A multi-stage anti-predator response increases information on predation risk

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SUMMARY

Optimal escape theory generally assumes that animals have accurate information about predator distance and direction of approach. To what degree such information is available depends not only on the prey's sensory capabilities but also on its behaviour. The structure of behaviour can strongly constrain or support the gathering of information. The ability of animals to collect and process information is therefore an important factor shaping predator avoidance strategies. Fiddler crabs, like many prey animals, escape predators in a multi-step sequence. In their initial response, they do not have accurate information about a predator's distance and approach trajectory and are forced to base their response decision on incomplete information that is not strictly correlated with risk. We show here that fiddler crabs gather qualitatively different visual information during successive stages of their escape sequence. This suggests that multi-stage anti-predator behaviours serve not only to successively reduce risk but also to increase the quality of information with regards to the actual risk. There are countless reasons why prey animals are not able to accurately assess risk. By concentrating on sensory limitations, we can quantify such information deficits and investigate how improving risk assessment helps prey optimise the balance between predation risk and escape costs.

Key words: multi-stage response strategy, escape behaviour, predator avoidance, fiddler crabs, vision, limited information.

INTRODUCTION

Optimal escape theory (Kramer and Bonenfant, 1997; Ydenberg and Dill, 1986) has been successfully used to predict behavioural responses of a wide variety of animals to approaching predators (e.g. Stankowich and Blumstein, 2005). These predictions assume that animals have accurate information with respect to the predator's distance and direction of approach. This is not always the case; some animals do not respond according to model predictions when predators approach them from different directions (e.g. Fernández-Juricic et al., 2005; Hemmi, 2005a). One reason for these discrepancies is that animals are not always able to collect the necessary sensory information, which is due, in large, to limits in resolving power and depth perception. In the context of predator avoidance, the most relevant traits of the visual system are arguably the extent of the visual field and the ability to accurately estimate distance (Blackwell et al., 2009; Cronin, 2005). Crucial for depth perception is not only visual acuity but also the distance between the eyes, which limits stereoptic depth judgements (e.g. Collett and Harkness, 1982; Zeil, 2000). Accurate estimation of approach trajectory is thus particularly difficult for small animals and for those that need to respond at large distances.

Fiddler crabs have limited visual information on a predator's identity, distance and direction of approach (Hemmi, 2005a; Hemmi, 2005b). Not knowing who is approaching from how far away and how directly makes it difficult to decide when to retreat. Given the cost of ignoring a predator, limited information is likely to lead to very sensitive but unspecific response criteria, and as a consequence, fiddler crabs escape from almost anything that moves in the sky (Layne et al., 1997; Hemmi, 2005a; Hemmi, 2005b). Like many other animals, fiddler crabs respond to predators in stages (Hemmi and Zeil, 2005). When they first detect a predator they interrupt their activity and freeze. Freezing has two likely consequences: firstly, it

makes the crabs more difficult to detect, and secondly, it brings their own visual system to rest, reducing motion blur and thereby decreasing noise in the visual input. If the predator continues to approach, the crabs run home towards their own burrows but often remain at the entrance.

Once close to their refuge the animals can afford to let the predator approach more closely and can extract more reliable information on its distance, speed, size and direction of approach, and possibly also its shape (identity). The crabs retreat underground only if the predator approaches further. It is this final step that is likely to be the most costly part of the escape sequence. After entering their refuge, the animals cannot further update their information with respect to the external world and are forced to enter a time-consuming waiting game with their predators (e.g. Hugie, 2004), leading to lost opportunities. The duration of predator-provoked refuge use in fiddler crabs has been shown to significantly exceed that of un-provoked refuge use, and the duration of provoked refuge use depends on the nature of the threat (Jennions et al., 2003; Wong et al., 2005). This suggests that before going underground, crabs are trying to assess not only the current but also the future threat posed by an approaching predator. We therefore predict that the crabs, in this step of their response sequence, should use a qualitatively different response criterion, rather than simply increasing the threshold of the criterion used in the earlier flight response.

