



Predator avoidance in fiddler crabs: 1. Escape decisions in relation to the risk of predation

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The risk of predation is a strong force shaping many aspects of animal behaviour. Early detection and efficient avoidance strategies not only help prey to survive, but also limit the negative impact predation has on other aspects of their lives. The type of antipredator strategy an animal uses must depend on its ability to collect accurate information on the risks to which it is exposed. However, models attempting to predict when a prey animal should escape from an approaching predator often assume that the prey has accurate information on a predator's distance and direction of approach. To test whether such models could be applied to a prey animal with restricted sensory capabilities, I explored the predator avoidance behaviour of the fiddler crab *Uca vomeris* by approaching crabs with small dummies intended to mimic a hunting tern. The crabs responded strongly and reliably to the simple dummies. They were clearly sensitive to risk and responded more often and earlier, the further away they were from their refuge. The probability of response was most strongly influenced by how directly and therefore how closely the dummies approached the crabs and reached 100% for very direct approaches. Surprisingly, however, the crabs responded later when the dummies approached them more directly. I argue that this counterintuitive result reflects a lack of reliable information on the predator's distance and movement relative to the crab and its refuge, because like many small animals, crabs cannot measure the distance to a predator. I conclude that general models attempting to predict when animals should respond to an approaching predator need to incorporate the information that prey animals have available at the time of response.

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Predation has an overwhelming influence on the behaviour of prey and affects many aspects of their lives (reviewed in Ydenberg & Dill 1986; Lima & Dill 1990; Sih 1994; Lima 1998). The strength of this influence depends on the prey's ability to detect and avoid an approaching predator. The earlier the detection and the faster the prey can move relative to the predator, the further from shelter it can venture. However, because predator evasion is costly in terms of time and energy, animals should not immediately flee when they detect a predator, but should adjust their response timing according to the particular circumstances of a threatening situation (Ydenberg & Dill 1986). In other words, to avoid unnecessary and costly responses, prey animals should try to assess risk and tailor their responses accordingly.

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A large body of literature shows that animals are indeed sensitive to the risk of predation and that they adjust their behaviour accordingly (e.g. Ydenberg & Dill 1986; Lima & Dill 1990). However, an important and so far often neglected aspect of predator–prey relationships is how prey animals perceive predation risk (Lima & Dill 1990). This is despite the fact that the mechanisms with which animals perceive and learn about the risk of predation have been shown to influence their behavioural options and change the predictions of theoretical models (e.g. Luttbegg & Schmitz 2000; Luttbegg 2002; Welton et al. 2003; Fernández-Juricic et al. 2004; Koops 2004).

The threat a predator poses once it has been detected by a prey animal depends on many factors, including its identity, which determines its speed and hunting style, and the prey's own speed and distance from its refuge. In addition, it is commonly assumed that predation risk depends on the predator's distance and direction of approach relative to the prey and its refuge. The risk is expected to increase if the predator approaches more directly, approaches faster or approaches from a direction

that forces the prey to run towards the attacker in order to reach its refuge. The prey animal is expected to respond earlier, that is at larger predator distances, as the risk increases (e.g. Ydenberg & Dill 1986; Kramer & Bonenfant 1997; Cooper et al. 2003). For instance, the model developed by Kramer & Bonenfant (1997) successfully predicts the relationship between a predator's approach direction (a human) and the distance at which woodchucks, *Marmota monax*, initiate their flight to a refuge. The model assumes that animals time their response in such a way that they reach the refuge earlier than the predator, by a certain margin of safety. The implicit assumption is that prey animals are able to measure not only the distance between themselves and the predator, but also the distance between the predator and the refuge. Yet, such distance judgements are nontrivial visual tasks, especially over the large distances involved (e.g. Collett & Harkness 1982). Furthermore, judging the distance between two objects irrespective of the direction from which they are viewed is a computationally complex task which we cannot necessarily assume animals are able to perform. In many situations, prey will not be able to measure the distance and approach speed of a predator and will even have difficulties identifying it. This is especially so for small prey or when decisions have to be made very quickly. If prey animals have incomplete information about a predator's approach trajectory, models such as the one proposed by Kramer & Bonenfant will fail to predict the response distance, although simple rules of thumb might allow prey to overcome such limitations (Bouskila & Blumstein 1992; Koops & Abrahams 1998; Welton et al. 2003).

Fiddler crabs provide an ideal model system to test model predictions on optimal escape for an animal with limited sensory capabilities. The crabs rely exclusively on vision to detect predators (Land & Layne 1995; Layne et al. 1997; Layne 1998), but their eyes do not allow them to resolve much spatial detail (Land & Layne 1995; Zeil & Al-Mutairi 1996). Simple dummies can therefore be used to test responses to predators (e.g. Nalbach 1990; Land & Layne 1995; Layne 1998) or even conspecifics (Zeil & Layne 2002; Hemmi & Zeil 2003c). Owing to their small size and eye design, the crabs are unable to measure reliably the distance to an approaching predator or dummy (Collett & Harkness 1982; Zeil et al. 1986) even though they are able to measure the distance to objects on the ground (Hemmi & Zeil 2003b). In addition, the crabs' small home range and high burrow fidelity (Crane 1975; Montaque 1980) make it possible to control accurately many parameters of a predator, such as its size, distance and direction of approach, in the crab's natural environment. It also allows one to measure the relative positions of the crab, the predator and the refuge with high spatial and temporal resolution (e.g. Hemmi & Zeil 2003a).

Despite their visual limitations, fiddler crabs are risk sensitive, both in the short and in the longer term. At close range, fiddler and other crabs that are not able to enter a refuge are sensitive to an attacker's direction of approach and escape in the opposite direction (Nalbach 1987; Frix et al. 1991; Ens et al. 1993). The time that resident crabs remain in their burrow after a simulated

attack depends on the distance of large and close objects (Jennions et al. 2003). In the long term, when faced with an increased level of predation, the crabs' mating system changes from one where females leave their burrow to choose a mate to one where males have to take the risks of searching for a mate (Koga et al. 1998).

In this paper I tested whether the Kramer & Bonenfant model applies to an animal that does not have complete information about a predator's distance and direction of approach. I related the timing of the crab's escape run to the movement and the size of dummy predators and thus related responses to actual risk. In the companion paper (Hemmi 2005), I investigated the consequences the quality of information available to prey animals has on their behavioural options (Lima & Dill 1990; Sih 1992; Koops & Abrahams 1998; Koops 2004) by measuring the visual cues that trigger the crabs' responses and by analysing their information content in relation to the predator's actual movements as they are described here.

METHODS

Apparatus

I conducted experiments with *Uca vomeris* on the mudflats of Bowling Green Bay, south of Townsville, Queensland, Australia (19°24.03'S, 147°6.9'E). A camcorder (Sony TRV110 or Sony TR705E) mounted on a tripod about 1.6 m above ground level was used to monitor a small patch of mudflat 0.8–1.1 m² in size. The camera was arranged such that the responses of several crabs could be recorded simultaneously.

