

Burrow surveillance in fiddler crabs

I. Description of behaviour

Jan M. Hemmi* and J. Zeil

Visual Sciences, Research School of Biological Sciences, Australian National University, GPO Box 475, Canberra, ACT 2600, Australia

*Author for correspondence (e-mail: jan.hemmi@anu.edu.au)

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Summary

When defending resources, animals need to reliably detect and identify potential competitors. Animals that live at high population densities would be expected to be efficient in this aspect of resource defence since the time lost in false alarms could be substantial and the failure of identifying a competitor could be very costly. How does an animal decide whether another animal is or is not a threat to a resource or a territory?

Fiddler crabs [*Uca vomeris* (McNeill)] operate from burrows that they guard and defend vigorously against other crabs. The crabs live in dense populations, with many animals inhabiting one square metre of mudflat. We describe here the behavioural responses of foraging crabs to repeated presentations of small crab-like dummies approaching their burrows. We explore the relationship between the probability and the timing of burrow defence responses, the crab's behavioural state, and the visual appearance and direction of approach of the dummies. We

find that the probability of response of resident crabs is independent of the relative position of crab and dummy but is strongly affected by the dummy's position and movement direction relative to the crab's burrow. The critical stimuli are the dummy's distance from the crab's burrow and whether the dummy is moving towards the burrow or not. The response distance (dummy–burrow distance) increases with the crab's own distance from the burrow, indicating that the crabs modify their assessment of threat depending on their own distance away from the burrow. Differences in dummy size and brightness do not affect the probability or the timing of the response.

We discuss these results in the context of fiddler crab social life and, in a companion paper, identify the visual and non-visual cues involved in burrow defence.

Key words: resource defence, burrow defence, visual behaviour, competitor, territory, fiddler crab, *Uca vomeris*.

Introduction

Resource defence costs time and energy and can lead to injury or even death (Huntingford and Turner, 1987). When animals decide how much of their time and energy they should allocate to guarding and defending a resource, they must make a number of assessments including the value of the resource, the probability of it being exploited, the cost of guarding it and the costs of actively defending it against a competitor. For instance, animals that are able to assess the relative strength of a competitor should have a selective advantage, and the evolutionary consequences of strategies dealing with competitors have been extensively studied (Maynard Smith and Parker, 1976; Parker, 1974). Equally, there should be quite a significant selection pressure on animals to efficiently discriminate between threatening and non-threatening events. Especially in dense populations, animals must balance the need to respond appropriately to real threats with the time and energy costs of false alarms. But what constitutes a competitor? How does an animal decide whether another animal is a threat to the resource it guards? These are trivial questions when confrontations over resources are direct, but

they are more difficult to answer when the decisions have to be made from a distance, as is often necessary when animals defend large territories where they cannot be everywhere at once or when they guard a central resource such as a nest. Defending a resource from a distance requires information on its location, the spatial constellation between the resource and a potential competitor and an assessment of the probability that the competitor is indeed a threat to the resource.

Fiddler crab societies are an interesting model system in which such questions can be addressed experimentally within the animals' natural social context. The crabs live in high-density colonies and occupy small, overlapping home ranges that are centred around the important resource of their burrow. In this and a companion paper (Hemmi and Zeil, 2003a), we describe the 'knowledge base' of burrow surveillance and defence in fiddler crabs (*Uca vomeris*). We ask what aspects of a threatening situation the crabs take into account when they decide whether to respond to an intruder and what sensory cues they use to make this assessment. Our main focus is on the use of vision in these crabs and how they exploit the

particular geometry of the flat world they inhabit to organise behaviour.

Fiddler crabs are small, semi-terrestrial crabs that are active during low tide on the inter-tidal mudflats and sandflats of tropical and subtropical estuaries. Most species are diurnal and work to a tight schedule of a few hours a day with most of their time spent feeding, while the remaining time is divided between burrow maintenance, social interactions, grooming and predator avoidance (e.g. Caravello and Cameron, 1987; Crane, 1975; Wolfrath, 1993). Each crab operates from its own burrow, which it defends vigorously against other crabs. Among males, burrow ownership is contested in partially ritualised, and often drawn-out, fights (e.g. Crane, 1975; Hyatt and Salmon, 1978; Jennions and Backwell, 1996; Jones, 1980; Pratt et al., 2003).

The burrow is a very important resource for the crabs (for reviews, see Crane, 1975; Montaque, 1980; Zeil and Layne, 2002). It offers protection from aquatic predators during high tide and from aerial and terrestrial predators during low tide, when the crabs are active on the surface. It provides a safe refuge for moulting animals and for females while incubating their eggs. The burrow protects the crabs from desiccation during their activity on the surface by offering them access to water, which is needed for respiration and feeding. How crucial burrows are as the only protection against predators is illustrated by the behaviour of crabs that have lost their burrow and are wandering through the colony in search of a new home. These wanderers are vulnerable to predation and protect themselves by approaching burrow owners. Although they are reliably chased away by resident crabs, wanderers remain oriented towards the foreign burrow and, in case of danger, are able to use it as a temporary refuge by following the resident crab down into its burrow (Crane, 1975; Ens et al., 1993; Zeil and Layne, 2002).

In addition, the location of a fiddler crab burrow plays a significant role in determining the owner's social environment and its access to food. The burrow serves as a central hub from where the crabs venture out on their feeding excursions, which, in the case of our study species (*U. vomeris*), take them rarely more than 1 m away from the burrow. The crabs repeatedly return to their burrow to defend it against other crabs, to take refuge from predators or to replenish their water supply (Zeil, 1998).

The degree of burrow fidelity appears to vary considerably, both between and within species, depending on predation levels, social system, food availability and possibly also on the substratum properties affecting the stability of burrows (deRivera and Vehrencamp, 2001; Ens et al., 1993; Genoni, 1991; Hyatt and Salmon, 1978; Koga et al., 1998; Montaque, 1980; Salmon, 1984, 1987; Wolfrath, 1993). In *Uca vocans*, a species closely related to *U. vomeris*, burrow fidelity appears to be very weak (Altevogt, 1955), and in some populations of *U. vomeris* only females remain with their burrow for extended periods of time (Salmon, 1984). By contrast, in our study population, both males and females appear strongly attached to their burrows, at least within one activity period. Burrow

fidelity is possibly enhanced by the fact that the burrows are deep and that unoccupied burrows are destroyed by the incoming tide, due to the soft ground. Such a high-density, shelter-based, central foraging system must exert immense pressure on burrow owners to not only guard their resource against conspecifics but also to be efficient in avoiding over-responding to the presence of burrow-owning, non-threatening neighbours. A crab that would not be able to distinguish between resident neighbours and potential burrow snatchers would spend a large part of its time guarding its burrow.

Here, we describe the circumstances that trigger burrow defence in foraging fiddler crabs. We moved small, simple, dummy crabs (see also von Hagen, 1962; Hyatt and Salmon, 1978; Land and Layne, 1995a; Salmon and Stout, 1962) across the substrate towards the burrows of resident crabs and determined if and when the crabs responded to the approaching dummy by rushing back to the burrow entrance. The sensory cues that fiddler crabs use to make their assessment are explored in a companion paper (Hemmi and Zeil, 2003a). A brief report on some of our results has been published elsewhere (Hemmi and Zeil, 2003b).

Materials and methods

Apparatus

All experiments were conducted with *Uca vomeris* (McNeill) (Ocypodidae: Brachyura: Decapoda) in the mudflats of Bowling Green Bay, south of Townsville, Queensland, Australia (approximately 19°25.6' latitude, 147°6.9' longitude). A camcorder (Sony TRV110 or Sony TR705E) was mounted on a tripod about 1.6 m above a small patch of mudflat, with its zoom set to maximum wide-angle to give a recording area of approximately 0.8 m × 1.1 m. The camera was arranged such that the burrow of an adult male (focal animal) was at the centre of the recording area, which also viewed several other crabs (peripheral animals), the responses of which were also analysed. There was no statistical difference in the responses of focal *versus* peripheral crabs for any of the statistical analyses we performed (all $P > 0.1$).

The crab dummies consisted of small plastic cylinders, mounted on a Perspex sled, which was slightly larger than the dummies themselves. The dummies were black or white and were one of seven different sizes (Fig. 1A). Most experiments (484 of the total 633 experiments analysed) were performed with a dummy size of 2.25 cm × 1.2 cm. The dummy was attached to a monofilament line, which was fed around two tent pegs that were ~3–4 m apart and allowed the dummy to be moved along a straight line, which we will call the 'dummy track', by manually pulling on the monofilament line (Fig. 1B). With this arrangement, the observer could control the dummy while sitting about 5–6 m away. The dummy was moved with an approximately constant velocity. Due to the nature of the substrate and the fact that dummies were moved by hand, some variations in speed within each run could not be avoided. The mean velocity ranged from 3 cm s⁻¹ to 14 cm s⁻¹ between experiments (mean ± s.d. = 7.8 ± 1.9 cm s⁻¹).

