparrows, for example, convey little information to their flock mates when a predatory threat is detected as the departure of birds induced by an actual attack cannot be easily distinguished from non-threat departures (Lima 1995). More generally, even if individuals are alerted to the existence of a predatory threat, by relying on others, uncertainty may still surround the magnitude of the risk that is posed (see also Giraldeau et al. 2002). This can conceivably have important implications for how individuals should respond to the threat (if at all), and for how long. Surprisingly, few studies have explicitly investigated prey behavior under this biologically meaningful scenario. A notable exception was research that manipulated information available to yellowhammers (*Emberiza citrinella*) to test the response of these birds to a flying sparrowhawk

(*Accipiter nisus*) (van der Veen 2002). Birds that heard a conspecific's alarm call, but could not actually see the threat, had less complete information about predation risk than those which saw the predator. As a consequence, the former engaged in greater alert-perching behavior and took longer to resume feeding. It remains to be tested whether the response observed in that study applies generally to other taxa, especially those that retreat into refuges (e.g., burrows, holes) when threatened. Hiding in a refuge may not only conflict directly with an individual's ability to engage in other activities (Cooper 1999; Diaz-Uriarte 1999; Downes 2001; Stapley and Keogh 2004), but also restrict the acquisition of any further information regarding the predatory threat (Hugie 2003, 2004). How much reliance, then, should refuge-seeking species place on the behavior of conspecifics in dictating their own response to a perceived threat?

The sand fiddler crab (*Uca pugilator*) inhabits intertidal sandflats in mixed-sex colonies along the Atlantic coast of subtropical and temperate North America (Crane 1975). Fiddler crabs construct burrows in the substrate and take shelter in their retreats during high tide but are surface active when the tide is out. Because fiddler crabs feed by extracting organic material from the surface sediment (Reinsel and Rittschof 1995), they must exit their burrows to feed. Individuals must also leave their burrows to find or court a mate (Pope 2000). When out on the surface, fiddler crabs are vulnerable to predation from a variety of animals including birds, mammals and reptiles (Crane 1975; Frix et al. 1991). Crabs respond to potential predators in a graded manner that reflects the gravity of the perceived threat. Specifically, individuals may freeze as an initial response, run back to the burrow entrance or, if the perceived predatory threat is sufficiently high, retreat down into its burrow (Land and Layne 1995a, b; Layne et al. 1997). A predator-mediated, threat-induced burrow retreat is a rapid response and is easily distinguished from the non-threatened behavior of crabs returning down their burrows to wet their gills or to excavate their burrows (Jennions et al. 2003). Crabs, however, also run to the burrow to ward off an intruder or, in the case of males, to attract potential mates (Christy and Salmon 1991). Hence, crabs could, potentially, be confronted with uncertainty as to the motive behind the rapid retreat of their nearest neighbor (Lima 1995). Social mediation of behavior in fiddler crabs has been reported in a variety of contexts (Backwell et al. 1998; Backwell and Jennions 2004). Fiddler crabs may thus also be sensitive to the antipredator behaviors of their near neighbors al-

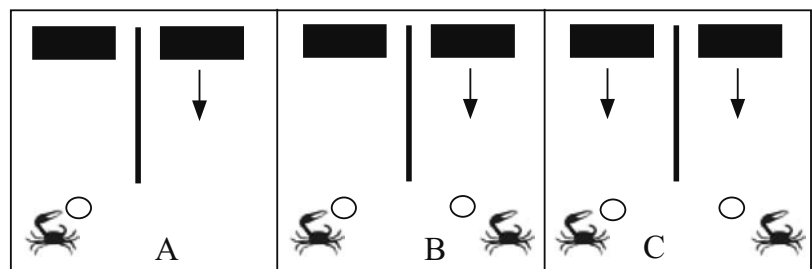
though this has not, until now, been specifically investigated (Jennions et al. 2003). In the light of these attributes, we set out to test the response of crabs that are directly confronted with a simulated predation threat versus those that are alerted to a threat via the response of a neighbor. We expect that the latter carries less information about the level of predation risk (van der Veen 2002). As a consequence, we predict that this should result in differences in both (1) the immediate response of individuals and (2) the time it takes for crabs to resume normal activity.