Fiddler crabs face a large number of predators, most commonly birds, using different hunting strategies (e.g. Zwarts 1985; Ens et al. 1993; Backwell et al. 1998; Koga et al. 1998; Iribarne & Martinez 1999). The dummies I used model the behaviour of the main local predator of *Uca*, the gull-billed tern, *Gelochelidon nilotica*. The terns fly in a smooth, horizontal motion a few metres above the ground into the wind scanning for prey. When they detect a crab, the terns stall and dive down in an attempt to catch it (Land 1999). The dummies consisted of small, black styrofoam spheres threaded on a monofilament line which was tightly strung between two poles about 4–6 m apart. This allowed me to move the dummy along a straight line, which I call the dummy track, by manually pulling on the monofilament line (Fig. 1), while sitting about 5–6 m away. The size and the height of the dummy were varied systematically, between three sizes (1.6, 2.4 or 3 cm diameter) and three heights (5, 15 and 24 cm). The dummy moved with an approximately constant velocity ($\bar{X} \pm \text{SD} = 22.7 \pm 5.8$ cm/s). As the dummy was normally outside the field of view of the camera when the crabs responded, the entire set-up was recorded from several metres away with a second, horizontally directed camera. Using the information from these two cameras, I could calculate the relative position between the crab and the dummy at all times.

The horizontal distance between the crabs and the dummy track ranged from 0 to 73 cm. In a typical experiment, the dummy would approach the crabs from a

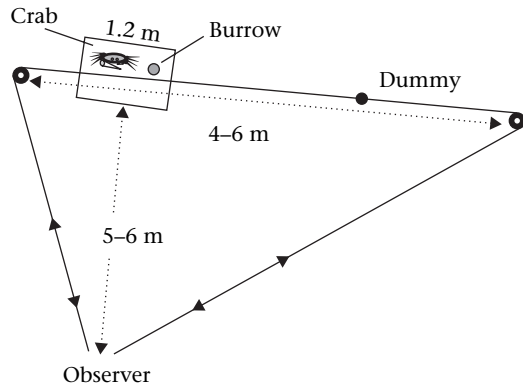


Figure 1. The dummy was moved along a track 4–6 m long, a stretch of fishing line tightly strung between two poles in the ground. The observer controlled the dummy from about 5–6 m away by means of another fishing line wrapped around the poles and attached to both sides of the dummy. The small rectangle represents the recording area of the video camera looking down on to the crabs and their burrows.

starting distance of about 300 cm ($\bar{X} \pm \text{SD} = 279 \pm 42$ cm), move past the crabs and then return to its original position. Each dummy approach (trial) was filmed from above and from the side for later analysis. Before the experiment started, the crabs were given 5–20 min to resume their normal foraging behaviour. No ethics approval was required to undertake this study.

Video Analysis and Response Measures

The film sequences were digitized at 240-ms intervals. Although the crabs' escape speed is very fast, this temporal resolution is adequate, because their normal foraging speed is very slow. To determine the X/Y-coordinates of crabs, burrows and dummies I used a video analysis program written in C and Matlab (Hemmi & Zeil 2003a). A response was considered to have started in a given frame if a crab moved at least 0.7 cm towards its burrow during the 240-ms interval preceding this frame and at least 2 cm over a three-frame interval (720 ms) starting at the previous frame. A relative measure for the crabs' response strength was calculated based on the entire path of the crabs. This measure expresses in percentages of the initial distance how far a crab moved towards its burrow during a trial. For the analysis of the timing of the response, I defined the position of the dummy and of the crab in the last frame before a crab reached the response criteria as their position at the time of response. The response speed was measured as the maximum speed during a crab's first response.

Selection of Trials

As the experiments were conducted in the natural setting, the crabs responded not only to the dummy but occasionally also to other crabs, to predatory birds and to other events beyond my control. The data set thus contains a number of responses that were unrelated to the dummies' movements. To keep such responses to

a minimum, and to make sure that all trials used in the analysis were as homogeneous, comparable and, with respect to variables of interest, as unbiased as possible, I used the following criteria to include trials in the final analysis: (1) there was no bird or crab interference during the trial; (2) crabs were at least 5 cm away from their burrow at the start of the trial; (3) the crabs had to be within the recording area when they responded to the dummy. A crab contributed at most its first 50 responses to the analysis (there was little or no habituation to the approaching dummy during the experiment, as the analysis will show). A total of 527 trials met these criteria and were subsequently analysed. I used excluded trials to calculate the number of presentations a crab had seen before a particular trial, except where the crab was underground during the entire trial and did not see the dummy.

Statistical Design and Analysis

The data were collected from seven set-ups. A set-up is an experimental setting where the camera and the dummy apparatus were placed in a particular location on the mudflat to film the responses of several crabs to repeated presentations of a dummy predator. The dummy presentations within a set-up were organized in blocks of nine trials. Each block contained a randomized presentation of the three dummy heights and, within each dummy height, a randomized presentation of the three dummy sizes. Dummy size was nested within dummy height to minimize the disturbance to the crabs required by changing the track height. Up to six blocks were presented within one set-up.

A lack of orthogonality in the data precluded the use of an ANOVA for the statistical analysis. Instead, I used a mixed model approach (Schall 1991; McCulloch & Searle 2001). A generalized linear mixed model was used to analyse the probability of a response (GLMM, GenStat 2002) and a linear mixed model (REML, GenStat 2002) to analyse the response distance and the response speed. I took into account individual components of variation between and within crabs (crab identity, GLMM, REML), between set-ups (set-up identity, REML) and between dummy presentations (trial identity, REML), by treating them as random factors. Random factors in mixed models are equivalent to the block structure in the analysis of variance. The GLMM model used the logit as a link function where $\text{Logit}(p) = \log(p/(1-p))$, with p = the probability of response. In all cases, the models were selected by sequentially fitting parameters of interest. A final model was then constructed including only those terms that reached significance at the 5% level. The statistical significance of the individual model parameters were tested with the Wald statistic (McCulloch & Searle 2001). The Wald statistic is a large sample approximation of the F test used in the analysis of variance. Interactions between (potential) model terms were tested for significance, if there was a reason to believe that they might be relevant. All REML models were checked graphically for outliers and for a normal error distribution.

RESULTS

Predator Avoidance Behaviour

To the human observer, the crabs' responses to the dummies were indistinguishable from their responses to real aerial predators. At first they froze, that is they stopped feeding and remained still. They then initiated a sudden, fast home run towards their burrow, where they usually stopped at or in the burrow entrance. During the third and last stage, the crabs retracted their eye stalks and disappeared underground, where they remained for a few minutes before reappearing. (Nalbach 1987, 1990; Land & Layne 1995). The following analysis describes only the second stage of the escape behaviour, the home run.