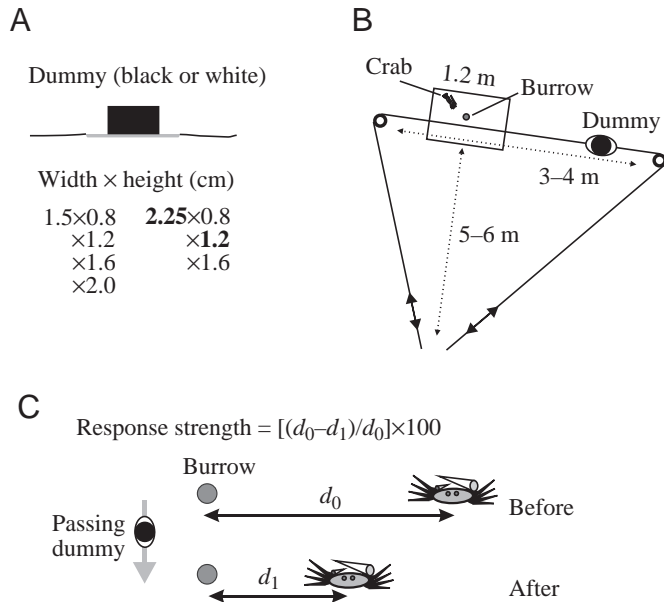


Fig. 1. Dummies, experimental set-up and measurement of response strength. (A) The dummy's size and appearance from the side. Bold dimensions indicate the most frequently used dummy. (B) The dummy was moved along a straight line (dummy track) between two tent pegs. The observer controlled the dummy from a distance by means of a fishing line wrapped around the tent pegs and attached to both sides of the dummy. The small rectangle represents the recording area of the video camera, centred on the focal crab's burrow. (C) The crab's response strength was measured as the distance the crab moved towards its burrow during a dummy presentation ($d_0 - d_1$) relative to the initial distance before the response (d_0).

The dummy track was arranged such that it passed the burrow of the focal crab at a closest distance of about 10 cm ('track distance'). The distance of the dummy track from the burrows of peripheral crabs was not controlled and ranged from 5 cm to 55 cm. In a typical experiment, the dummy would approach the burrow of the focal crab from ~1–1.5 m away, move past the closest point to the burrow for a short distance and then return to its original position. In a small number of trials, the dummy did not reverse its direction but left the area on the opposite side of the burrow from where it approached. Each dummy approach was filmed for later analysis.

Video analysis

The film sequences were digitised at 240 ms frame intervals via an IEEE 1394 card in a computer running a Linux/Slackware operating system. The x and y coordinates of crabs and dummies were determined using a video analysis program written by Jan Hemmi in C and Matlab and corrected for optical and perspective distortions. The program automatically tracks all crabs in a sequence. Because crabs can leave the recording area, disappear by entering their burrows or become cryptic against the mottled mudflat background, the operator had to manually track the crabs when the program failed to do so. Based on the x and y coordinates of the crabs, the dummy

and the burrow, a response was considered to have started in a given frame if a crab moved at least 0.66 cm towards its burrow during the 240 ms time interval preceding this frame and at least 2 cm over a three-frame interval (720 ms) starting at the previous frame. Responses were not counted as such if the crab responded after the dummy had reached its closest point to the burrow for the first time (74 of the 493 cases in which crabs responded or 15%). This was necessary as most of these late responses (60) occurred after the dummy turned around at the end of the track to move back to its starting position and therefore completely changed the geometry of the particular experiment. A special analysis, however, concentrates on these late responses (Fig. 9). The position of the dummy and the crab in the last frame before a crab reached the response criterion was then taken as their position at the time of response. This response criterion is used in the probability analysis outlined below. In addition, we calculated a relative measure for the crab's response strength based on the entire path of the crab (Fig. 1C). This measure expresses as a percentage how far a crab moved towards its burrow during an experiment. The reference distance is the largest crab–burrow distance before the crab responded.

Selection of trials for the final analysis

As we worked in the natural setting, the crabs not only responded to the dummy but also to other crabs, to predatory birds or to other events beyond our control. The data set thus contains a number of responses that were unrelated to the dummy's movements. In order to keep such responses to a minimum, and to make sure that all experiments used in the analysis were as homogeneous and unbiased as possible with respect to variables of interest, we used the following criteria to include trials into the final analysis: (1) there was no bird or crab interference during the trial; (2) the dummy approached to at least 1 cm of its closest point to the burrow; (3) crabs were at least 5 cm away from their burrow at the start of the experiment; (4) the crabs were within the recording area when the dummy entered the recording area and (5) for each crab only the first 50 dummy presentations were included. A total of 633 experiments met these criteria and were subsequently analysed. Excluded experiments were still used to calculate the number of dummy presentations a crab had been exposed to prior to a particular experiment, except where the crab was underground during the entire trial and did not see the dummy.

Statistical analysis

As we took repeated measurements for each crab, the statistics used needed to take possible crab-to-crab variation into account. This was done in the framework of a Generalised Linear Mixed Model (GLMM) to analyse the probability of a response (GenStat, 2000; Schall, 1991), while response distance, the response speed and the response strength were analysed in a Linear Mixed Model (REML; GenStat, 2000). By fitting crab identity as a random term, all these analyses take repeated measures on individual crabs into account and adjust the probability calculations accordingly. As the values

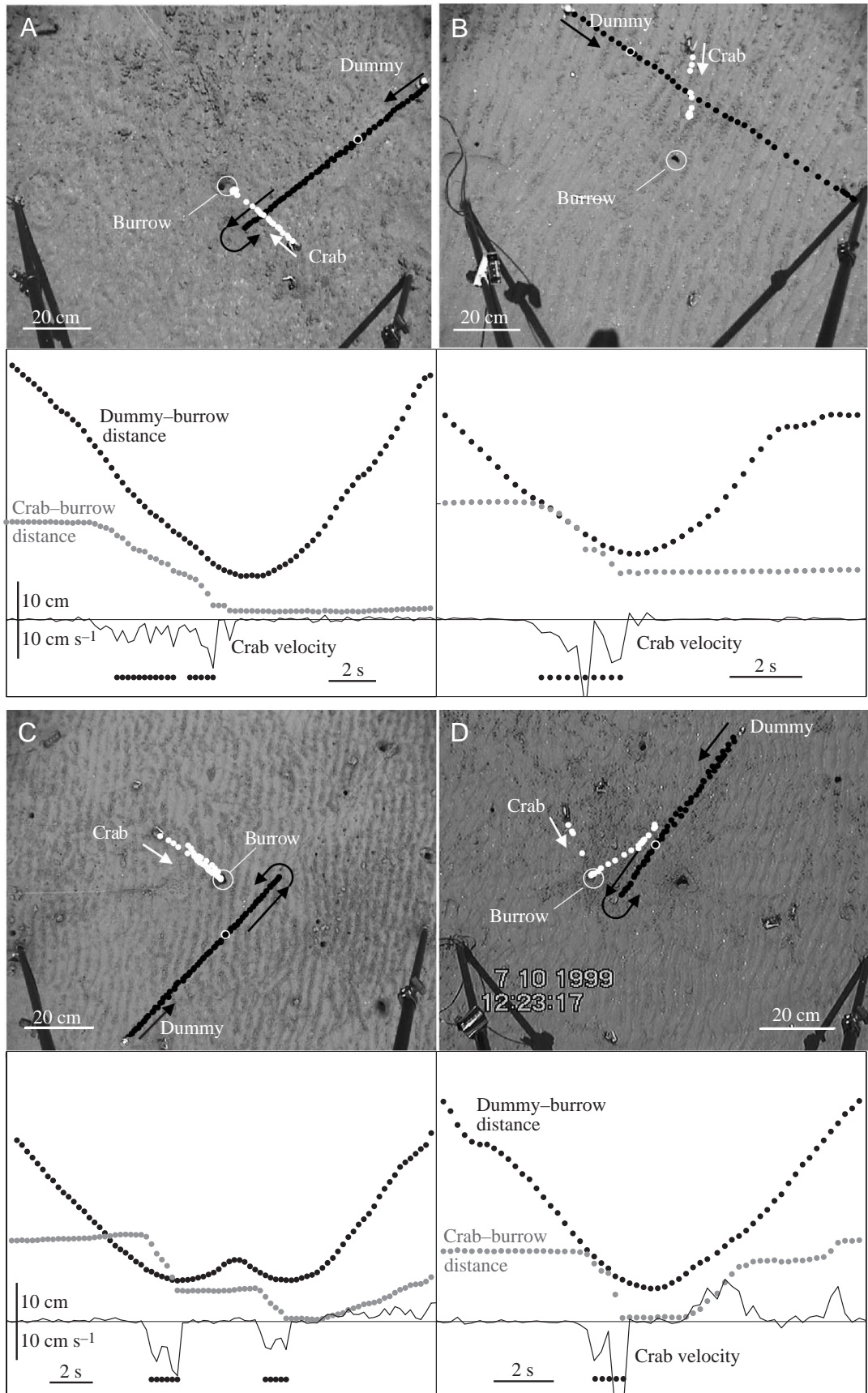


Fig. 2. Four examples of crab responses to the approaching dummy. The four images show a bird's eye view of the mudflat at the time the dummy enters the field of view. Consecutive dummy positions are marked with black dots, and crab positions with white dots ($\Delta t=240$ ms). The onset of a crab's response is marked by a small white ring around the dummy's position at that point in time. Burrows are marked by large white circles. The graphs below the four images show the distance of the dummy (black dots) and of the crab (grey dots) from the crab's burrow over time. The crab's velocity towards its own burrow (cm s^{-1}) is shown as a continuous line at the bottom, whereby negative velocity values indicate that the crab travelled towards the burrow. Time samples during which the movements of the crabs meet the criteria for a response are marked by a black dot below the velocity trace. Further explanations can be found in the text.

of the response strength are limited in range between 0% and 100%, we first applied a logit transformation. A statistical model was constructed by sequentially testing terms of interest. The final model included only those terms that reached significance at the 5% level. The significance of an individual term was tested by calculating the Wald-statistic associated with dropping the term from the full model. We then checked for some of the interactions between the final terms and also for some interactions between these terms and other previously excluded terms if we had a good reason to believe that they might be important. The final models are described in the Results section. All REML models were checked graphically for outliers and for a normal error distribution. Where fitted values were calculated for a certain variable, all other variables were set to their mean values.