Here we measured the visual information fiddler crabs use to decide when to retreat underground in response to an approaching dummy predator. Their decision criterion, when compared with the initial home run, is based on more accurate visual information that better predicts predation risk. Multi-stage escape behaviour, which is generally thought of as a stepwise reduction of risk, therefore also needs to be viewed as a strategy to optimally cope with limited information. Although in the case of fiddler crabs it is the visual

system that limits the availability of information, there are many other reasons why prey animals may not be able to fully assess predation risk. Irrespective of the source of uncertainty, we argue that multi-stage escape responses are an adaptation to deal with such limited information.

MATERIALS AND METHODS
Study species
Fiddler crabs, *Uca vomeris* McNeil (Ocypodidae: Brachyura: Decapoda), are central place foragers that feed on tropical and subtropical mudflats during low tide. Each crab occupies its own burrow from which it makes regular feeding excursions. When faced with predatory birds or approaching humans, individual crabs always return to their own burrow, irrespective of whether or not this is the closest refuge. Experiments were conducted on the mudflats of Bowling Green Bay, Townsville, Australia (19°24′S, 147°7′E) in October 2005.

Experimental procedure
Three video cameras (Panasonic NV-GS150GN, Belrose, NSW, Australia), fixed to metal poles 1.6 m above the mudflat, continuously recorded crab behaviour over an area of approximately 0.9 m × 1.4 m each (Fig. 1). A black styrofoam ball of 2.9 cm diameter was used as the dummy predator (see Hemmi, 2005a; Hemmi and Merkle, 2009). A monofilament fishing line wrapped around a driving wheel allowed the ball to be pulled along a 20 cm-high dummy track (Fig. 1A). A battery-driven electric drill attached to the driving wheel moved the dummy at one of three speeds (see also inset Fig. 4B): slow ($19.3 \pm 2\,\mathrm{cm\,s^{-1}}$), medium ($36.3 \pm 3\,\mathrm{cm\,s^{-1}}$), and fast ($70.7 \pm 7\,\mathrm{cm\,s^{-1}}$). This setup enabled the experimenter to remotely control the dummy. The dummy predator, modelled on the hunting behaviour of the gull-billed tern (Land, 1999), reliably elicits anti-predator responses in fiddler crabs (e.g. Hemmi, 2005a). After completing the experimental setup, crabs were given at least 10 minutes to resume normal foraging behaviour before the experiment started.

During what we call a 'run', a dummy approached the recording area from a distance of at least 6 m, moved past all three cameras, before returning to its starting position (Fig. 1A). These 'runs' were repeated every 2–3 min. We replicated this setup in five different locations, each time presenting nine dummy runs consisting of three randomised blocks. Each block consisted of three runs, one at each dummy speed, in a randomised sequence.

Video analysis and response measurements
We digitised the video footage with dvgrab (modified open source Linux software) and extracted the behavioural data with custom-made Matlab software. All crabs were assigned to their individual burrows, and their positions were tracked at 200 ms intervals. Camera images were calibrated by removing lens distortion effects, and a checkerboard test pattern was used to determine the positions of the cameras relative to each other and to the ground (Bouguet, http://www.vision.caltech.edu/bouguetj/calib_doc/). The pulling line that moved the dummy also moved two patterned wheels, each visible to one of the video cameras. From the wheel rotations we were able to calculate the exact position of the dummy relative to the crabs, even when the dummy itself was not visible in every image.

As in previous work, a home run was considered to have occurred whenever a crab moved at least 3 cm towards its burrow during a three-frame period (600 ms). The start of the response was assigned to the first of these frames in which the crab had moved at least 1 cm during one 200 ms interval. A burrow descent was recorded when a crab entered its burrow to the point where it became invisible. Responses were only counted if they occurred during the incoming dummy movement, i.e. while it moved from its start position towards the turning point (Fig. 1A). The decision to run home was assumed to have occurred one frame (200 ms) prior to when the response was measured. The burrow descent decision was considered to have occurred two frames (400 ms) before a crab had fully disappeared. This was necessary as our criterion for a crab to have descended underground is very conservative and required the crab to become completely invisible. In most situations, the crabs were already clearly heading underground in the frame before the response was registered. Changing the criterion from 200 ms to 400 ms, however, made little difference. The biggest effect of varying this criterion was on the crab–dummy distance for the fastest dummy speeds. Had we assumed a 200 ms decision time for the underground response, the three survival curves would actually have become even more similar (Fig. 4C). A 400 ms decision time for the home run, however, would have slightly exaggerated the differences found between the survival curves (Fig. 4A).