Methods

All experimental work was carried out during diurnal low tide (± 3 h) in September 2004 at Little Sippewissett Marsh, Cape Cod, Massachusetts, USA. Experiments took place on the high marsh along exposed sand flats and gently sloping sandy creek banks. For each trial, we first located two crab burrows situated in close proximity to one another. On Cape Cod, the distribution and density of sand fiddler crabs varies seasonally. Crab densities can be as high as 93 crabs/m² during late spring but decline through the summer (Connell 1963). As the number decreases, the dispersion pattern of *U. pugilator* changes from a uniform distribution to one that is spatially patchy (Connell 1963). At the time of our study, burrows clustered in small groups were common along unvegetated sand flats and creek banks bordered by dense marsh and open water. Testing in these areas allowed us to avoid more open and densely populated areas where the behavior of many neighbors would otherwise have been difficult to control (Pope 2000). The burrow distance between focal pairs was a mean \pm SD of 28.6 ± 12.5 cm.

The experimental setup involved pushing an opaque plastic divider 2 cm into the sand (length of divider = 47 cm, height = 23 cm). The length of the divider was oriented perpendicular to, but 5 cm behind, the straight line distance separating the two burrows. We then positioned a gray cylinder 40 cm behind each of the two burrows (length of cylinder = 36 cm, height = 11.5 cm). Each cylinder was tied to a 2.5 m length of white string which was used by the observer to pull the cylinder 10 cm towards the crab burrow in a simulated 'predator' attack (Fig. 1). Pulling a stimulus tethered to string has previously been successfully used to study visual perception and behavior in *U. pugilator* (Land and Layne 1995a). Fiddler crabs

Fig. 1 Experimental setup. **A** Control. **B** One scare. **C** Two scare. Arrow indicates the movement of the cylinder



categorize stimuli as dangerous (or not) by their position relative to their visual horizon (Layne et al. 1997). Objects moving above the visual horizon are perceived as a threat. Hence, crabs are expected to view an oncoming cylinder (whose height rises above the visual horizon) as a threat, but not the string pulled along the ground. The opaque sheet provided a visual barrier so that a given crab was unable to see the cylinder behind its neighbor's burrow. The crabs, however, could see one another as they fed near their respective burrows. After setting up the experimental apparatus, the observer sat quietly in a chair approximately 2 m in front of the burrows. Focal crabs soon emerged and resumed feeding. As in previous studies, crabs did not appear to be affected by the presence of the observer nor the placement of stationary foreign objects near their burrows (Christy et al. 2002, 2003a, b; Jennions et al. 2003).

We used three treatments to test whether crabs cue in on the response of their near neighbor to predators. In "one scare" trials ($N=32$), the observer pulled the cylinder behind one of the crabs such that the 'scared' crab's neighbor could not see the actual threat but could see the response of the scared crab. The scared and non-scared crabs were randomly predetermined before the cylinder was pulled. In "two-scare" trials ($N=32$), the observer pulled the cylinders behind both crabs simultaneously. In these trials each crab could see both the threat and the response of its neighbor. As a control ($n=32$), we also set up trials where a cylinder was pulled when a neighbor crab was absent or below its burrow. This allowed us to confirm that (1) the movement of the neighbor's cylinder behind an opaque screen was not, somehow, being perceived as a threat and (2) any response was not due to more distant crabs reacting to the cylinder. Trials from each of the three treatments were conducted in random order and within the same general location. For all trials, we scored the response of crabs on a scale from 1 to 4 (Table 1). We also measured the time to resumption of normal activity (i.e., the time it takes to resume feeding). If crabs retreated into their burrows, we also recorded, for up to 300 s, the time it took for crabs to re-emerge. Because we used naturally settled crabs, trials included both same-sex and separate-sex 'pairs'. Male and female sand fiddler crabs do not differ in their retreat speed when threatened, nor in the time to re-emergence after a scare (Frix et al. 1991). The carapace length of focal crabs measured a mean \pm SD of 18.07 ± 2.36 mm, with no significant difference in size

between the sexes (two-sample t -test, $t=1.17$, $N_1=N_2=80$, $P=0.24$).