Figure 2 shows four examples of crab responses to an approaching dummy, of which the scenes in Fig. 2a, b are typical. In Fig. 2a the crab sat still while the dummy approached, until it suddenly rushed back to its burrow, in a single fast and uninterrupted run. The crab in Fig. 2b initially kept moving away from its burrow. It then stopped and as the dummy continued to approach, it rushed home. Figure 2c, d shows slightly more unusual responses. The crab in Fig. 2c executed a fast home run after it had allowed the dummy to approach to within 40 cm. To reach the safety of its burrow, the crab had to run directly towards the approaching dummy, which at the time of response was almost exactly above the crab's burrow entrance. Figure 2d shows an example where the crab responded in a more graded fashion: it was only the

third and fastest of the three distinct responses that brought the crab to the entrance of its burrow.

Both the regularities and the variability in the responses can be appreciated from Fig. 3, which shows the full set of results that I used in the analysis. Clearly, the bird dummies, which were just small black styrofoam balls, were very effective in eliciting escape responses in these crabs. Of the total of 527 trials, the crabs responded in 461 cases (87%; Fig. 3a, b) and ignored the dummy in only 66 trials (13%; Fig. 3c, d). In 95% of the 461 trials where the crabs did initiate a response they retreated to within 2 cm of their burrow, where they probably had tactile contact with the entrance. If the crabs responded to the approaching dummy, they did so before the dummy reached its closest point to them, as can be seen by the absence of grey dots in Fig. 3c, d. In only two cases did crabs respond later and were therefore considered not to have responded at all, leaving 459 responses out of 527 trials for the following analyses.

The Probability of Response

The trials where the crabs did not respond to the dummy were not a random subset of all trials, but were clearly defined by the geometrical constellation between the dummy, the burrow and the crab. A generalized linear mixed model (GLMM, GenStat) was used to isolate the parameters that influenced whether the crabs responded. However, the high overall response probability (87%)

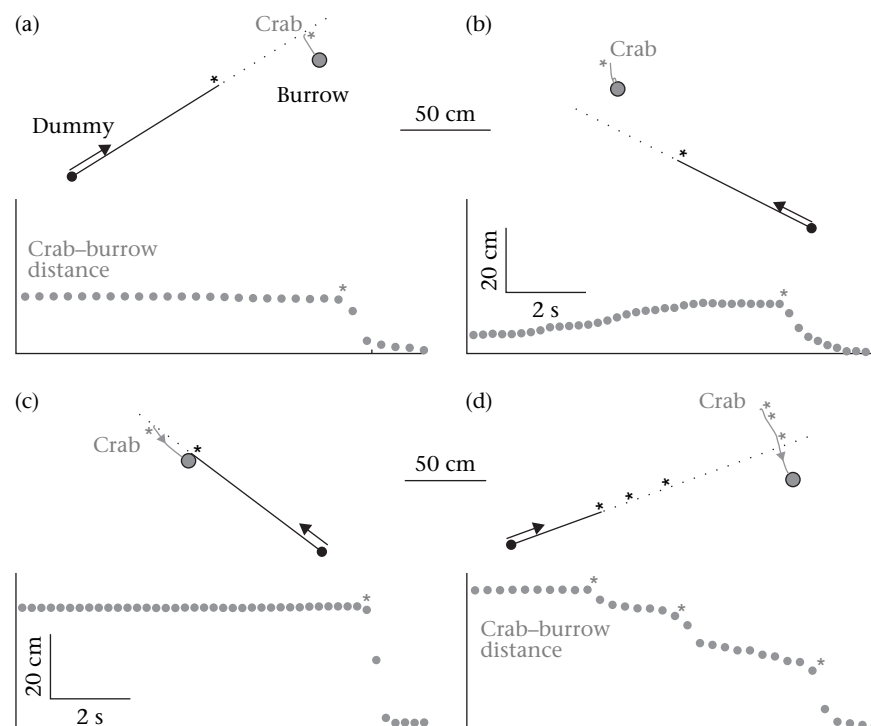


Figure 2. Four examples of crab responses to a bird dummy. The top part of each panel depicts a bird's-eye view of the mudflat, showing the dummy track in relation to the crab and its burrow. The position of the crab and the dummy at the start of the crab's response is marked by an asterisk next to the crab's path (light grey line) and next to the dummy's track (black straight line), respectively. The graphs below each panel show the crab-burrow distance over time. The onset of the response is again marked by an asterisk. Consecutive crab-burrow distances are shown at intervals of 240 ms.