A

Camera field of view
Burrows
Dummy start position
Approach direction
Turning point
Dummy track
1m
Pulling line
8 m
Observer

B

Dummy
Crab–track distance
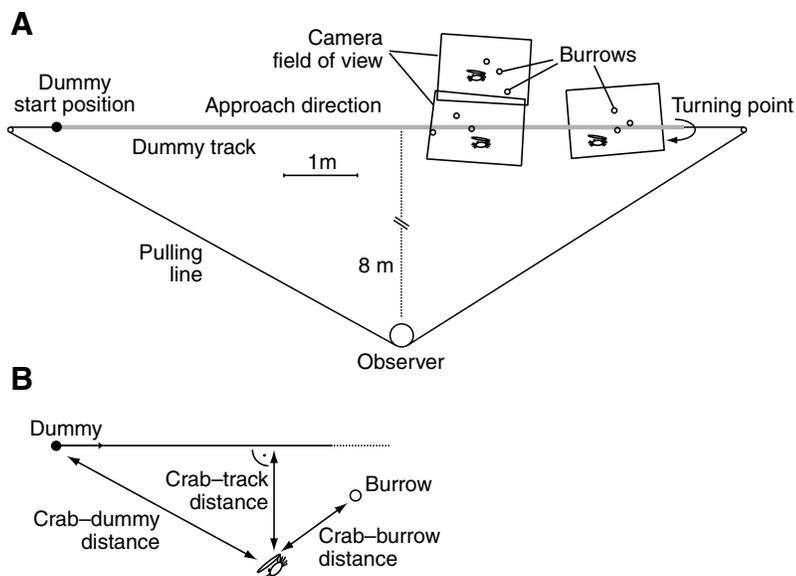Burrow
Crab–dummy distance
Crab–burrow distance

Fig. 1. (A) Experimental setup. A typical arrangement of the field of view of three cameras, the dummy track, crab burrows, the dummy and the experimenter. Digital cameras recorded the crabs' responses to the approaching dummies. During a 'run', the dummy moved to the end of the track, where it turned around to go back to its starting position. (B) The geometry of the response situation: crab–dummy distance, crab–track distance and crab–burrow distance. Crab–track distance and crab–burrow distance were measured at the onset of dummy motion, crab–dummy distance at the time of response.

For home runs we only considered crabs that were at least 5 cm away from their burrow at the start of the run (Hemmi, 2005a). This ensured that a home run could be scored by the criterion defined above. For each valid run, we determined the crab–dummy distance, crab–burrow distance and crab–track distance (Fig. 1B). All crabs that left the cameras' field of view during the dummy movement or that were involved in an interaction with another crab were excluded from the analyses. From the geometry of the situation, we could then calculate the apparent size (the angular size of the dummy predator as seen from the crab's point of view) and apparent speed of the stimulus (the angular speed of the dummy as seen from the crab's point of view).

Statistics

Data from both the burrow descent and the home run decision were analysed in the context of a survival analysis using a Cox model (Collett, 2003). Cox proportional-hazards model allows the effects of several risk factors on the probability to die, or as in our case, to respond to an ever-more threatening stimulus to be analysed. The advantage of this approach is that we do not have to divide the data into those runs/crabs that do respond and those that do not. The survival curve combines the probability of response together with the response timing (in our case response distance or stimulus angular size). However, it is very easy to disentangle the two effects visually; survival curves clearly provide the information at what distances the crabs responded to the approaching dummy. For the home-run data, the final Cox model contained three terms: dummy speed, crab–track distance and crab–burrow distance. For burrow descent, the model contained only two terms, dummy speed and crab–track distance. Dummy speed was fitted as a factor, all other terms as variates. For the burrow-descent decision, crab–track distance is the same as burrow–track distance. As in a typical regression analysis, the significance of each model term was judged by comparing models that differed by only one term. All terms of the final model made a statistically significant contribution to that model at the 5% level. Statistical significance was judged using a simple permutation approach applied to the full Cox model (Good, 2005). This non-parametric approach allowed us to avoid making assumptions about the underlying distribution of our data while taking into account the experimental and repeated-measures design. To test statistically for the effects of approach speed, dummy speed was randomly permuted 10,000 times across the responses of each individual crab. The score of our statistical measurement, the residual deviance of the Cox model, a measure of residual variance left in the data, was computed on our original, un-permuted data set and was then compared with the scores of the permuted data sets. Significance was judged by calculating the percentage of permutations that resulted in a score that was more extreme or equal to the score calculated from the un-permuted data set. As usual, P-values thus indicate the probability that the measured effect was due to chance alone. By permuting strictly within individual crabs we eliminated crab-to-crab variability from the analysis. All of the other variables, such as the distance between the crab and its burrow and the distance between the crab and the dummy track, over which we had no control during the experiment, were permuted within individual dummy approaches, thereby taking into account the block design of the experiments. Computations were performed in R (R Development Core Team, Vienna, Austria) using the survival package v.2.34-1.