Statistical analyses

We used Kruskal–Wallis nonparametric analysis of variance to evaluate overall group effects in the initial response of crabs to the perceived threat and the time taken to resume activity. Comparisons between and within treatments were analysed using Mann-Whitney U -tests and Wilcoxon signed ranks tests respectively. In the case of multiple pair-wise comparisons, alpha levels were adjusted using the Bonferroni procedure and reported accordingly in the text. We used nonparametric survival analyses to compare the time of re-emergence and resumption of activity between groups of crabs that hid. Cases in which crabs did not re-emerge or resume activity within 300 s from the time they first entered their burrows were recorded as "right censored" for the purpose of the survival analyses (SYSTAT 2002). All statistical analyses were conducted in SYSTAT v. 7.0.

Results

Initial response to predatory threat

There was a significant difference in the response of crabs to our simulated predatory threat depending on whether or not individuals witnessed the threat for themselves (Table 2; Kruskal–Wallis test, $H=121.03$, $P<0.001$). Control crabs were neither threatened directly nor were they able to see the response of a threatened neighbor. Such crabs generally continued feeding when a cylinder, screened from view by the opaque partition, was pulled on their neighbors' side. The reaction of control crabs differed from the response of crabs that were threatened directly (control crabs versus crabs in two scare treatment: Mann-Whitney U -test, $U=1024$, $P<0.001$; control crabs versus threatened crabs in one scare treatment: Mann-Whitney U -test, $U=5$, $P<0.001$), as well as crabs that were privy to the response of a threatened neighbor but were not, themselves, threatened (i.e., control crabs versus non-threatened crabs in one scare treatment: Mann-Whitney U -test, $U=261$, $P<0.001$). Crabs that were not threatened directly in the one scare treatment also responded differently to both their threatened

Table 1 Description of behavioral response of crabs to simulated threat

Score	Description
1	No reaction. Crab continues to feed without any obvious signs of disturbance
2	Freeze. Crab stops feeding and assumes a stationary stance
3	Return to burrow entrance. Crab scuttles back to the entrance of its burrow but does not enter
4	Descent into burrow. Crab scuttles back, and retreats into burrow

Table 2 Tally of responses by crabs to simulated threat

Treatment	Response			
	No reaction	Freeze	Return to burrow	Descent into burrow
Control	26	4	2	0
One-scare				
Threatened	0	0	5	27
Non-threatened	12	7	5	8
Two-scare	0	0	1	63

neighbor (Wilcoxon signed ranks test, $z=4.18$, $P<0.001$) and crabs in the two scare treatment (Mann-Whitney U -test, $U=892$, $P<0.001$). Although 12 crabs continued feeding, the other 20 non-threatened crabs in the one scare treatment reacted to the behavior of their threatened neighbor by freezing, retreating to their own burrow entrance or, in some cases, by entering their burrows (Table 2). By contrast, the majority of crabs that were directly threatened in both the one- and two-scare treatment retreated down their burrows.

Resumption of activity

The time taken for crabs to resume their activity after a perceived predation threat was related to the initial response of the crab. Individuals that merely froze or scuttled to their burrow entrance resumed activity sooner than those which retreated down their burrows (Kruskal–Wallis test, $H=38.74$, $df=2$, $P<0.001$, Fig. 2). The time it took

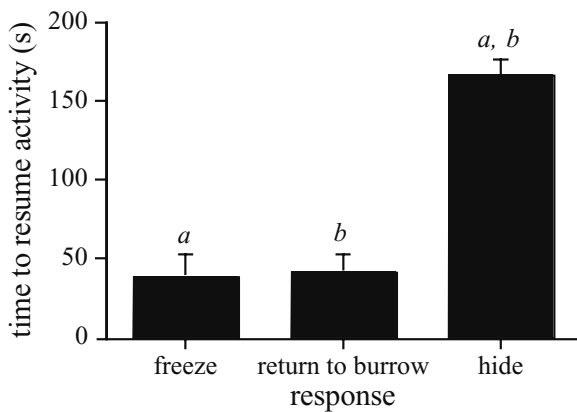


Fig. 2 Time taken to resume activity depending on the initial response of crabs. Lowercase letters indicate significant differences after Bonferroni correction ($\alpha=0.017$)