Results

General description of burrow surveillance in *Uca vomeris*

Resident crabs respond to the approaching dummy in a similar fashion as they would to a real crab intruder. Fig. 2 shows four examples of burrow defence responses to approaching crab dummies. The scene in Fig. 2A shows a crab slowly retreating to its burrow, always staying closer to the burrow than the dummy (see the distance vs time plot below the image in Fig. 2A). This is the most common type of response, although the crabs are usually slightly faster. The crab in Fig. 2B first attempts to block the dummy's way and then allows it to pass on the outside, staying between the dummy and the burrow. The crab in Fig. 2C responded late, initially allowing the dummy to approach closer to the burrow than it was itself. When the crab finally does respond, it stops as soon as the dummy has reached its closest point to the burrow and starts to move away on the other side. The crab sits still until the dummy turns around at the end of its track and approaches the burrow for the second time. This time the crab moves all the way back to the burrow, where it remains until the dummy has passed the closest point for the second time, at which point the crab resumes foraging. Fig. 2D shows another late response, starting at the moment the dummy has reached about the same distance from the burrow as the crab has. At this point, the crab, a female, responds with a fast and complete return to the burrow. As soon as the dummy changes direction and returns to its starting point the female leaves her burrow to chase the dummy. During the chase she keeps both feeding claws fully extended and lifted high, a behaviour often seen during aggressive interactions between females (von Hagen, 1993).

In most cases, the crabs responded strongly to the approaching dummy. The strength exceeded 80% in 72% of the responses (Fig. 3). In fact, in more than 93% of all responses the crabs made sure they ended up closer to the burrow than the dummy. However, even though more than half of the crabs (54%) returned to within 2 cm of their burrow (solid black line in Fig. 3), in only 27 cases (6%) did the crab enter its burrow and disappear below ground. Their usual

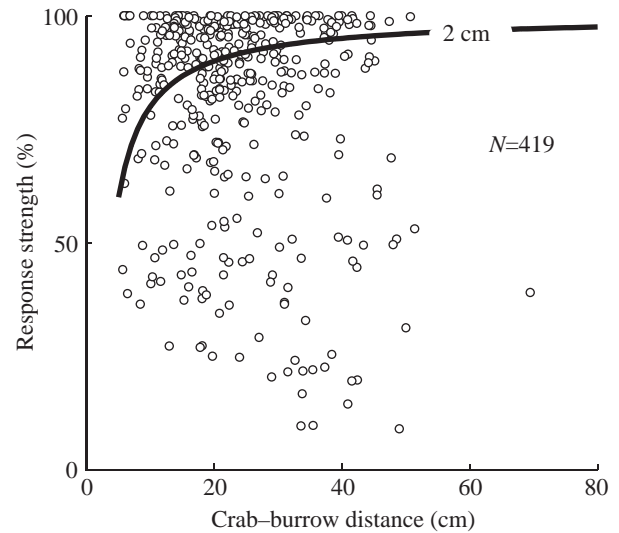


Fig. 3. How the response strength (see Fig. 1C) depends on crab-burrow distance. The solid line indicates the value of response strength needed for a crab to move from its current position to within 2 cm of the burrow. At a distance of 2 cm, the crabs are likely to have tactile contact with the burrow entrance.

behaviour was to sit at or near the burrow while the dummy was in the vicinity. While sitting in the burrow entrance, the crabs often pivot around to track the dummy as it moves past, threatening it with their claws. Occasionally, males wave their enlarged claw while retreating and even attack the dummy, hitting it with their claw, or try to block the dummy's path. These responses are very different from the crabs' responses to an approaching bird predator or a bird dummy. Confronted with a bird dummy (a 2 cm black ball moving 10–30 cm above ground), the crabs respond earlier and run towards their burrow at a higher speed and in many cases disappear underground. The responses to dummies moving on the substrate, by contrast, are usually slower and coordinated with the movement of the dummy, as if the crabs are trying to make sure they always stay closer to the burrow than the dummy. In a display of parallel processing, the crabs often continue feeding while they slowly retreat to their burrows and therefore appear to minimise the impact the response has on their feeding time. Both male and female *U. vomeris* respond with burrow defence to the approaching dummy. This is in contrast to *Uca pugnax* and *Uca pugilator*, in which males – who try to attract females into their burrows for underground mating – take dummies lacking an enlarged claw to be females (Aspey, 1971; Crane, 1975; von Hagen, 1962). *Uca vomeris*, however, mate on the surface at the entrance of the female burrow (Crane, 1975; Salmon, 1984), and females or female-like dummies are not tolerated near male burrows.

We summarize the data set to be used in the following analysis in Figs 4, 5 and define the variables 'track angle', 'track distance' and 'crab side', which are needed to describe the geometry between the crab, the dummy and the burrow in Fig. 6.

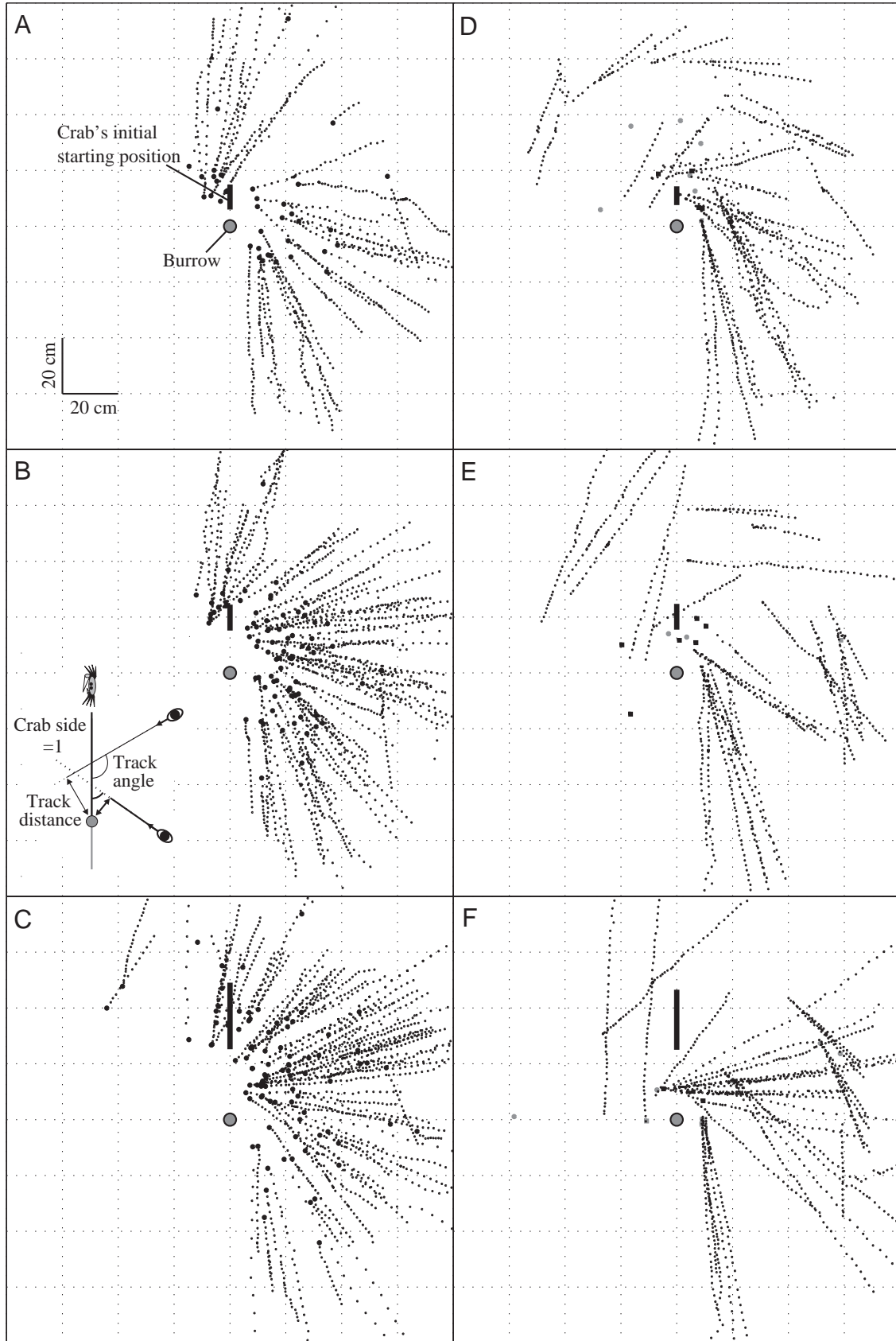


Fig. 4. Summary of the data set used in the analysis for all experiments in which the extended dummy track intersected the vertical line defined by the crab's home vector on the crab side of the burrow (crab side = 1; see inset in B). Consecutive dummy positions are shown in a coordinate system defined by the crab's home vector. The data from different experiments were moved and rotated such that the crab's home vector always points vertically down towards the burrow, which was placed at the centre of each panel (grey circle). The trajectory of the dummy is shown from the moment it became visible in the recording area until the crab responded to the dummy or until the dummy reached its closest point to the burrow. The thick, vertical, black line above the burrow shows the range of crab starting positions for all the experiments accumulated in the respective panel. (A–C) All trials in which the crabs responded to the dummy; (D–F) all trials in which the crabs did not respond to the dummy, or where they responded late, after the dummy had reached its closest approach to the burrow. The three rows of panels sort the dummy presentations according to the crab–burrow distance, with increasing distance from top to bottom (A,D: 5–15 cm; B,E: 15–25 cm; C,F: 25–55 cm). The position of the dummy at the time a crab responded has been marked by an enlarged symbol: a dot indicates that the response occurred on the dummy's first approach, a square indicates that the crab responded after the dummy changed direction at the end of its track and was moving back towards its starting position. In addition, a black symbol indicates that the crab responded while the dummy was approaching the burrow, whereas a grey symbol indicates that the dummy was moving away from the burrow when the response occurred. As the tracks are only shown up to their closest point to the burrow, some of the dots and squares do not lie directly on the printed section of a path in panels D, E and F. All tracks are shown to move from right to left to increase the clarity of the figure. To achieve this, tracks were mirrored at the vertical home vector where necessary.