RESULTS

Crabs reliably responded to the approaching dummy predator by running home to their individual burrows. At the entrance of the
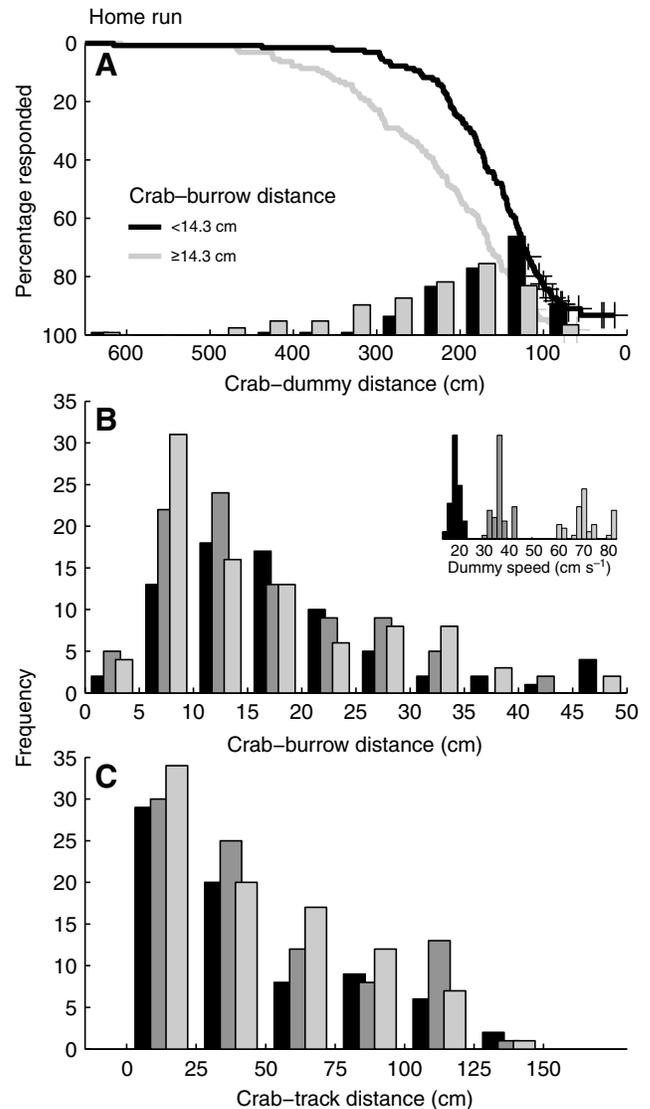

Fig. 2. (A) Crabs that were further away from their burrow (light grey line and bars) responded earlier, i.e. at a larger distance to the approaching dummy predator, than those closer to home (black line and bars). Lines show the inverted empirical cumulative distribution function and bars show the probability that a crab responded as the dummy moved though a certain distance bin. The inverted cumulative distribution function, also known as a survival curve, shows the percentage of crabs that have responded before the dummy reached a certain distance to the crab. Crosses indicate censored data points, where the dummy had reached its closest possible distance to the crab. The data have been divided into two groups: near and far, according to whether crabs were closer or farther away than median distance to the burrow. N=127 in each group. (B) Distribution of crab–burrow distances at the time the dummy started to move. (C) Distribution of crab–track distances at the time the dummy started to move. The histograms in B and C have been divided into three groups according to the speed of the moving dummy (inset B, black=slow, grey=medium, light grey=fast).

burrow they often paused before retreating underground or resuming other activities. Over 95% of all crabs ran home in response to the approaching dummy, and crabs that were further away from their burrow and therefore more exposed, responded earlier (Fig. 2A, N=254, P=0.0003) (see also Hemmi, 2005a).