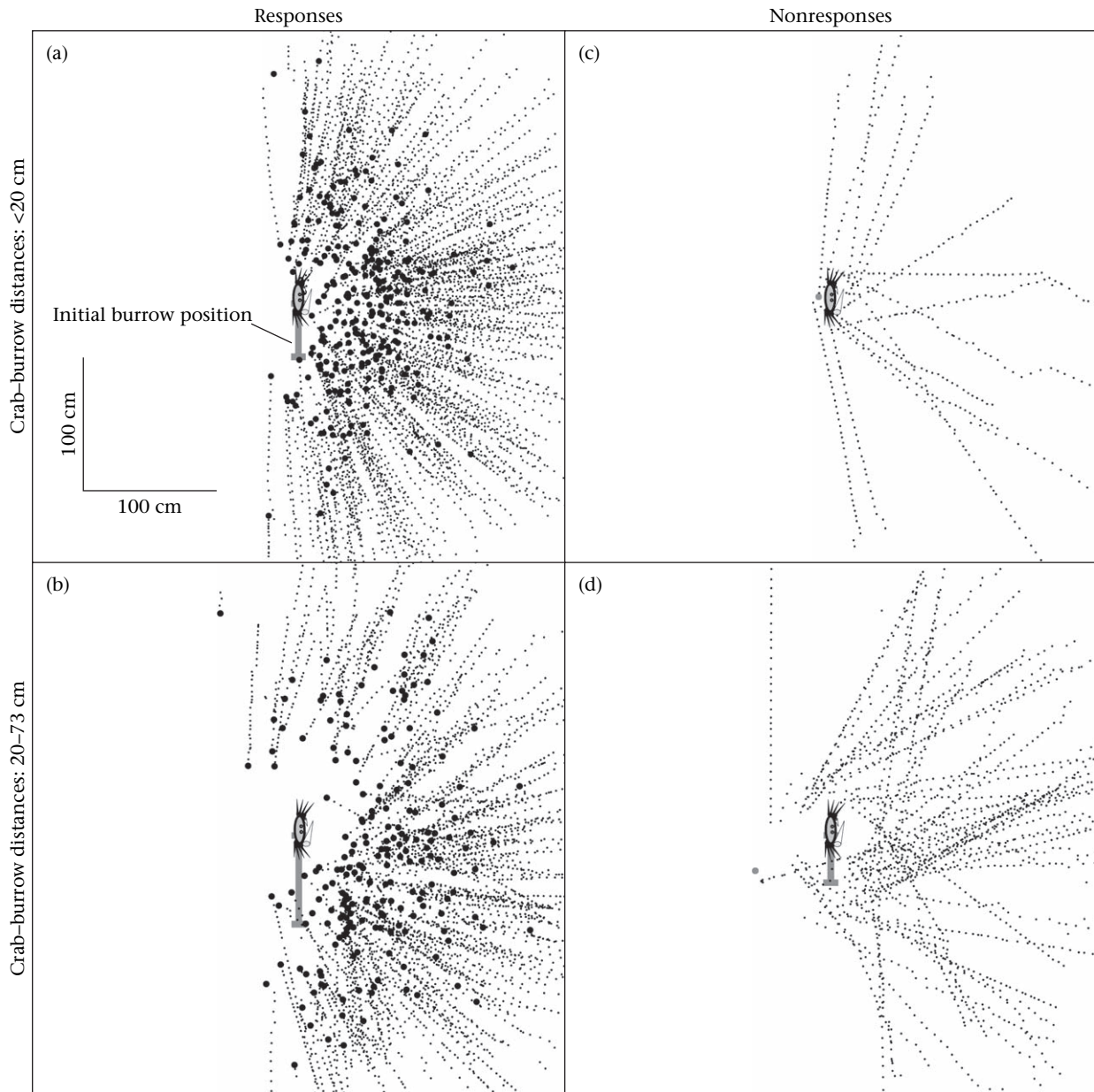


Figure 3. Summary of the data set used in the analysis. The panels show dummy paths in a coordinate system defined by the crab's home vector (positions are shown every 240 ms). (a) and (b) All trials in which the crabs responded to the dummy. (c) and (d) All trials in which the crabs did not respond to the dummy or where they responded late, after the dummy had reached its closest point to the crab (a and c). Crab–burrow distance = 0–20 cm; (b and d) 20–73 cm. Vertical grey lines below the crab's position show the range of burrow positions relative to the crab at the start of the trial for all trials accumulated in the respective panel. The position of the dummy at the time a crab responded is marked by an enlarged dot. Large grey dots in (c) and (d) indicate that the crab responded after the dummy had reached its closest approach. To increase the clarity of the figures, all tracks are shown to move from right to left by flipping tracks across the crab's home vector where necessary.

coupled with the strong predictive power of the approach direction (crab–track distance, Fig. 4a inset) caused the model to become unstable when too many other terms were included. I therefore applied a much more stringent term selection procedure. With one exception only, those terms were included that achieved significance when fitted in isolation. This restricted the statistical model to two terms, the crab–track distance and the dummy height. I made an exception for the term crab–burrow distance,

because crab–burrow distance is positively correlated with crab–track distance, but has the opposite effect on the response probability. Its effects were therefore masked when fitted in isolation from crab–track distance.

Table 1 and Fig. 4 summarize the results of the statistical analysis. The main determinant of the response probability was the dummy's approach direction relative to the crab (crab–track distance), which I measured as the horizontal distance on the ground between the crab and

the dummy track (Fig. 4a). The crabs were more likely to respond if the dummy approached them more directly. In fact, the probability of response was essentially 100% when the dummy approached the crab directly but dropped below 50% for less direct approaches.

The crabs were more likely to ignore an approaching dummy, if they themselves were closer to the burrow (Fig. 4b). The model fit (solid line) reached almost 100% at larger crab–burrow distances (40–60 cm). The model fit does not follow the raw data as well as expected because the crab–track distance and the crab–burrow distance are

positively correlated, but have opposite effects (Fig. 4b, inset). The correlation results from the fact that most burrows were relatively close to the dummy track (median = 14 cm). Large crab–track distances were thus more likely to occur when the crabs moved far from their burrow.

In addition, the crabs were slightly more likely to respond to the dummies that moved higher (24 cm) above ground than to those that moved along lower tracks (Fig. 4c). Changing the dummy's height had two effects: first, it determined how directly the dummy could approach the crab, an effect already seen in the variable crab–track distance (Fig. 4a). Based on this effect, one might predict that an increase in height should lead to a decrease in response probability, which was clearly not the case. Second, dummy height affected how high an approaching dummy appeared in the crab's visual field. The observation that dummy height increased the response probability therefore suggests that the apparent elevation was one of the visual cues that determined whether crabs responded (Hemmi 2005).

I found no convincing evidence that the crabs' sex (GLMM: $\text{Wald}_1 = 0.05$, $N = 527$, $P = 0.826$) or size ($\text{Wald}_1 = 2.53$, $N = 527$, $P = 0.112$) influenced the escape probability, regardless of whether these variables were added to the final probability model, or whether they were tested individually.

Distance or Direction of Approach?

Response probability was thus most strongly influenced by the distance from the crab to the dummy track. Crab–track distance, however, determined not only how directly the dummy approached, but also how closely it could approach. For instance, at large crab–track distances, the dummy never came close to the crab (large crab–dummy distance), but its path also never pointed directly at it. If crab–dummy distance were the main factor causing the crabs to respond, one would expect that for a given crab–dummy distance the probability of response should be independent of the track's distance. If, on the other hand, the crabs were sensitive to the dummy's movement