The dummy paths in Figs 4, 5 are shown in a coordinate system defined by the crabs' home vectors. The data have been split in three ways: (1) Fig. 4 shows all the trials where the dummy's extended track intersects the vertical line defined by the home vector on the crab side of the burrow (crab side = 1; Fig. 4B, inset), while Fig. 5 shows all the trials where the dummy track intersects the line of the home vector beyond the burrow (crab side = 0; Fig. 5B, inset); (2) the data set within each figure is split according to the starting distance of the crabs from their burrows (panels A,D: 5–15 cm; B,E: 15–25 cm; C,F: 25–55 cm) and according to (3) whether the crabs responded (panels A–C) or not (panels D–F; see the figure legends and methods for additional details). Because the data in Figs 4 and 5 are shown in a coordinate system defined by the crabs' home vectors, a crab that moved during the dummy presentation produces a change in direction of the dummy path. Most dummy paths are straight, however, indicating that in the vast majority of our experiments the crabs did not move significantly prior to responding to the dummy.

What determines whether a crab responds?

The crabs do not respond to every dummy approach. Crabs outside the 1 m² of recording area almost never responded to the dummy. The crabs only take note of the dummy when it

Table 1. Results of the Generalised Linear Mixed Model analysis (N=633)

Term*	d.f.	Wald [†] /d.f.	P
A (Burrow) track distance	1	15.64	<0.001
B Track angle	8	4.89	<0.001
C Crab side	1	5.71	0.017
D Presentation repeat	5	5.47	<0.001
E (Crab) track distance	1	0.37	0.543
F (Crab) track distance × approach side	2	0.29	0.748
G Crab sex	1	0.12	0.734
H Crab size	1	0.01	0.930
I (Crab) burrow distance	1	2.53	0.112
J Dummy size	1	0.18	0.669
K Dummy brightness	1	1.21	0.271
L Dummy speed	1	2.75	0.097
M Dummy direction	1	0.06	0.804

*Variables are measured at the start of the experiment.

[†]The Wald statistic is a measure of statistical significance. Larger values indicate higher significance.

approaches their own burrow. This can be verified by inspecting the dummy paths in Figs 4 and 5. Panels D–F of both figures show the paths when the crabs did not respond; in these cases, clearly more tracks passed the burrow at a distance of >20 cm compared with those in which the crabs responded (panels A–C). The 'response panels' show predominantly radial paths pointing towards the burrow. As we show below, the particular geometry of a trial, i.e. the relationship between a crab, its burrow and the dummy's direction of approach, is indeed an important factor determining the probability of response.

We used a GLMM to test for the influence of a variety of factors on the crabs' probability of response when faced with the approaching dummy. Since no interactions reached significance, the final model contained four significant terms:

$$\text{Logit}(P) \approx \beta_0 + \beta_1(\text{track distance}) + \beta_2(\text{track angle}) + \beta_3(\text{crab side}) + \beta_4(\text{presentation repeat}) + \text{error}.$$

Random term: crab identity; N=633; logit=log[P/(1–P)].

Table 1 lists the statistical output for these terms, for some of the interactions and for other terms of interest that failed to achieve significance. Three of the four significant terms in the final statistical model – (burrow) track distance, track angle and crab side – describe the geometrical situation of each experiment (Fig. 6).

Track distance

As expected, the distance of the dummy track to the crab's burrow is the single most important factor determining the response probability (Table 1A). The probability decreases sharply with increasing distance, by about 80% over a range of 60 cm (Fig. 7A).

The (burrow) track distance, the closest distance between the crab's burrow and the dummy track, is a measure of how

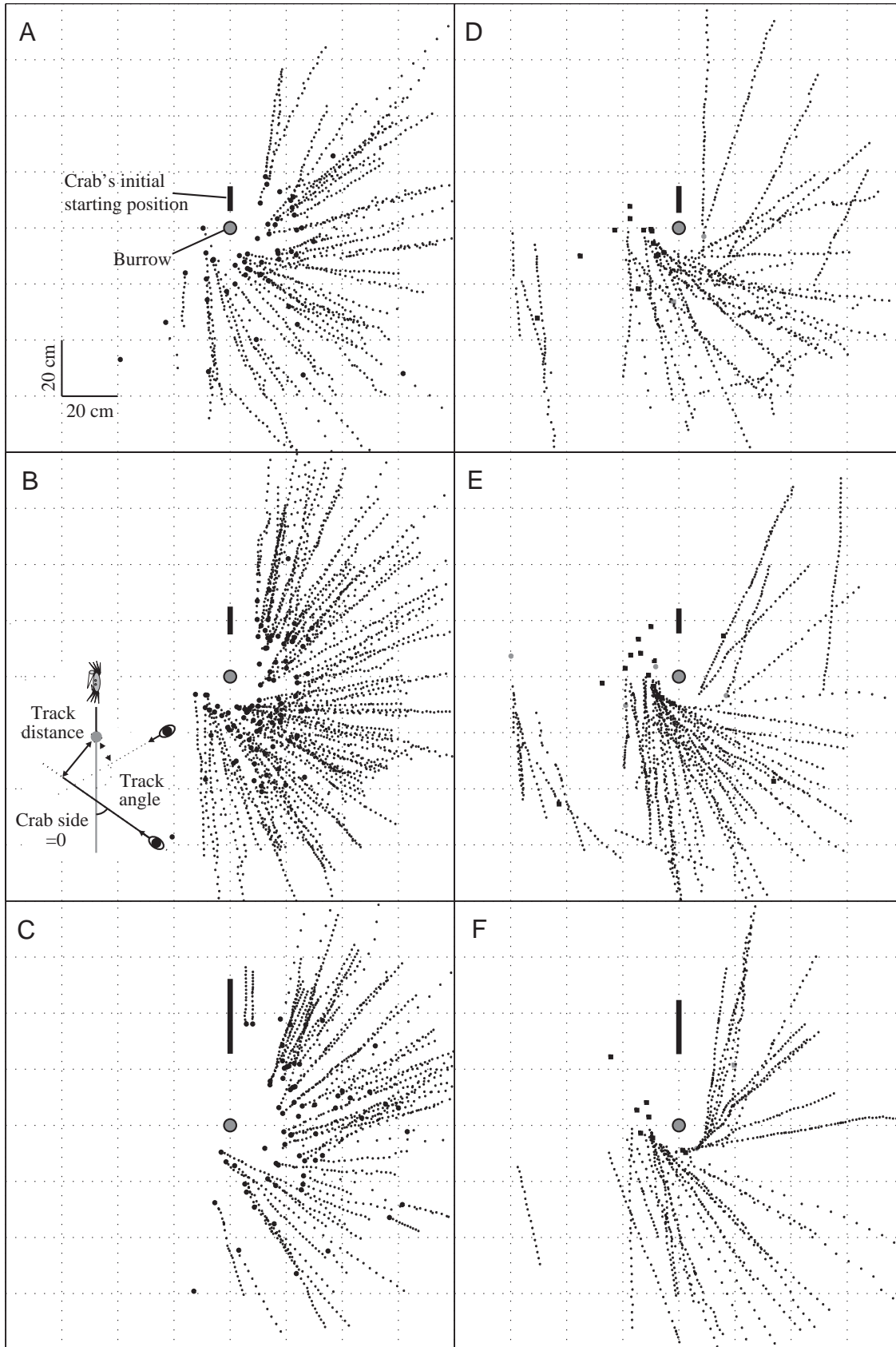


Fig. 5. Summary of the data used in the analysis for all the experiments where the extended dummy track intersected the vertical line defined by the crab's home vector on the side of the burrow opposite to the crab (crab side = 0; see inset in B). All other conventions as in Fig. 4.