The distance of the crab or burrow to the dummy track, a measure of the directness of the dummy's approach, had an important effect
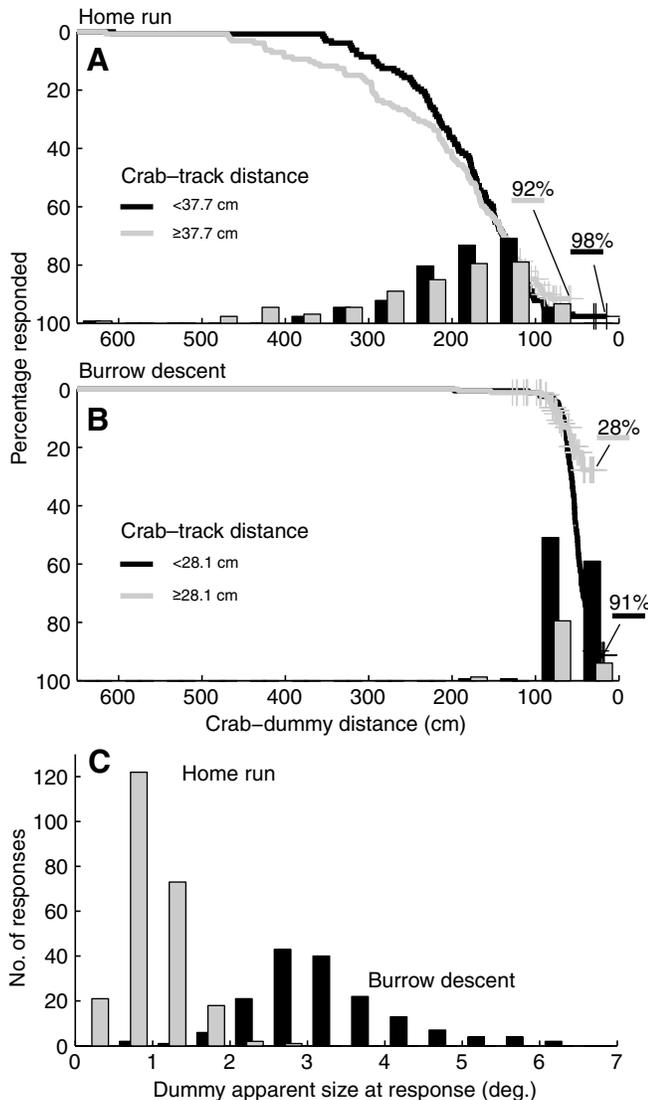
Fig. 3. Crabs further away from the dummy track were less likely to respond to the approaching dummy. The data have been separated into two groups, near (≤median) and far (>median), according to the distance between crabs and the dummy track. N=127 in each group. (A) Home run: crabs closer to the dummy track (black bar and lines) respond later to the approaching dummy but are overall slightly more likely to respond than those farther away (light grey bar and lines). (B) Burrow descent: crabs with burrows close to the dummy track (black bar and lines) are much more likely to go underground than those farther away (light grey bar and lines). N=157 in each group. There is, however, no clear difference between the two groups in their response distance (histograms). (C) The apparent size of the dummy at the time the crabs respond for the home run (grey bars) and the burrow descent (black bars). Other conventions as in Fig. 2.

on both the home run and the burrow descent (Fig. 3A,B). Crabs closer than the median distance of 37.7 cm to the dummy track were more likely to run home (98%, endpoint black line in Fig. 3A, N=254, P=0.0005) than those further away (grey line, 92%). Crabs responded later, however, when approached more directly (black line in Fig. 3A, N=237, P=0.012), even though more directly approaching predators are likely to be more dangerous (see also Hemmi, 2005a).