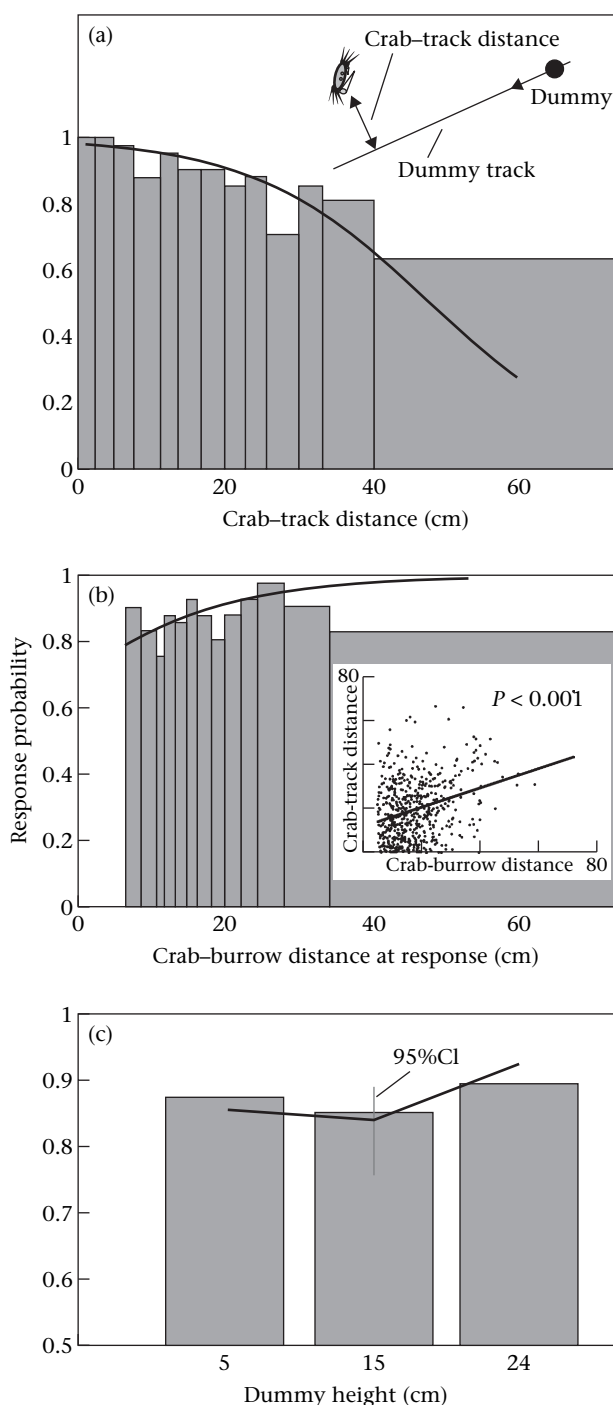


Figure 4. The effects of the three significant terms that influenced the crab's probability of response. (a) Crab–track distance: the ground distance between the crab and the dummy track (inset). It measures how closely and how directly the dummy approached the crab. The histogram shows the crab's probability of response as a function of crab–track distances. The width of each distance bin has been adjusted to contain an approximately equal number of trials ($N_{\text{bin}} = 42$ or 43). Wider bars indicate a sparser sampling along the X axis. This has been done only to show how the data are distributed. The black solid line is the probability of response as predicted by the statistical model. (b) Crab–burrow distance. Conventions for the histogram as before. The solid line indicates the predicted values based on the statistical model. The scatter plot inset shows how crab–track distance depends on crab–burrow distance. A linear regression line has been fitted to the scatter plot. (c) Dummy height. The black solid line shows the probability of response as predicted by the statistical model. The vertical grey line marks the 95% confidence interval around the fitted value for dummies that moved 15 cm above ground.

Table 1. Probability of response: results of the generalized linear mixed model analysis*

Fixed model terms†	df	Wald	P
Crab-track distance	1	37.99	<0.001
Crab-burrow distance	1	17.76	<0.001
Dummy height	2	22.43	<0.001

*(GLMM; $N = 527$); random model: crab identity.

†Variables were measured at the start of each trial.

direction, one would expect the opposite result: for a given crab-dummy distance the probability of response should depend on the crab-track distance. Figure 5a shows that at large crab-dummy distances (>100 cm) dummies that approached crabs more directly (smaller crab-track distance) were less likely to induce a response than dummies

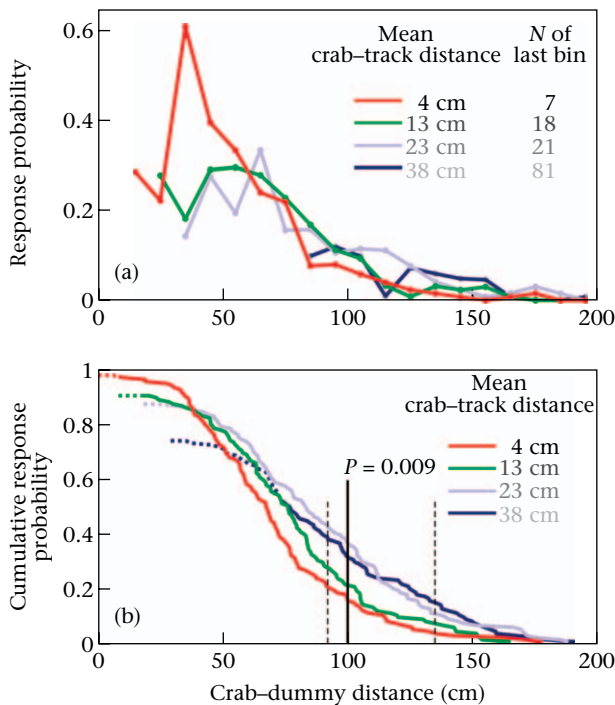


Figure 5. The effects of crab-dummy distance on the response probability for four ranges of crab-track distance. The bin width for the crab-track distances was chosen such that each bin contained equal numbers of trials ($N_{\text{bin}} = 134$ or 135), resulting in the following bins: 0–8.8, 8.81–18.9, 18.91–30, 30.1–76 cm with a mean crab-track distance per bin of 4, 13, 23 and 38 cm, respectively. (a) Positional response probability. The probability was calculated for fixed crab-dummy distance bins 10 cm wide. As most crabs would already have responded earlier, the estimates for the closest crab-dummy distance are based on a relatively small number of runs (N of last bin). (b) For the cumulative response probability, the portion of each of the four curves that falls below the curve's upper crab-track distance limit (8.8, 18.9, 30, and 76 cm) is not strictly comparable to the other curves and is therefore shown as a dotted line. This is because crabs obviously cannot respond to a dummy at a distance of, for instance, 40 cm, if the dummy cannot approach that closely because of a large crab-track distance. The vertical dashed lines indicate the range of crab-dummy distances over which the response probabilities for the four curve differ significantly at the 5% level.

that approached less directly (larger crab-track distance). This can be seen more clearly in Fig. 5b. The probability that a crab responded before the dummy approached to within 100 cm is significantly smaller for smaller crab track-distances (GLMM: $\text{Wald}_1 = 6.77$, $N = 527$, $P = 0.009$). The response cut-off at 100 cm is somewhat arbitrary. However, any cut-off between 92 and 135 cm (Fig. 5b) leads to the same conclusion. As the dummy came closer, this effect disappeared or even reversed (Fig. 5a) such that for small crab-dummy distances, dummies that moved directly towards a crab appeared to be more likely to elicit a response. The direction of motion relative to the crab thus clearly mattered. However, Fig. 5a also shows that the distance between the crab and the dummy itself was important. The probability of response increased strongly as the dummy approached the crab for all crab-track distances. This effect appears to be the main reason why the overall probability of response (Table 1) was higher for dummies that approached the crabs more directly (Fig. 5b, end-points of the four curves, Table 1). Dummies that did not approach the crabs directly were restricted as to how close they could approach.

The Response Timing

The crab-track distance thus influenced both the probability and the timing of the response (Fig. 5). Overall, the crabs were more likely to respond to dummies that approached them more directly, but they paradoxically responded later to these dummies. In the following analysis I investigate in more detail which parameters determined the response distance, that is the three-dimensional distance between the crab and the dummy at the time the first response was initiated. The median response distance was 79.4 cm and 75% of the responses occurred when the dummies were between 47.9 cm and 129.5 cm away (Fig. 3). The results of the linear mixed model analysis (REML, GenStat) are summarized in Table 2.

