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RESEARCH ARTICLE

Evidence of predictive selective attention in fiddler crabs during escape in the natural environment

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ABSTRACT

Selective attention is of fundamental relevance to animals for performing a diversity of tasks such as mating, feeding, predation and avoiding predators. Within natural environments, prey animals are often exposed to multiple, simultaneous threats, which significantly complicates the decision-making process. However, selective attention is rarely studied in complex, natural environments or in the context of escape responses. We therefore asked how relatively simple animals integrate the information from multiple, concurrent threatening events. Do they identify and respond only to what they perceive as the most dangerous threat, or do they respond to multiple stimuli at the same time? Do simultaneous threats evoke an earlier or stronger response than single threats? We investigated these questions by conducting field experiments and compared escape responses of the fiddler crab *Gelasimus dampieri* when faced with either a single or two simultaneously approaching dummy predators. We used the dummies' approach trajectories to manipulate the threat level; a directly approaching dummy indicated higher risk while a tangentially approaching dummy that passed the crabs at a distance represented a lower risk. The crabs responded later, but on average more often, when approached more directly. However, when confronted with the two dummies simultaneously, the crabs responded as if approached only by the directly approaching dummy. This suggests that the crabs are able to predict how close the dummy's trajectory is to a collision course and selectively suppress their normally earlier response to the less dangerous dummy. We thus provide evidence of predictive selective attention within a natural environment.

KEY WORDS: Escape behaviour, Predator avoidance, Crustaceans, Vision, Multiple simultaneous predators, Natural environments

INTRODUCTION

The risk of predation has an important influence on animal behaviour because of the severe consequences of a failed escape response (Ydenberg and Dill, 1986; Lima and Dill, 1990; Sih, 1994; Lima, 1998; Preisser et al., 2005; Creel and Christianson, 2008; Clinchy et al., 2013). A fast and accurate response to a perceived threat is key to a successful escape. However, many animals have relatively limited sensory and neural processing capabilities and yet they have to make vital decisions in often complicated environments with multiple attentional distractors, and multiple potential

predators. There is a large body of literature investigating how animals assess the risk imposed by approaching predators and how they incorporate this information into their decision-making process (Lima and Dill, 1990; Gursky-Doyen and Nekaris, 2007; Ferrari et al., 2010; Yager, 2012; Humphreys and Ruxton, 2018). The strategies prey animals adopt when faced with a single predator depend on many factors such as the speed, size and hunting style of the predator, as well as the prey's own speed and distance from its refuge (Lima and Dill, 1990; Hemmi, 2005a; Hemmi, 2005b; Gursky-Doyen and Nekaris, 2007; Yager, 2012; Humphreys and Ruxton, 2018).

In natural environments, prey animals rarely detect and respond to stimuli in isolation and often face multiple threatening stimuli. Yet, only a handful of studies have explored escape strategies in multiple-predator scenarios (McIntosh and Peckarsky, 1999; Amo et al., 2004; Geist et al., 2005; Cooper et al., 2007). Given that failing to respond appropriately can be lethal, and that escape actions are energetically costly and take time away from other important activities (Sih et al., 1990; Dill and Fraser, 1997; Sih, 1997; Martín and López, 1999), we might expect that animals have evolved efficient strategies to deal with the presence of multiple predators.

There is a range of potential options available to prey when faced with multiple predators. Ideally, prey might adjust their response behaviour to minimise the combined risk from all identified predators (Sih, 1987). For instance, prey might escape in a direction which maximises the distance from all predators. This strategy requires a 'divided attention' mechanism. Alternatively, prey could assess the risks of all predators individually, identify the predator that poses the highest risk, and then respond to that predator in isolation (McIntosh and Peckarsky, 1999; Geist et al., 2005; Amo et al., 2004). In this strategy, prey require a selective attention mechanism and would suppress the response to a less threatening predator to avoid a more dangerous one (McIntosh and Peckarsky, 1999; Geist et al., 2005; Amo et al., 2004). In a worst-case scenario, prey might simply integrate the information from all predators and respond to the average signal. This might work well in some situations, for instance when two predators approach from the same side of the animal, but not in others, such as when predators approach from opposite directions, where the prey may not respond at all. Additionally, as the risk posed by multiple predators is likely to be greater than the risk posed by a single predator, multiple predators might evoke earlier or faster responses (Geist et al., 2005), and/or may increase the duration or frequency of refuge use (Ydenberg and Dill, 1986; Kramer and Bonenfant, 1997; Amo et al., 2004; Cooper et al., 2007).

Fiddler crabs are an important food source for a large variety of avian predators (e.g. Zwarts, 1985; Ens et al., 1993; Iribarne and Martinez, 1999) and often encounter several predators at any one time. The crabs rely exclusively on visual information to detect predators (Nalbach, 1990; Land and Layne, 1995; Layne et al.,

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1997; Layne, 1998) and they typically respond to predators by running to their burrow entrance, before descending underground if the threat persists (Nalbach, 1990; Land and Layne, 1995; Jennions et al., 2003; Hugie, 2004).