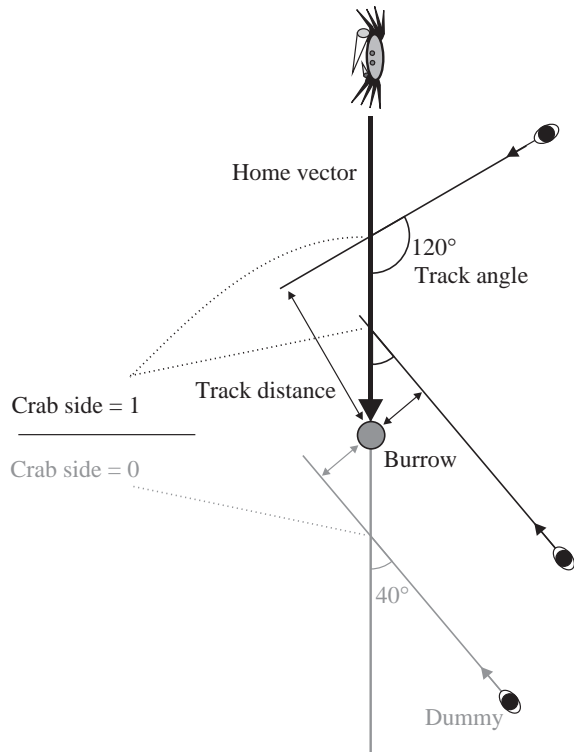


Fig. 6. Definition of track angle, track distance and crab side, the three parameters used to describe the dummy trajectory relative to the burrow and the crab's home vector. 'Crab side' measures whether the dummy track intercepts the line defined by the crab's home vector on the crab side of the burrow (crab side = 1) or on the opposite side (crab side = 0). The variable is needed because there are always two paths that have a particular combination of track angle and track distance.

directly the dummy approaches a crab's burrow, but it also measures how closely a dummy can approach the crab's burrow. The effect of track distance therefore suggests that the crabs are either sensitive to the dummy's position or motion relative to the burrow. At this point, it is not possible to test for the influence of the dummy–burrow distance directly because this distance is not defined for trials where the crabs did not respond. However, a special analysis presented below will distinguish between the influence of the dummy's direction of motion and its distance from the burrow. To make sure that the relevant variable is indeed the distance between the track and the burrow and not between the track and the crab, we removed the (burrow) track distance from the model and fitted the (crab) track distance instead. (Crab) track distance is clearly not significant (Table 1E), even when we allow for a difference in response depending on whether the dummy approaches from the crab side of the burrow or not (Table 1F). The crabs thus assess the dummy's position or its path relative to their burrow and not relative to themselves. In other words, the crabs make their decision to respond not in an egocentric frame of reference but in one that is centred on the burrow (Hemmi and Zeil, 2003b). The dummy paths in Figs 4

and 5A–C strongly support this conjecture in a qualitative way. Whenever the dummy approaches from the crab side of the burrow (i.e. from the top in the figures), the crabs usually allow the dummy to come very close but respond when it threatens to overtake them. When the dummy approaches from the opposite side of the burrow, however, the distance between the crab and the dummy at the time of response is much larger. Note that the dummy's distance to the burrow is similar in both cases. Below, we will provide further evidence that the crabs initiate their response independent of their own distance from the dummy (Fig. 11B).

Track angle and crab side

The dummy's approach direction relative to the crabs' home vector (track angle) strongly affects the probability of responses (Table 1B). For statistical purposes, track angles were sorted into 20° bins from 0° to 180° and fitted as a categorical variable (d.f.=8). The probability is high whenever the dummy approaches from the crab side of the burrow; that is, for track angles larger than 100° (Fig. 7B). The probability drops off sharply towards smaller approach angles and reaches its lowest probability when the dummy approaches the burrow from directly opposite the crab (track angle <20°).

Crab side is a measure of whether the dummy track crosses the extended home vector on the crab side of the burrow or on the opposite side. Crab side has two values, 0 and 1, and was needed to achieve a complete geometrical description of each trial. Each track angle can have either value of crab side. The influence of crab side (Table 1C) on the probability of response is weak and only just significant. The crabs are more likely to respond to the dummy when it crosses the home vector on the side of the burrow occupied by the crabs themselves (Fig. 7B).

The effect of repeated dummy presentations

The variable 'presentation repeat' (Table 1D) counts the number of dummy approaches a given crab has already been exposed to before a given experiment and can therefore be used as a measure of how the probability of response is affected by the repeated presentations. Since the time course of this effect was not known, presentation repeat was fitted as a categorical variable with degrees of freedom (1–5, 6–10, 11–20, 21–30, 31–40, 41–50; Fig. 7C). The first two bins were kept smaller, because habituation is more likely to have an effect early on in a series of experiments. The estimated response probability of crabs decreases monotonically with increasing presentation repeat (solid black line).

Crab characteristics

Neither crab sex (Table 1G) nor size (Table 1H) influenced the probability of response, which was also independent of the distance the crabs were away from their burrows at the start of an experiment (Table 1I).

The role of intrinsic dummy characteristics

So far, we have mainly analysed variables that describe the way the dummy moved with respect to the crab and its burrow

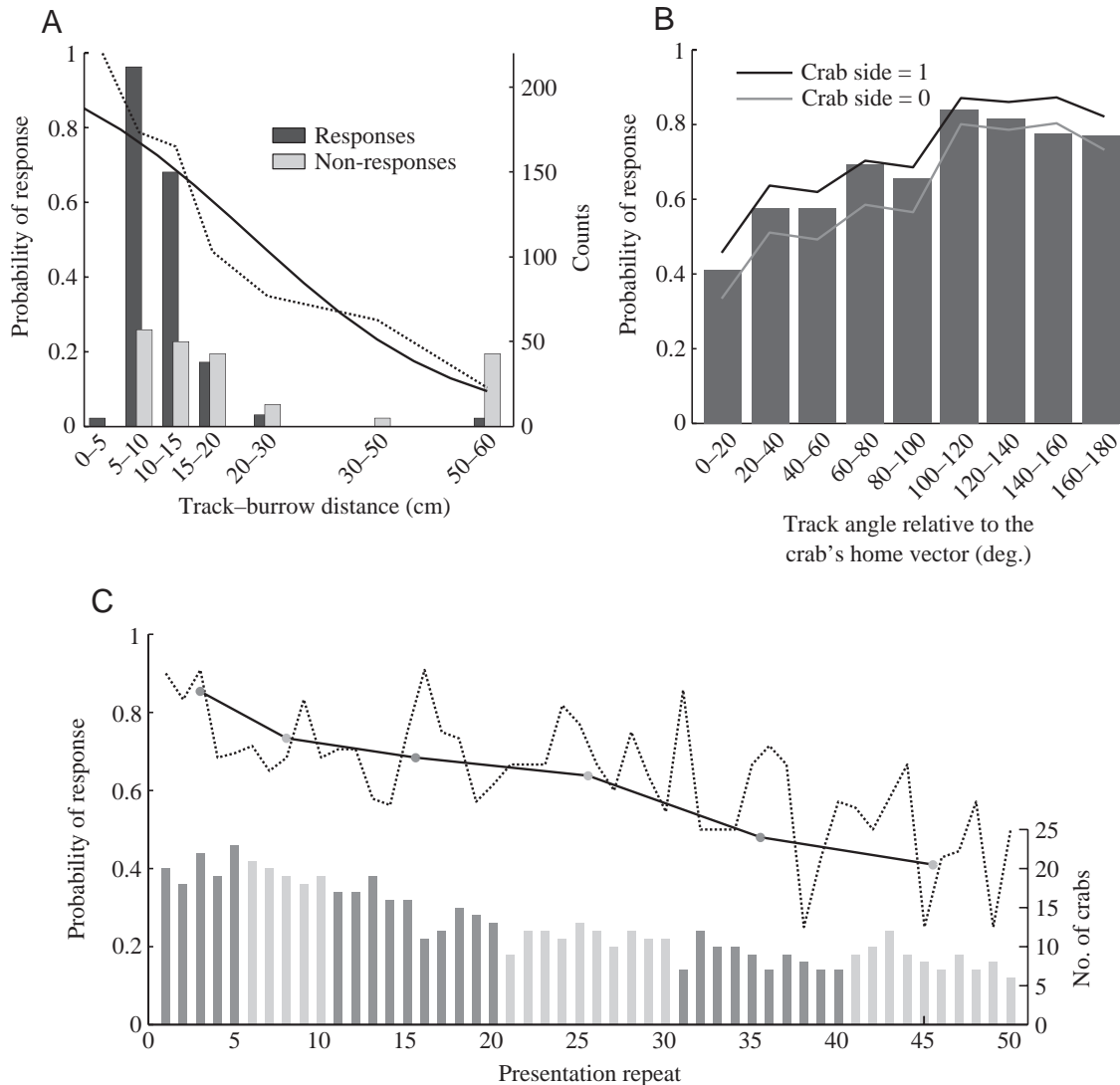


Fig. 7. The effects of the four significant terms that influence the crab's probability of response (see Table 1). (A) The distance of the dummy track from the crab's burrow (track distance; see Fig. 6). The histogram shows the number of experiments where the crabs responded (black) and the number of experiments where the crabs did not respond (grey) for a number of different track distances (right scale). The dotted line connects the probability of response for each bin of the histogram (left scale). The solid line shows the probability of response as fitted by the statistical model. (B) The effects of track angle and crab side (see Fig. 6). The vertical bars show the probability of response based on the raw data for the different approach directions, and the solid lines are fitted values based on the statistical model (grey, crab side = 0; black, crab side = 1). (C) The effect of repeated dummy presentations on the probability of response. The dotted line shows the probability of response over the number of successive dummy presentations. The model fit is shown by the grey dots joined by a solid line. The number of experiments for each value of presentation repeat, i.e. the number of crabs contributing to this value, is indicated by the histogram at the bottom of the figure. The two shades of grey group the values of presentation repeat that correspond to the six levels fitted in the statistical model.