Distance and Direction of Approach

A comparison of the raw data in Fig. 3a, b suggests that the main parameter affecting the crab-dummy distance at the time of the response was the crab's distance from its own burrow (Table 2). Figure 6a shows a scatter plot of the

Table 2. Response distance: results of the linear mixed model analysis*

Fixed model terms†	df	Wald	P
Crab-burrow distance	1	56.95	<0.001
Approach direction	2	6.77	0.034
Dummy size	2	35.34	<0.001
Dummy height	2	27.63	<0.001
Dummy height*Crab-track distance	2	19.92	<0.001
Mean dummy speed	1	3.96	0.046

*(REML; $N = 459$); random model: set-up identity + crab identity + trial identity.

†Variables were measured at the time of response.

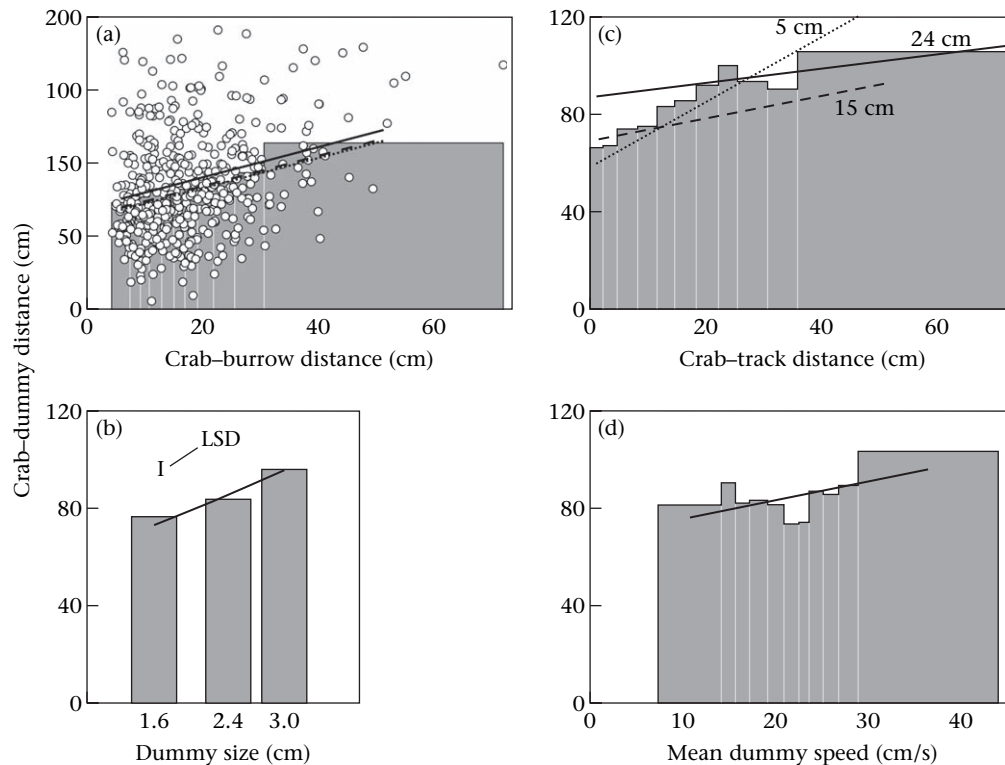


Figure 6. The variables affecting the crab's response timing. The black lines in all four panels are the model fits to the data, at mean values for all the other parameters in the model. Histogram conventions as in Fig. 4. (a) Crab–burrow distance. Model predictions are shown for the situation where the dummy approached the crab from the opposite side of the burrow (solid line) from the side (dashed line) or from the crab's side of the burrow (dotted line). (b) Dummy size. The small vertical line is the least significant difference (LSD) between any two sizes. (c) Crab–track distance. The three lines show the model fit for the relation between crab–track distance and response distance for a dummy height of 24 cm (solid line), a dummy height of 15 cm (dashed line) and a dummy height of 5 cm (dotted line). (d) Dummy speed.

crab–burrow distances against the response distances. The mean response distance increased with crab–burrow distance (histogram in Fig. 6a). On average, for every centimetre the crab moved away from its refuge, the response distance increased by just over 1 cm. Note that, in contrast to the prediction of Kramer & Bonenfant (1997), the slope of the relation between the crab–burrow distance and the response distance was unaffected by the approach direction of the dummy relative to the crab's home vector (its home direction; REML: $Wald_2 = 1.65$, $N = 459$, $P = 0.438$). The crabs did, however, respond slightly earlier to dummies that approached from across the burrow (within 60° of the home vector, solid line, Fig. 6a) compared to dummies that approached from the crab's side of the burrow (more than 120° of the home vector, dotted line) or from 60 – 120° relative to the crab's home vector (dashed line). This effect, however, was very small (Table 2) and statistically not very robust. It became nonsignificant when the angular binning of the dummy's approach direction was changed from 60° bins to either 90° or 30° bins.

Dummy Size, Track Distance and Dummy Height

Not surprisingly, fiddler crabs responded earlier to larger dummies (Table 2). An increase in the size of the dummy

from 1.6 to 3 cm led to a 21-cm increase in the response distance (Fig. 6b, black line), which, however, is clearly smaller than the 51-cm increase one would expect if the crabs responded to the apparent size of the dummy, i.e. its angular size at the retina.

We have already seen that the crab–track distance affected the distance to the dummy at which the crabs initiated their response (Fig. 5). This effect depended on the height of the dummy (Table 2). The effect of crab–track distance was stronger (steeper slope) for the lower dummies. Overall, however, the crabs responded earlier to the higher dummies, especially at small crab–track distances. In addition, the histogram in Fig. 6c suggests that the effect of the crab–track distance diminished for larger crab–track distances (>25 cm). The crab track–distance was measured as a horizontal distance on the ground (Fig. 4a) to keep the variable independent of the track height (dummy height). The interaction between the dummy's height and the crab–track distance could therefore be caused by the increased three-dimensional distance between the crab and the track. This was not the case, however. Replacing the horizontal crab–track distance with the three-dimensional distance did not change the model result. None of the coefficients changed by more than 10% and the interaction between dummy height and crab–track distance remained clearly significant (REML: $Wald_2 = 14.23$, $N = 459$, $P < 0.001$). The

dummy height thus had an effect independent of, or in addition to, increasing the three-dimensional crab-track distance. The main result of this analysis, namely that the response distance decreased as the dummy moved more directly towards a crab, confirms the results presented in Fig. 5.

Dummy Speed

Unfortunately, I was not able to move the dummy at a uniform speed. On average, the dummy accelerated slightly during its approach before it slowed down again when it came closer to the crabs. The dummy's distance to the crab and the dummy's speed are thus negatively correlated for experimental reasons, making it impossible to analyse the relation between the response distance and the dummy's speed at the time of response. However, the average dummy's speed over the entire approach (crab–dummy distance of 250–50 cm) is not affected by this and was therefore used in the analysis, although I expect it to underestimate considerably the true effect of the dummy's speed. None the less, the dummy's average approach speed had a marginal effect on the response distance. The crabs responded slightly earlier if the dummy approached faster (Fig. 6d, Table 2; see also Hemmi 2005).