The burrow descent usually does not immediately follow the home run but the crabs wait and make a second decision whether

and when to retreat underground. The mean or median response distance for the burrow-descent response (crab–dummy distance at the time of response) is less than one third of that of the home run (compare distributions in Fig. 3A,B).

The effect of the dummy's approach trajectory (crab–track distance) was much stronger for the burrow-descent response than for the home run. While 91% of crabs that were closer than the median distance of 28.1 cm to the track disappeared underground as the dummy approached (endpoint black line in Fig. 3B), only 28% of those farther away retreated into their burrow (grey line in Fig. 3B, N=314, P<<0.0001). There was, however, no clear difference in the timing of this response. Irrespective of how directly they were approached by the dummy, crabs descended into their burrow at approximately the same distance to the dummy (Fig. 3B).

The dummy's apparent size at the time of response is much larger for the burrow-descent response (black bars in Fig. 3C) than for the home run (grey bars in Fig. 3). This is a direct consequence of the differences in respective response distances.

Speed dependence

Dummy speed affected the underground response in a different way to the home run. Crabs ran home earlier, i.e. at a larger crab–dummy distance, when the dummy moved faster (Fig. 4A, N=254, P<<0.001) (see also Hemmi, 2005b). The overall home-run response probability, however, was independent of dummy speed. The increase in response distance for faster approach speeds is consistent with our earlier evidence, that retinal speed is part of the criterion crabs use to decide when to run home (Hemmi, 2005b). If the home-run decision is based on the dummy's apparent speed, we would predict that the distribution of apparent speeds at the time of response is independent of the dummy's real speed. This is precisely what we found. Even though fast dummies (light grey bars in inset Fig. 4B) were almost four times faster than slow dummies (black bars), the distribution of apparent speeds, at the time of response, was almost identical (Fig. 4B, N=254, P<0.014). Note that if the dummy's apparent speed at the time of response is the same for different dummy speeds, its distance at the time of response is necessarily different and *vice versa*. The broad speed distributions demonstrate clearly that the crabs did not respond at a set apparent speed (Fig. 4B). Being the same for different dummy speeds, however, the distributions suggest, that the crabs' decisions were based on a measurement that correlated with the dummy's apparent speed (see also Hemmi, 2005b).

The same dummy was treated very differently when crabs sat at the burrow entrance. The results show exactly the opposite pattern to what we saw for the home run. The response distance was identical for all three dummy speeds (Fig. 4C, N=314, P=0.21) but the distribution of apparent speeds at the time of response varied widely (Fig. 4D, N=314, P<<0.001). The crabs responded to fast and slow dummies at the same distance (Fig. 4C) but at very different apparent speeds (Fig. 4D).