during a trial. Are there any intrinsic dummy characteristics that affect the crabs' probability of response? Neither the dummy's size (Table 1J), brightness (i.e. whether it was black or white; Table 1K) nor speed (Table 1L) affected the crabs' probability of response. However, as the dummy track was fixed for each experimental set-up, the compass bearing from which the dummy approached a crab's burrow was always the same. To test whether the crabs associate the repeatedly approaching dummy with a certain compass direction, we changed the dummy's approach direction by rotating the track

90° around the burrow of the focal crab in 17 experiments. This was done after the crabs had had extensive exposure to the dummy approaching from the initial direction (at least 14 experiments per crab). While the change in direction did not affect the crabs' probability of response (Table 1M), it did increase the response strength from a mean of 83% to 96% (REML; $N=419$, d.f.=1, Wald/d.f.=7.48, $P=0.006$). This increase is consistent with the interpretation that the dummy approaching from a new direction was perceived as being different from the initial dummy, even though the two were

physically identical. This indicates again that the crabs do not simply evaluate the dummy in an egocentric frame of reference. While the dummy always approached from the same external compass direction during the initial habituation period, the crabs themselves frequently changed the direction in which they foraged and thus would have seen the dummy approach from a number of different directions relative to their own home vector. As the crabs keep their longitudinal body axis always approximately aligned with their burrow (Ens et al., 1993; Land and Layne, 1995b; Zeil, 1998), the dummy would have been seen in different parts of their visual field.

We also tested whether a change in the size of the dummy during the course of the experiment had a similar effect. There was no difference in the response probability or of the response strength regardless of whether we used all available trials for the statistical analysis ($N=31$) or only the first two trials with a new dummy size per crab ($N=12$) (all $P>0.35$).

The critical parameters: the distance from the burrow or the direction of travel?

As mentioned earlier, the (burrow) track distance influences two different parameters: how close to the burrow the dummy can get (minimal dummy–burrow distance) and how directly the dummy moves towards the burrow (see Fig. 6). The strong influence of the (burrow) track distance on the probability of response of the crabs may therefore either indicate that the crabs are sensitive to the distance between the dummy and their burrow or that they are sensitive to the direction of the dummy's path. For large track distances, for instance, the dummy can never come very close to the burrow, but its path also never points directly at the burrow. If distance were the main factor, we would expect that, for a given dummy–burrow distance, the probability that a crab responds should be independent of the track's direction relative to the burrow. If, on the other hand, the crabs were sensitive to the direction of the dummy path, we would expect that for a given dummy–burrow distance, the probability of response should be higher for tracks that have a trajectory that points more directly at the burrow (small burrow track distance). This difference should increase as the dummy gets closer to the burrow, because it should then be easier for the crabs to assess the direction of the dummy's path relative to the burrow. Fig. 8 shows the relationship between the probability of response and the dummy's distance from the burrow for three ranges of track distances. The overall shape of the three curves is very similar: all three curves show a strong increase in the probability of response as the dummy gets closer to the burrow, with only a slightly lower probability for larger track distances.

For a statistical test of these differences, we used a GLMM model identical to the one presented above, but this time we only counted responses if they occurred before the dummy reached a distance of 20 cm to the burrow. In essence, we now check whether the (burrow) track distance affects the probability that a crab responds before the dummy reaches a burrow distance of 20 cm (cumulative probability of the three

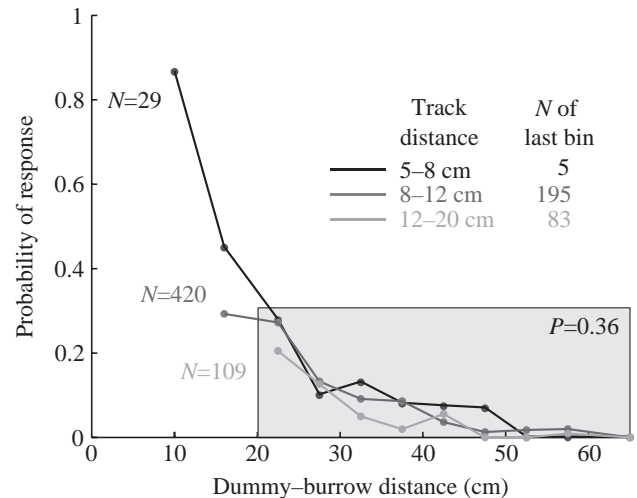


Fig. 8. The effect of dummy–burrow distance on the probability of response for three different ranges of track distance. The binning used for the dummy–burrow distance was: 5–8 cm, 8–12 cm, 12–20 cm, and 5 cm-wide bins for distances larger than 20 cm. For each track distance, binning started at the upper end of the distance range (e.g. at 20–25 cm for 12–20 cm track distances). To make the results for different dummy–burrow distances directly comparable, we adjusted the probability for slightly different bin widths in such a way that all values reflect the probability that a crab responds during a 5 cm movement of the dummy. For the meaning of the grey area, see text.

curves over the distances marked by the grey area in Fig. 8). The previous model checked for the influence of track distance on the cumulative probability of the entire curves. In order to do this in an unbiased way, we had to limit the data set to track distances below 20 cm, such that each included track allowed the dummy to approach to within 20 cm of the burrow. This limitation on its own did not affect the statistical model. However, the probability that a crab responds before the dummy reaches a distance of 20 cm from the burrow is independent of the track distance (GLMM; $N=558$, d.f.=1, Wald/d.f.=0.85, $P=0.356$). The significance of the other three parameters in the model remained unchanged. The result of this analysis is not affected by the exact response cut-off used (e.g. 20 cm). We cannot categorically rule out a small influence of the dummy's path direction, due to the limited number of data points at large and very small (<5 cm) track distances. However, the analysis shows that the dummy's distance to the burrow is the dominating factor that determines the response probability of burrow owners and not the direction of the dummy's path relative to the burrow.

There is yet another way to approach the question of whether the crabs are sensitive to the direction in which the dummy is moving. It became very clear during the experiments that the crabs responded almost exclusively as the dummy approached the burrow but ignored it when it moved away. To test this, we used a subset of our experiments in which the dummy moved at least 5 cm past the burrow (Fig. 9A). The selection criterion was chosen in such a way that the dummy had to move more

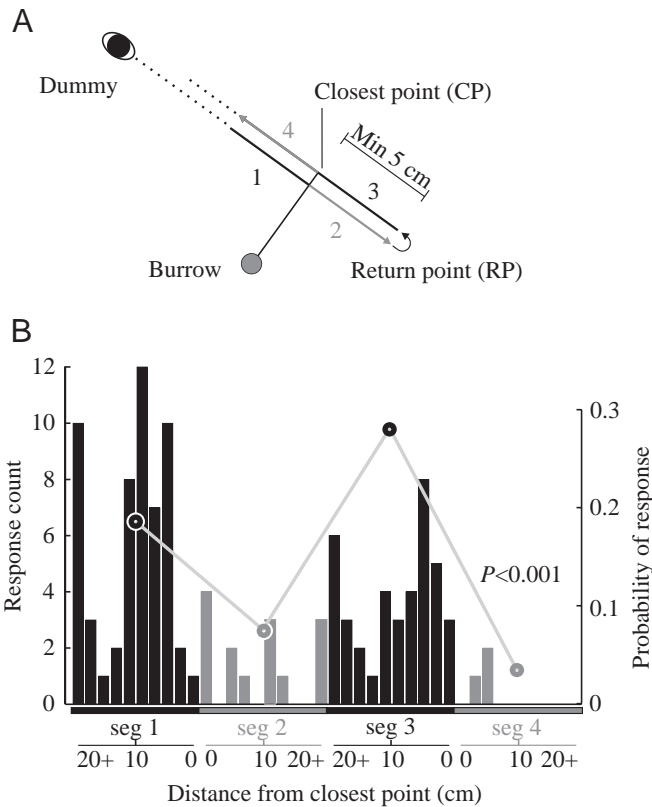


Fig. 9. Response probability and the movement direction of dummies. (A) Definition of the four track segments close to the burrow that were used in the analysis and the movement direction of the dummies in these segments. (B) The number of responses in each segment (histogram) and the probability of response per segment as fitted by the statistical model (dots joined by a solid line). Each segment has been divided into ten 2 cm-wide bins sorted according to their distance from the closest point (CP). The distances are sorted in the same way as a dummy would move through them during an experiment. The dummy–burrow distance is decreasing for segments 1 and 3 and increasing for segments 2 and 4. The response probability clearly differs between the four segments (GLMM; d.f.=3, Wald/d.f.=11.95, $P < 0.001$).

than 5 cm beyond the closest point to the burrow (CP) before reversing direction at the return point (RP), including all experiments where the crabs did not respond, or responded late, after the dummy had moved past CP (Fig. 9A). Based on the distance that the dummy had moved past CP we then defined four equal length segments on the dummy's path (Fig. 9A). Experiments in which a crab responded to the dummy before the dummy reached segment 1 were excluded and only the first response of a crab was counted. All remaining experiments were analysed regardless of whether the crabs reacted or not. If a crab responded to the dummy during a given segment, the remainder of that experiment was then ignored in the probability calculations for the subsequent segments. This selection process left us with 232, 176, 162 and 123 trials to compare the probability of response for segments 1–4, respectively. We can state the following, non-exclusive

hypotheses: (1) The probability of response should decline from segment 1 to segment 4 because sensitive crabs would respond early, and we should see an accumulation of insensitive crabs towards later segments. (2) If the crabs are sensitive to the direction of movement of the dummy, we would expect the probability of response to be higher when the dummy approaches the burrow (segments 1 and 3) compared with when the dummy moves away from the burrow (segments 2 and 4). Otherwise, the probability of response should be the same for all segments.