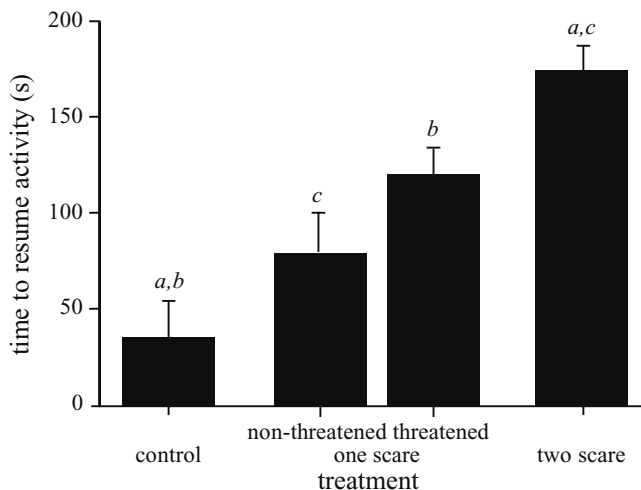


Fig. 3 Time taken to resume activity in each treatment. Lowercase letters indicate significant differences after Bonferroni correction ($\alpha=0.008$)

for crabs to resume their activity also differed between treatments (Kruskal–Wallis test, $H=25.48$, $df=3$, $P<0.001$, Fig. 3).

Among the crabs which actually hid (Table 2), we found no difference in emergence times between threatened and non-threatened crabs in the one-scare treatment (mean time to emerge by threatened crabs = 174 s, non-threatened crabs = 181 s; survival analysis, $\chi^2=0.03$, $df=1$, $P=0.87$) nor did we find a difference in time taken to resume activity between these two groups (mean time to resume activity by threatened crabs = 223 s, non-threatened crabs = 194 s; survival analysis, $\chi^2=0.21$, $df=1$, $P=0.65$). A comparison of threatened crabs that hid in the one-scare treatment versus crabs that hid in the two-scare treatment revealed that the latter took significantly longer to emerge than the former (mean time to emerge by threatened crabs in one-scare treatment = 174 s, two-scare treatment = 217 s; survival analysis, $\chi^2=4.10$, $df=1$, $P=0.04$). There was, however, no difference in the time taken to resume normal activity (mean time to resume activity by threatened crabs in one-scare treatment = 194 s, two-scare treatment = 231 s; survival analysis, $\chi^2=2.61$, $df=1$, $p=0.11$).

Discussion

Fiddler crabs responded to the predator-mediated, threat-induced behavior of their nearest neighbors even when they, themselves, were not privy to the threat. However, while crabs that actually saw the threat generally entered their burrows, crabs that only saw the response of their neighbor exhibited a greater range of behaviors. This included freezing, running back to the burrow, retreating into the burrow and, in some cases, no reaction at all. There are a number of reasons why crabs exhibited such a range of responses. First, the information conveyed by the rapid retreat of a neighbor may have been equivocal. In some species, such as Embirizid sparrows, individuals may have difficulty distinguishing between behaviors that are induced by a predatory threat and those that are not (Lima 1995). Similarly, in fiddler crabs, dashing back to the burrow may not only be indicative of an imminent predatory threat since crabs are also known to effect a rapid retreat towards their burrows in response to an intruder and/or to attract a prospective mate (Christy and Salmon 1991). Hence, it is possible that some crabs may not have regarded the rapid retreat of their neighbors as an actual antipredator response.