Repeated Presentations

The crabs did not habituate over 50 dummy presentations as shown for the probability of response (Fig. 7a) and for the response strength (Fig. 7b). Response distance tended to decrease slightly over time (REML: $\text{Wald}_5 = 9.38$, $N = 459$, $P = 0.095$; Fig. 7b). However, the fitted value for the last 10 experiments was only

11% smaller than the fitted value of the first five trials (Fig. 7b). Considering the large number of consecutive dummy presentations, the absence of significant habituation documents again how relevant the dummies were for the crabs.

Neither crab size (REML: $\text{Wald}_1 = 1.51$, $N = 459$, $P = 0.219$) nor crab sex ($\text{Wald}_1 = 0.48$, $N = 459$, $P = 0.487$) had any effect on the response distance.

Response Speed

The crabs not only adjusted the timing of their response to the situation with which they were confronted, but also varied the speed with which they ran back to their burrow. Crabs reached speeds of up to 70 cm/s (Fig. 8a, b) and accelerated regularly at 400–500 cm/s² with a maximal acceleration of just over 600 cm/s². An REML analysis, which again used set-up identity + crab identity + trial identity as its random model, found two variables that affected the speed with which crabs responded ($N = 459$). If a crab ran home in several stages (e.g. Fig. 2d), I used the running speed of the first stage in the analysis.

The overwhelming factor influencing the response speed was the crab's own distance from its burrow (REML: $\text{Wald}_1 = 39.81$, $N = 459$, $P < 0.001$; Fig. 8a). To make sure that the increase in response speed was not only due to the coarse temporal sampling, I resampled a small selection of trials every 40 ms. This slightly increased the speed estimates (Fig. 8b, black versus grey points). The difference, however, was independent of the crab–burrow distance, which remained a significant factor (REML, random model: crab identity: $\text{Wald}_1 = 16.00$, $N = 29$, $P < 0.001$). The inset in Fig. 8b shows that the crab–burrow distance changed not only velocity, but also acceleration. In addition, the crabs varied their speed according to their distance to the dummy at the time they responded ($\text{Wald}_1 = 19.68$, $P < 0.001$). The correlation coefficient (-0.067) is negative, indicating that the crabs ran home at a more leisurely pace the earlier they responded to the dummy.

DISCUSSION

Why Crabs Respond to Dummy Predators

The crabs took the simple dummies very seriously indeed, as demonstrated by their reliable and strong responses which did not habituate even over 50 presentations (Fig. 7). While it would have come as no surprise that the crabs repeatedly respond to a real predator, the dummies I used did not look anything like real birds. The main local predator, the gull-billed tern is about 33–38 cm long, with white body and wings. However, the crabs could not distinguish between the dummies and real bird predators for two main reasons. First, the visual resolution of crab eyes is limited (Land & Layne 1995; Zeil & Al-Mutairi 1996) so that crabs could not resolve any details of the (dummy) predator's shape at the time they initiated their response. In 95% of cases, the crabs responded when the dummy's apparent size was less than

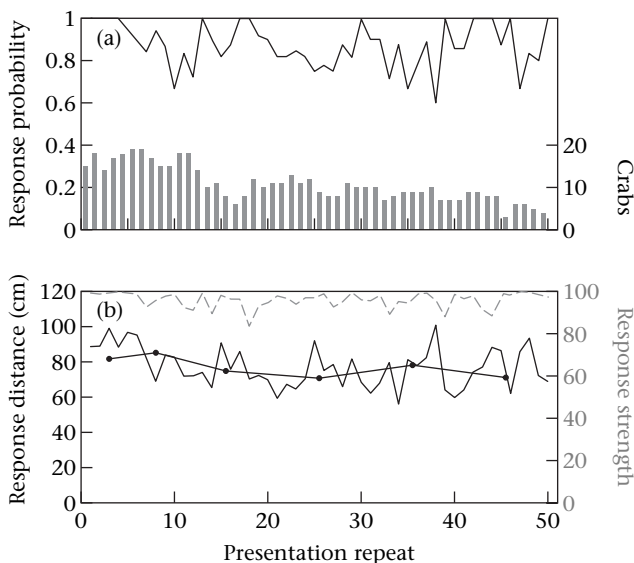


Figure 7. The effects of repeated dummy presentations. (a) The response probability (solid line). The histogram shows the number of crabs that contributed to each estimate of the response probability. (b) Response strength (grey, dashed line) and response distance (solid line). Line with dots shows the model fit.

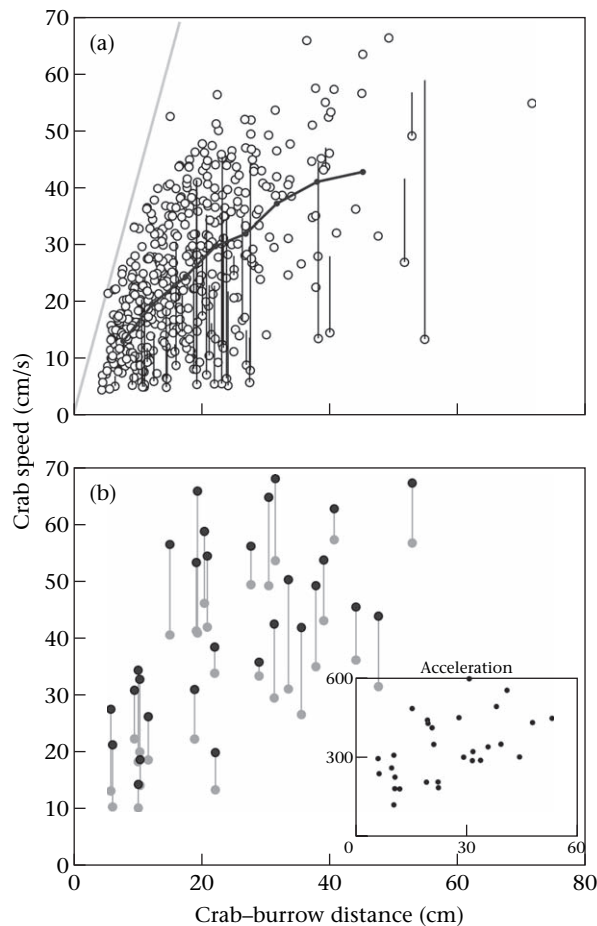


Figure 8. The crabs' escape speed as a function of their distance from the refuge. (a) The crabs' initial escape speed in relation to crab-burrow distance. If a crab's first response was not its fastest one, I added a thin vertical line that connects the crab's initial escape speed (circles) with the position of its highest speed recorded in the same experiment. The grey line indicates the highest speed that could in principle be measured (one-frame interval). (b) Trials ($N = 29$) covering a wide range of crab-burrow distances were selected to reanalyse crab speed at a higher temporal resolution. No more than five trials per crab were included. The two estimates for each trial are connected by a solid, vertical line. The original estimates (grey dots) are based on a 240-ms sampling interval and the re-estimates (black dots) are based on a sampling interval of 40 ms. Inset: the maximum acceleration the crabs achieved in the same 29 trials is shown as a function of the crab-burrow distance. To measure acceleration, the speed profiles were smoothed (mean of two consecutive readings), to reduce the effect of digitizing noise.