DISCUSSION

When faced with danger, the fiddler crab *U. vomeris* responds in multiple stages (Hemmi and Zeil, 2005). We have shown here that they use qualitatively different visual information to initiate each of the two most costly stages of this escape sequence. The burrow-descent response was not triggered immediately following the home run but much later at less than one third of the home-run response distance. Crabs run home to their burrow early during a predator's approach and their escape criterion is highly unselective. Almost all of the crabs within the recording area returned to their burrow each
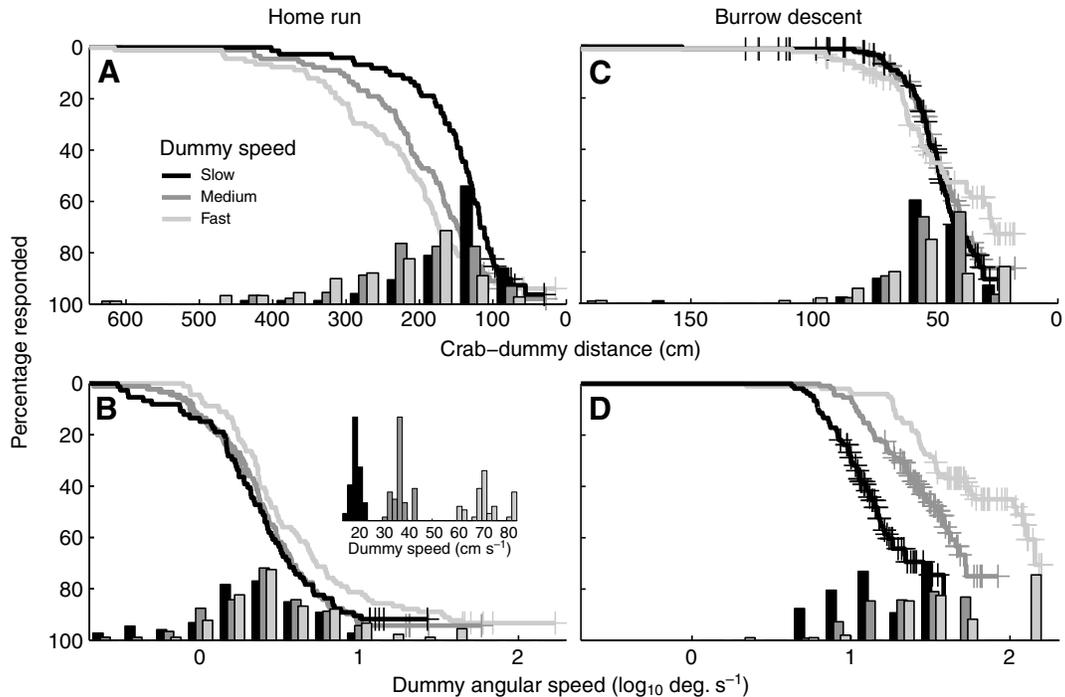
Fig. 4. The response criterion crabs use to decide when to respond to the approaching dummy predator is speed-dependent for the home run (A,B), as shown by the equal apparent speed of the dummy at the time of response (B) but not for the burrow-descent response (C,D). The data have been separated into the three groups according to the speed of the approaching dummy (inset B, black=slow, grey=medium, light grey=fast) and are plotted against the dummy's distance to the crab (A,C) and against the dummy's apparent speed as seen by the crab (B,D). Note the difference in scale between A and B. The two panels A and B and the panels C and D, respectively, show the same data plotted in two different ways. The inset in B shows the distribution of measured dummy speeds at the time the crabs ran home. See Results for further detail. Other conventions as in Fig. 2.

time the dummy predator approached. By contrast, the burrow descent is triggered later and only those crabs that were approached directly actually escaped underground (Fig. 3B). Over 70% of crabs farther away than 28.1 cm from the dummy's approach trajectory remained on the surface and in visual contact with the predator. This difference in selectivity reflects the accuracy of the visual information available to the crabs during the two stages of their response.

The decision to run home
The results of Fig. 4A,B show that the home-run decision is sensitive to the apparent speed of the approaching predator. However, apparent speed is not the only visual characteristic of the predator that influences response timing. Apparent size, retinal elevation (Hemmi, 2005a; Hemmi, 2005b), contrast (Smolka, 2009) and stimulus history (Hemmi and Merkle, 2009) have also been shown to affect the home-run decision. The strong retinal speed dependence, however, highlights the unspecific nature of this early escape decision and leads to many false alarms. Retinal speed does not always reflect actual risk, and indeed crabs run away from almost anything that moves above the visual horizon (Layne, 1998). Using retinal speed as part of the decision criterion means that faster predators will trigger earlier escapes. It also means, however, that crabs will respond later to a more dangerous, directly approaching predator (Fig. 3A). This is because the apparent speed of an object decreases as the object approaches the observer more directly (see Hemmi and Zeil, 2005). So, whilst crabs are clearly influenced by a predator's approach trajectory, they cannot interpret this information correctly, as their response criteria confounds speed and approach trajectory.

Fiddler crabs are, therefore, unable to truly assess the directness of the approach when they first respond to a predator. The resulting

discrepancies between optimal escape theory (e.g. Kramer and Bonenfant, 1997) and crab behaviour have already been discussed by Hemmi (Hemmi, 2005a; Hemmi, 2005b). Crabs, however, are nonetheless clearly risk-sensitive; when they are farther away from their refuge they respond earlier than when closer to home (Fig. 2) (see also Hemmi, 2005a), a common characteristic found in many animals (Stankowich and Blumstein, 2005). As predators can approach from any direction, the crab–burrow distance has no influence on the crabs' ability to detect the predator. The observation that the crabs adjust the response distance to the predator based on their own distance to the burrow, therefore, also illustrates that the home run is not simply triggered by a detection threshold. Rather, the crabs are making a decision when to respond to an already visible stimulus.