The number of responses is clearly much higher for track segments 1 and 3 than for segments 2 and 4 (Fig. 9B), and the response probability is significantly different for the four segments (GLMM; d.f.=3, Wald/d.f.=11.95, $P < 0.001$; Fig. 9B). In fact, the crabs respond much more often when the dummies move through segments 1 and 3 than through segments 2 and 4. An inspection of the pair-wise standard errors of the linear transformation of the model shows that all four segments differ significantly from each other. Two of these comparisons are especially interesting. Segment 3 has a higher probability of response than segment 2, demonstrating that the crabs distinguish between an approaching and a retreating dummy. On such a coarse scale, therefore, the crabs are sensitive to the dummy's direction of movement relative to the burrow. It is important to keep in mind that if there were a general decrease in the probability of response towards later segments, we would actually expect segment 3 to show a lower probability of response than segment 2. The second interesting comparison is between segments 1 and 3. The fact that the probability of response is higher in segment 3 suggests that the crabs are somehow sensitised by the directional change in movement direction of the dummy at the return point. The crabs often responded almost immediately as the dummy changed direction, especially if the dummy was still close to the burrow. This is not obvious in Fig. 9B because the return points fall into different bins along the histogram.

What determines the response distance?

The previous analysis has shown that the distance between the dummy and the crab's burrow and the geometry of the dummy approach are the most important predictors of whether or not a crab responds. In the following analysis, we investigate what parameters determine the response distance, which we define as the distance between the dummy and the burrow at the time the crabs initiate their response. An inspection of Figs 4 and 5 suggests that crabs respond when the dummy has reached a certain distance from the burrow, irrespective of the dummy's approach direction. The median response distance is 24.5 cm, and 75% of the responses occur when the dummy is between 14.2 cm and 42.4 cm (upper and lower 12.5th percentile) away from the burrow (Fig. 10).

To test which factors affect the response distance, we performed an REML (Table 2). The response distance was log transformed to achieve a satisfactory error distribution. The final model had the following form:

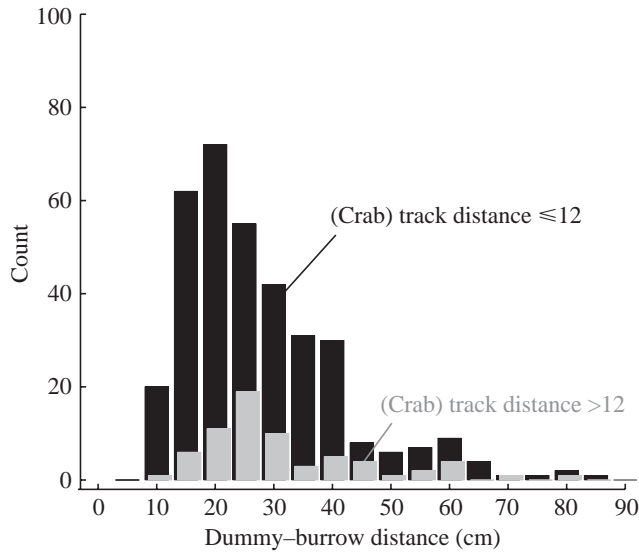


Fig. 10. Histogram of dummy-burrow distance (response distance). Black bars represent response distance distribution for track distances of ≤ 12 cm; grey bars represent response distance distribution for track distances of > 12 cm.

$$\log_e(\text{dummy-burrow distance}) \approx \beta_0 + \beta_1(\text{track distance}) + \beta_2[(\text{crab burrow distance})] + \beta_3[\text{track distance} \times (\text{crab burrow distance})] + \beta_4(\text{trial index}) + \beta_5(\text{track angle}) + \beta_6(\text{crab side}) + \text{error}.$$

Random term: crab identity; $N=419$.

The effect of the crab's distance from its burrow

The main parameters affecting the response distance are the track's distance from the crab's burrow (Table 2A) and the crab's distance from its own burrow at the time of response (Table 2B). Also significant is the interaction between these two variables (Table 2C). The relationship between the response distance and the (crab) burrow distance depends on the (burrow) track distance and *vice versa*. The larger the track distance, the smaller the effect of the (crab) burrow distance. For small track distances (i.e. larger dummy-burrow distances, when they are further away from the burrow), the crabs respond earlier [Fig. 11A; dashed line (track distance = 10 cm) and open dots]. However, when the track is ≥ 20 cm away from the burrow (solid line and filled dots), the crab-burrow distance has no influence on the response distance (dummy-burrow distance).

Track angle and crab side

Track angle has a very weak effect, which is statistically only just significant, on the timing of the response (Table 2E). The effect of crab side just fails to be significant (Table 2F). Dummies that would intersect the extended home vector on the crab side of the burrow (crab side = 1) trigger a response slightly earlier, and dummies that approach on a low track angle are allowed slightly closer to the burrow. However, the response distance is remarkably constant, no matter where the

Table 2. Results of the Linear Mixed Model Analysis ($N=419$)

Term*	d.f.	Wald†/d.f.	P
A Track distance	1	31.24	<0.001
B (Crab) burrow distance	1	31.42	<0.001
C Track distance \times (crab) burrow distance	1	12.67	<0.001
D Presentation repeat	5	7.16	<0.001
E Track angle	8	2.15	0.028
F Crab side	1	3.76	0.053
G Crab size	1	0.01	0.911
H Crab sex	1	0.00	0.995
I Dummy size	1	0.19	0.662
J Dummy speed	1	0.31	0.576

*Variables are measured at the time the crab initiates its first response.
†The Wald-statistic is a measure of statistical significance. Larger values indicate higher significance.

dummy comes from. Fig. 11B shows that the crabs respond at a roughly equal dummy-burrow distance, irrespective of the dummy's approach direction, which is irrespective of where relative to the home vector the crabs see the dummy. The statistical difference between the track angles is mainly based on the fact that if the dummy approaches from across the burrow, as seen from the crab's perspective, the crabs respond late, allowing the dummy to come slightly closer to the burrow than for the other approach directions [Fig. 11B, lightest grey lines (track angles $< 20^\circ$)].

The effect of repeated presentations on the timing of the response

The crabs adjust their behaviour to repeated dummy presentation by allowing later dummies to approach the burrow more closely before they respond (Table 2D). The effect is surprisingly small, however (Fig. 11C): over the course of ~ 50 trials, the dummy-burrow distance at the moment of response decreased by only 30%.

Crab and intrinsic dummy characteristics

As in the case of the response probability, neither the sex nor size of the crabs (Table 2G,H) nor the size nor speed of the dummies influenced the response distance (Table 2I,J).

The most striking result of the analysis of the response timing is that the crabs retreat towards their burrows when the dummy has reached a certain distance from the burrow, irrespective of its approach direction. In addition, the crabs adjust this response distance according to their own distance from the burrow: they respond earlier when they are further away from their own burrow.

Discussion

We have employed simple crab dummies to investigate how fiddler crabs assess and respond to events in the crowded visual world they inhabit. We exploited their need to survey and