Second, even if crabs had perceived the retreat of their neighbor as an antipredator response, they may still have regarded the seriousness of the predatory threat differently compared with crabs that actually saw the threat (Helfman 1989). For antipredator behaviors to be adaptive, prey are expected to respond in a threat-sensitive manner (Helfman 1989). This requires individuals to properly assess the risk, a process that requires prey to balance the costs and benefits of their actions (Sih 1997). The flight of a neighbor could alert individuals to a potential predatory attack but, without actually seeing the threat itself, some individuals may not perceive the situation as sufficiently grave to elicit a

hiding response. Less “drastic” behaviors such as freezing or retreating back to the burrow entrance have the advantage of placing crabs in a position where they can, potentially, acquire further information through heightened vigilance and, if necessary, facilitate a retreat back into the burrow if the threat increases. This is useful because crabs that only see the reaction of their neighbor also have less complete information about the threat. In yellowhammers, for example, response varied according to the amount of information available (van der Veen 2002). Birds that only heard a conspecific alarm, but did not see the hawk that induced the alarm, overestimated the predatory risk and, as a consequence, took longer to return to foraging activity.

Overestimating risk can have costly consequences, especially for refuge-seeking species such as fiddler crabs. This is because when fiddler crabs enter their burrows, time spent in their shelter must be traded against time spent on surface activities, such as feeding and mate searching. Retreating into a refuge can also severely limit the acquisition of additional information and force prey into a potentially uncertain position of having to decide how long to remain in a refuge before re-emerging (Hugie 2003). In our study, the initial response of crabs to a perceived predatory threat clearly had an effect on the time it took for individuals to return to other activities. Individuals that entered their burrows also took longer to return to normal activity than those which merely froze or ran to their burrow entrance.

When crabs retreated into their burrows, the time it took for them to return to the surface did not differ between individuals that actually saw the threat and those that did not. One possibility is that if crabs make the decision to hide after seeing the threat-induced response of their neighbor, the magnitude of the threat might be considered sufficiently high to elicit a comparable hiding time as though the crab had seen the predatory threat itself. It is worth bearing in mind, however, that re-emergence times will also be influenced by uncertainty as to whether, and for how long, the threat might be persisting on the surface (Hugie 2003, 2004). Intriguingly, crabs stayed underground longer in trials where both animals saw the threat compared to a crab who was threatened while its neighbor was not. Crabs, therefore, might view a threat as being more severe (and/or less equivocal) if they also see their neighbor retreat. Thus, for individuals that actually see a predatory threat directly, the flight of a neighbor might also contribute, in an additive way, to the perception of risk and subsequent hiding duration. In terms of re-emergence time, Pratt et al. (2005) suggested recently that crabs might be able to use substrate vibrations to gauge the activity of near neighbors when deciding how long to hide.

It is unlikely that the reactions of focal crabs in our study were induced, to any significant degree, by the movement of the predatory stimuli on their neighbor’s side. String-tethered objects have successfully been used previously to study visual perception and behavior of sand fiddler crabs (Land and Layne 1995a, b; Layne et al. 1997). Fiddler crabs are known to categorize stimuli as dangerous or not

by their position relative to their visual horizon (Layne et al. 1997). A piece of string pulled along the ground (i.e., below the crabs visual horizon) is not, therefore, perceived as a threat. A focal crab could not have seen its neighbor’s cylinder move since it was shielded by an opaque screen. It is conceivable, however, that crabs could have reacted to vibrations or sounds that resulted from pulling the cylinder on its neighbor’s side. However, had this been the case, we might have expected crabs in control trials to stop feeding and to take evasive action. Instead, the majority of crabs in these trials continued foraging, seemingly oblivious to the neighbor’s cylinder being pulled. Even though we specifically avoided open and densely populated areas for our study, this result also confirms that the response of more distant crabs (if any) are unlikely to have had a major impact on our test subjects.

Although the dynamics of refuge use by prey have attracted considerable theoretical and empirical attention, few studies have actually considered the role of conspecific behavior in guiding the response of individuals to perceived threat in refuge-seeking prey. The uniquely sensitive nature of antipredator response in such species makes it likely that, as in our study, social facilitation plays an important role in shaping prey behavior.

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