The decision to enter the burrow
The decision to escape below ground is based on qualitatively different visual information than the decision to run home. Predator speed, in this case, has no effect on response distance (Fig. 4C,D). This speed independence rules out speed-dependent decision cues such as a threshold for time-to-contact or looming (change in apparent size over time), both of which would be triggered earlier by faster dummies.

The fact that crabs respond at equal distance for different dummy speeds does not actually indicate that crabs are able to measure predator distance directly. It is very unlikely that they are able to do so (Collett and Harkness, 1982; Hemmi, 2005a). Our 2.9 cm dummy always moved at the same height and therefore both apparent size and elevation in the crabs' visual field or changes in apparent size and elevation are perfectly correlated with distance. To discriminate between these possibilities, we would need to manipulate dummy size and height.

Retinal elevation and retinal size, however, carry important risk-related information. Both predict predation risk more directly and more accurately than retinal speed. A larger retinal size indicates a larger or closer predator (Peters et al., 2008), both of which are more dangerous. Equally, for predators such as terns that fly parallel to the mudflat like our dummies, an increase in retinal elevation signals that the tern is approaching 'the observer'. What is important for the crabs is that a hunting tern cannot realistically approach closely without increasing its apparent size or retinal elevation. They could, however, come closer without increasing apparent speed. In the extreme case of a direct approach, there would be no displacement of the predator's image at the crab's eye. The only image motion cues a crab would perceive would be the looming edges of the predator's outline. Furthermore, by moving initially tangentially past a crab and then moving more and more directly towards it, an approaching predator could in fact decrease retinal speed during the early stages of the approach.

The crabs' ability to use this more accurate visual information for the burrow-descent decision depends crucially on the earlier execution of the home run, which brings the crabs back to the relative safety of their refuge with a relatively minor cost. Being close to safety, crabs can afford to let the predator approach more closely, before being forced to make the next decision. The extra wait time results in a strong increase in the apparent size of the approaching predator (Fig. 3C). Fiddler crabs have a minimum receptive field size of just less than one degree (Smolka and Hemmi, 2009). This increase in the angular size of the predator image on the crabs' ommatidial array thus greatly improves the crabs' ability to measure apparent size, retinal elevation or changes thereof.

The availability of a refuge

Prey animals not only have to decide when to flee from a predator but they also have to weigh up what the best course of action may be (e.g. Broom and Ruxton, 2005; Cooper and Wilson, 2007). The availability of a refuge must have a strong influence on the prey's choice of escape strategy. The early home runs observed in fiddler crabs, which are triggered by rather unspecific stimuli, make sense only if they bring the animals close to the relative safety of their refuge. Otherwise, the fast movements these escape runs generate would only attract attention, without increasing the animal's safety. It is therefore interesting to note that under laboratory conditions, where there is no refuge available, the criterion that triggers the escape run of a distantly related crab *Chasmagnathus granulatus* is not speed-dependent but is triggered by a fixed increase in the predator's apparent size (Oliva et al., 2007) (see also Nalbach, 1990). This decision criterion is more similar to that used by fiddler crabs in the field when they decide to retreat underground, suggesting that *Chasmagnathus* simply skips the early home run because it does not have a refuge to go to.

Predation risk and multi-stage escape responses

We have shown that fiddler crabs switch to qualitatively different visual cues that more accurately predict the risk of predation when executing later stages of their multi-stage escape response. Visual limitations in estimating predation risk are likely to be common in animals, especially those that have close-set eyes or those that need to make decisions early. Vision is, however, not the only source of uncertainty that will lead to a multi-stage predator avoidance strategy. There are many reasons why prey animals are unable to fully assess predation risk. Most fundamentally, every predator–prey encounter is an interaction between two players, both of which make decisions that evaluate and change the benefits and risks of previous and future decisions (e.g.

Lima, 2002). We therefore need to interpret the design of multi-stage predator escape responses not just as a stepwise approach to increased safety but also as a means to gain access to additional information on the actual risk of predation before making important decisions.

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