3.5° (median = 1.6° ; Hemmi 2005). A dummy with an apparent size of 1.6° covers less than two ommatidia in the horizontal and two or three ommatidia in the vertical direction (Land & Layne 1995; Zeil & Al-Mutairi 1996). This is clearly not enough to resolve any details of shape (as other animals are able to do in predator-prey interactions (e.g. Curio 1993; Evans et al. 1993)). Second, owing to their close-set eyes, the crabs do not have information on the dummy's distance when it is further than about 14 cm away (Collett & Harkness 1982; Zeil et al. 1986; Hemmi & Zeil 2003b). Although the terns are at least 10 times larger than my small dummy spheres, the crabs

cannot distinguish between a 3-cm object at 1-m distance and a 30-cm object at 10-m distance (e.g. Collett & Harkness 1982; Layne 1998). This inability of the crabs to judge distance, and therefore absolute size, is exemplified by a common observation in the field that the crabs are equally likely to flee from a soaring sea eagle, a small migrating butterfly or an approaching tern.

Predator Avoidance and Model Predictions

Kramer & Bonenfant's (1997) model made two specific predictions about when a prey animal should respond to a predator: (1) prey should respond earlier the further away they are from their refuge and (2) the slope of this relation should depend on the direction of the predator's approach relative to the direction between the prey and the refuge (the prey's home vector). When predators approach from the opposite side of the refuge, the response distance should be longer than when they approach from the prey's side of the refuge. The difference should be exactly twice the prey's distance from its refuge.

My results corroborate the first prediction in that the crabs responded earlier to an approaching predator the further away they were from their burrow (Fig. 6a), but do not agree with the second prediction. Although the crabs did respond slightly earlier when the dummy approached from beyond the burrow, the effect was much weaker than predicted and the adjustment did not depend on crab-burrow distance. This weak effect is probably caused by burrow defence responses. Crabs constantly monitor the area surrounding their burrow and respond by rushing home when other crabs approach the burrow too closely (Hemmi & Zeil 2003a). Burrow defence can accidentally be triggered by other crabs rushing home in response to a bird dummy. Such contaminating effects will tend to increase the response distance selectively in those cases where the dummy approaches from beyond a crab's burrow. The Kramer & Bonenfant model does clearly not apply to the antipredator responses of fiddler crabs.

The most likely reason for this is that fiddler crabs do not have the necessary information that is required by the model. If we restate the Kramer & Bonenfant model in terms of the distance between the predator and the prey's refuge, the difficulty of the prey's task becomes more evident. The model is based on the assumption that the prey needs to arrive at the refuge before the predator does and that it should do so with a constant margin of safety. This means that the position of the predator at the time the prey reaches safety should be a constant distance from the prey's refuge, irrespective of its approach direction or of the prey's initial position relative to the burrow. The distance depends only on the margin of safety. Therefore, the prey should allow the predator to approach to a specified distance to the refuge before initiating its response, independent of its approach direction. In other words, prey animals should evaluate the predator's position and motion in an allocentric frame of reference (i.e. relative to their refuge) rather than an egocentric frame of reference. An inspection of the raw data in Fig. 3a, b shows that this is clearly not the case in fiddler crabs. The black

dots, which indicate the positions of the dummy at the time of response, form an annulus around the position of the crab and not around the burrow, as predicted by the model. In contrast to burrow surveillance (Hemmi & Zeil 2003c), the crabs respond to predators in an egocentric frame of reference. In the context of burrow surveillance (Hemmi & Zeil 2003a, b), the crabs are able to judge the distance between a simulated crab intruder and their own burrow, because for objects on the ground, the elevation in the crab's visual field provides a cue to distance (Collett & Harkness 1982; Zeil et al. 1986; Collett & Udin 1988; Ooi et al. 2001; Hemmi & Zeil 2003b). For aerial predators, however, such distance cues are not available.

The fact that fiddler crabs do not follow the predictions of the Kramer & Bonenfant model also shows that the crabs have not found a rule of thumb to offset the lack of accurate information (Bouskila & Blumstein 1992; Welton et al. 2003). Theoretically, crabs could make assumptions about the size of their predators or about the height at which they fly, both of which would provide the crabs with a measure of absolute distance to the predator. However, such assumptions would be disastrous if the crabs face multiple predators of different sizes, predators that approach at different heights, or predators that have adopted different hunting techniques (Zwarts 1985; Iribarne & Martinez 1999).

My results show that the validity of the Kramer & Bonenfant model does not apply to animals that have restricted capabilities to make long-range distance judgements. I would predict that the model is also likely to fail in situations where prey animals have to make fast decisions, which will limit the quality of information they have available.

Who Gets Eaten?

If we scale up the distances at which the crabs responded to the small bird dummies to real birds, the crabs would on average respond when the terns were still 5–10 m away. Terns fly horizontally across the mudflat until approximately over a crab they see and then tend to swoop almost vertically downwards to pick it up (Land 1999). When my dummy passed more or less directly over the crabs (very small crab-track distance), all of the crabs had responded by the time the dummy had reached its closest point, which for a bird flying parallel to the ground would still be about 2 m away. In the example of a successful attack by a tern shown in Land (1999), it took the tern another 2.5 s to stall and land on the substrate to pick up the crab. Based on a speed of 60 cm/s (Fig. 8b) and an acceleration of 300 cm/s² (Fig. 8b, inset), the crabs can cover 54 cm in just the first second of their response. The consistency and early timing with which the crabs responded in the present study therefore seems to make it very unlikely that terns ever catch a crab. This suggests that the birds catch only those crabs that are (temporarily) without a burrow and wander over the mudflat (Iribarne & Martinez 1999). Indeed, the risk of predation appears to be so much higher for wanderers than for resident crabs, that some fiddler crab species change their mating system from

a female-searching to a male-searching system when the risk of predation increases (Koga et al. 1998).

In conclusion, while fiddler crabs avoid predators very reliably, their behaviour does not follow predictions from models that assume prey animals to have 'perfect' or 'complete' information about a predator's distance and direction of movement. The relation between the organization of predator avoidance behaviour in fiddler crabs and the information available to them is the subject of a separate analysis (Hemmi 2005).

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