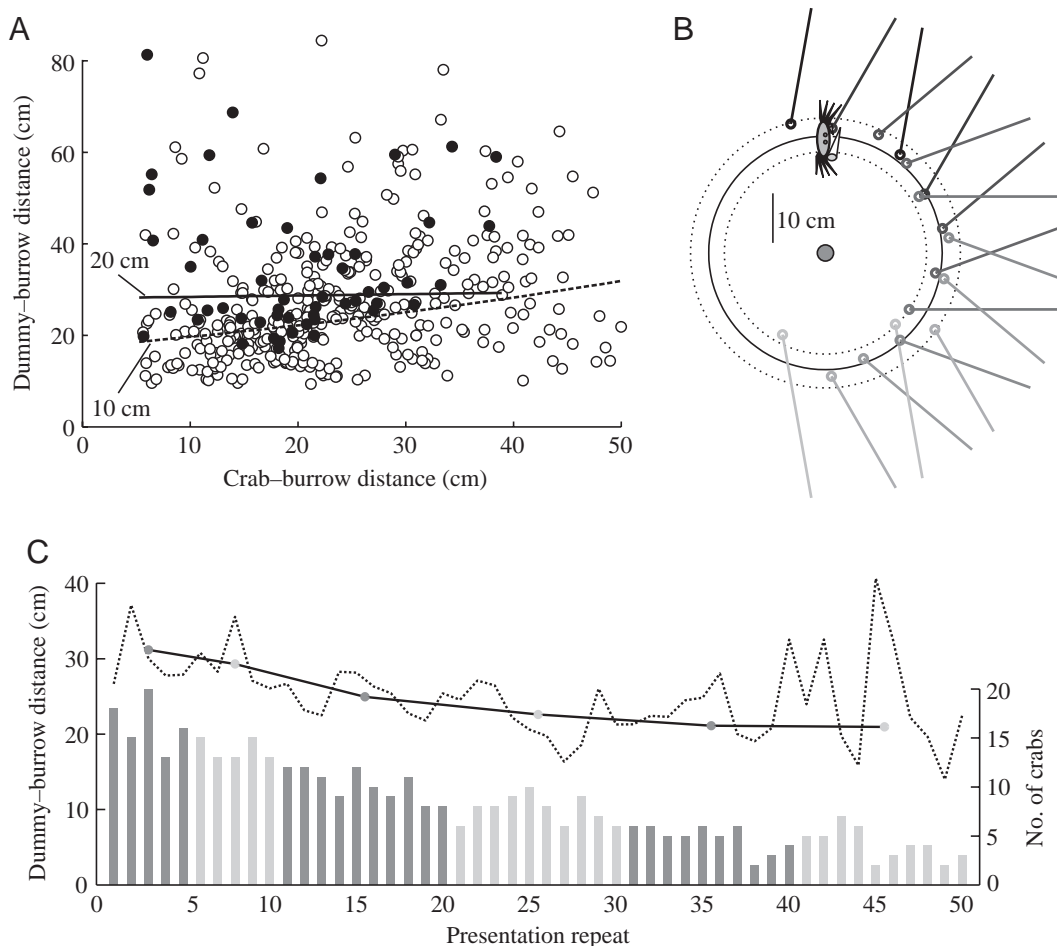


Fig. 11. The parameters that influence a crab's decision of when to initiate its response to the approaching dummy. (A) The influence of crab-burrow distance on the dummy-burrow distance at the time of the response. The data set has been split according to the track's distance from the crab's burrow: small burrow track distances of ≤ 20 cm are shown as open circles, and the corresponding model fit (track distance = 10 cm) as a dotted line. Larger track distances of > 20 cm and the model fit for a track distance of 20 cm are shown as filled dots and a solid line, respectively. (B) Response distance and the direction of approach of the dummy. The response distance is only slightly influenced by different track angles. The solid lines show the direction of dummy paths, and the large circles mark dummy positions at the time of response as fitted by the statistical model. The fitted response distance is shown for each of the nine approach directions (track angle) and the two values of crab side (see Fig. 6). Increasing track angles are shown in progressively lighter greys. Fitted values were calculated at the mean of all other parameters in the statistical model. The mean crab-burrow distance is 23.4 cm. Solid and dotted circles represent the mean response distance ± 2 s.e.m. (C) The effect of repeated dummy presentations on the response distance. The dotted line shows the mean response distances over successive dummy presentations. The grey dots joined by a solid black line show the model fits for the six categories of presentation repeat. The grey bars at the bottom of the panel show the number of experiments (crabs) contributing to each estimate. The two shades of grey indicate which presentation repeats correspond to the six categories of the variable presentation repeat used in the statistical modelling.

defend their burrows while foraging away from them to ask what criteria determine whether the crabs perceive a threat to their burrow or not.

On the most general level, our results show that the crabs took our simplistic dummies very seriously, even though they did not resemble real crabs in attributes other than their size and their position in the visual field of a crab observer (von Hagen, 1962; Land and Layne, 1995a). The crabs' overall probability of response is very high (Fig. 7C) and most responses are strong in that in the majority of trials the crabs retreat all the way back to their burrows when they become aware of a dummy (Fig. 3). The crabs habituate little to

repeated dummy approaches, with over 60% of the crabs continuing to respond even after 30 dummy presentations. This is in spite of the fact that the time pressure the crabs were subjected to during our experiments was severe. The crabs involved spent a significant amount of their time responding to the dummy. Burrow surveillance is of such significance to these crabs that each event is taken seriously, independent of the recent history. The decline we observed in the probability of response during the course of the experiments – rather than being based on sensory habituation – is probably indicating a change in the crabs' perceived balance between the burrow's resource value and the cost associated with its surveillance and

defence. Indeed, for some crabs it proved too much: many of them stopped participating in our experiments by disappearing below ground, while most other crabs were still active on the surface. A few crabs even abandoned their burrows and wandered off in search of a new one.

Our analysis identified the dummy's distance to the burrow of a crab as the single most important parameter that determines the crab's probability of responding by rushing back to the burrow. The probability of response declines sharply with increasing dummy–burrow distance (Figs 8, 10). The decision that the burrow needs defending is thus not made in an egocentric frame of reference but in one that is centred on the burrow. The crabs evaluate the dummy's movements relative to their burrow and not relative to themselves. This is also evident in Fig. 11B, where the mean distance between the dummy and the burrow at response time varies little for the different approach directions, but the distance between the dummy and the crab depends very strongly on where the dummy comes from. The ability of fiddler crabs to judge the distance between the burrow and an approaching dummy regardless of their own distance from the burrow is quite an astonishing feat of information processing. We will devote a companion paper to a detailed analysis of this problem (Hemmi and Zeil, 2003a).

While the dummy's distance from the burrow is clearly very important, the crabs are also sensitive to the general direction in which these crab-like dummies move. The probability that a crab responds to a dummy that is close to its burrow is about three times higher when the dummy moves towards the burrow than when it moves away from it (Fig. 9). Our results also reveal that the crabs use knowledge of their own distance from the burrow to modify their behaviour. The crabs respond earlier to an approaching dummy if they themselves are further away from the burrow (Fig. 11A).

Our dummies clearly do not look like real crabs, yet they were very successful in eliciting burrow defence. The reason for this is likely to be related to the limits of resolution of fiddler crab compound eyes. In the context of burrow defence, the crabs simply cannot afford to be choosy. They often need to respond to intruders at a large distance. At a mean crab–dummy distance of 30 cm at the time of the response, the angular size of our dummies was so small that they would be seen by, at most, a few ommatidia. This is clearly not enough to make sophisticated visual discriminations. Indeed, despite the male's massively enlarged claw, fiddler crabs are only able to distinguish between a male and a female crab at distances of 10–15 cm (Aspey, 1971; Land and Layne, 1995a). This might also be the reason why we failed to find differences in the response probability or response distance between male and female crabs or between crabs of different sizes. Similarly, intrinsic dummy characteristics, such as its size and the sign of its contrast against the mudflat background (white or black dummy), do not influence the crabs' probability of response or the response timing. Burrow surveillance responses are initiated at distances at which the crabs do not have sufficient information to distinguish between an intruder's size and sex

or between a crab and a simple dummy. The responses we observed are therefore only based on the dummy's position and motion. Our dummies not only didn't look like real crabs but they also moved differently. Burrow-less, wandering crabs frequently change direction and often approach other crabs (Zeil and Layne, 2002), whereas our dummies moved along a predictable straight line. We might therefore expect to see even higher probabilities of responses towards real crab intruders than the ones we found with dummies.

The observation that the crabs' probability of response actually increased when the dummy changed direction after passing the burrow, compared with the initial approach (Fig. 9), suggests that the crabs are indeed sensitive to such changes in motion direction. These changes might be another way in which the crabs attempt to distinguish between neighbouring resident crabs and potentially dangerous intruders.

Interestingly, the crabs respond more strongly when the same dummy approaches the burrow from a new compass direction, as if it was perceived as a new threat. It may be important to note in this context that resident crabs are able to remember the locations of the burrows of at least some of their neighbours based on path integration (Zeil and Layne, 2002). The direction from which a crab approaches might thus contain information on its identity. Keeping track of the approach direction of another crab with which a burrow owner has interacted before could therefore be part of a mechanism that allows fiddler crabs to avoid unnecessary interactions with their neighbours.

Our results show that the crabs are able to adjust their response behaviour according to the particular situation during which a conspecific approaches their burrow. They are sensitive to the intruder's distance (Fig. 8) and motion (Fig. 9) relative to their burrow, to changes in the direction of motion (Fig. 9), to the compass direction from where the intruder approaches and to their own distance from the burrow (Fig. 11A). The effects of all these factors are consistent with the hypothesis that the crabs try to minimise the time lost during burrow defence without increasing the risk of losing their burrow. It is not clear at this point why the crabs respond less often to dummies that approach from beyond the burrow (Fig. 7B). Two non-exclusive hypotheses that could explain this difference are based on strategic or perceptual considerations. Wandering crabs initially approach the burrow owners rather than the burrows themselves because the burrow entrances are not normally visible to the crabs from a distance of >15 cm (Zeil, 1998; Zeil and Layne, 2002). Burrow owners might therefore be more responsive to crabs approaching or overtaking them as mimicked by dummies approaching from the crab's side of the burrow. The result could also indicate that the crabs find it more difficult to make a judgement on the position and direction of movement of dummies that approach from beyond the burrow. The mean distance between the crab and the dummy at the time of the response is much larger when the dummy approaches from beyond the burrow (Fig. 11B). In fact, the crabs clearly respond to dummies that are up to 80 cm

away. At such a distance, the apparent size of the dummy is only 1.6° wide and <1° high, and the crabs would clearly find it difficult to accurately determine its position and motion relative to the burrow. Such a detection problem would lead to a higher percentage of crabs not responding to dummies approaching from these directions.

In summary, fiddler crabs protect their burrow against conspecifics by returning to its entrance whenever another crab approaches to within a certain distance of the burrow. Foraging crabs evidently know how far away they are from their burrows because the further away they are from home, the earlier and faster they respond to an approaching dummy. We know that crabs do not see their own burrows from more than 15 cm away, so their path integration system needs to provide them with information about the direction and distance in which their burrow lies (Cannicci et al., 1999; von Hagen, 1967; Zeil, 1998; Zeil and Layne, 2002). Burrow-surveying crabs thus need to be able to integrate visual information and information from the path integration system to assess another crab's position and movement relative to the burrow. Exploring how they are able to do this and unravelling how they could achieve the necessary 'sensor fusion' is the subject of the following paper (Hemmi and Zeil, 2003a).

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