Fiddler crabs are an excellent study system to investigate the role of visual attention in escape behaviour and examine how an animal with limited sensory capabilities responds to the complex task of responding optimally to multiple predators. Much is known about their visual system in terms of ocular anatomy, and its spatial and temporal resolution, providing essential information for the interpretation of crab behaviour. As a result, the impact of their well understood visual limitations on escape decisions has been extensively incorporated into studies focused on reactions to a single threat (Land and Layne, 1995; Zeil and Al-Mutairi, 1996; Hemmi, 2005a; Hemmi, 2005b; Hemmi and Pfeil, 2010; Smolka et al., 2011; Smolka et al., 2013). Because of their small size and the design of their eyes, fiddler crabs cannot resolve much spatial detail and identify the shape of predators at low resolution (Land and Layne, 1995; Zeil and Al-Mutairi, 1996; Smolka and Hemmi, 2009; Bagheri et al., 2020). For instance, compared with the human eye, which can achieve up to 60 cycles deg^{-1} (Campbell and Green, 1965), the fiddler crab compound eye has a maximum resolving power of only ∼2 cycles deg^{-1} in the acute zone (Bagheri et al., 2020). Consequently, crabs treat all moving stimuli above the horizon as potential threats (Land and Layne, 1995; Layne et al., 1997) and even simple dummy predators can provoke reliable anti-predator responses similar to those evoked by natural predators (e.g. Nalbach, 1990; Land and Layne, 1995; Layne, 1998; Hemmi, 2005a; Smolka et al., 2011).

Previous studies have shown that these crabs use visual cues such as retinal speed, angular size and elevation above the horizon to evaluate risk (Hemmi, 2005a; Hemmi, 2005b; Hemmi and Pfeil, 2010). Because of their reliance on retinal motion speed to trigger an escape run, crabs respond more often, but later, to directly approaching dummies, compared with those that approach tangentially (Hemmi, 2005a). This counter-intuitive result can be explained by the lack of depth perception and the importance of retinal motion in the escape decision (Hemmi, 2005b; Hemmi and Pfeil, 2010). Directly approaching dummies present less of a threat early on as their retinal image moves less, but they eventually come closer and elicit responses more reliably.

In contrast to the body of work on crab responses to single predators, the way in which fiddler crabs assess predation risk in the presence of multiple visual threats, what escape strategies are then elicited and therefore the role of attention is essentially unknown. We therefore aimed to investigate how fiddler crabs integrate their responses to simultaneous predatory threats under naturalistic conditions in the field. We measured the crabs' responses to two different dummy predators moving on two different approach trajectories: (1) a directly approaching, high risk, predator and (2) a tangentially approaching, lower risk, predator. By comparing the crabs' responses to predators approaching individually or simultaneously, we were able to show that crabs suppress the normally earlier responses to the lower risk predator and selectively respond to the higher risk predator which normally elicits later responses.

MATERIALS AND METHODS
Study species
Experiments were conducted in August 2017 on the intertidal mudflats near Learmonth (22°18S, 114°9E), south of Exmouth, Western Australia. We confronted fiddler crabs of the species

Gelasimus dampieri (Crane 1975) (formerly *Uca dampieri*) with either a single or two simultaneously approaching dummy predators while they foraged near their burrows in a natural social and physical environment. The crabs live in dense colonies and each crab occupies its own burrow, which it escapes towards in case of danger (Nalbach, 1990; Land and Layne, 1995; Jennions et al., 2003; Hugie, 2004; Zeil and Hemmi, 2006). Experiments were conducted by UWA AEC approved methods (UWA AEC project number RA/3/100/1515).

Experimental setup and procedure
Dummy predators were moved along the mudflat on two tracks made from thin, transparent, monofilament fishing line, wrapped around two posts (Fig. 1). Dummy predators were black plastic balls (e.g. Hemmi and Tomsic, 2015) with a diameter of 3 cm. A non-stretch polyfilament line connected each dummy to a motorised driving wheel and allowed us to move the dummies at a speed of 47.9±7.8 cm s^{-1} (mean±s.d.) with battery-driven electric drills. Similar dummy systems have previously been used to effectively evoke escape responses in crabs (e.g. Hemmi, 2005a, Hemmi and Pfeil, 2010, Hemmi and Tomsic, 2015). Two sets of two cameras (Sony Handycam HDR-CX550VE at 25 frames s^{-1}) were mounted on two metal poles and positioned in two nearby locations. Each set of cameras was placed next to one of the dummy tracks (Fig. 1). The cameras were approximately 1.7 m above the mud flat and each pair of cameras monitored the activity of crabs within an area of approximately 3–4 m^2.

The two dummy tracks were mounted at a height of approximately 20 cm above the ground and ran at approximately right angles to each other over two separate groups of crabs (group 1 and group 2; Fig. 1). For each group of crabs, the two tracks represented two different approach trajectories: direct and
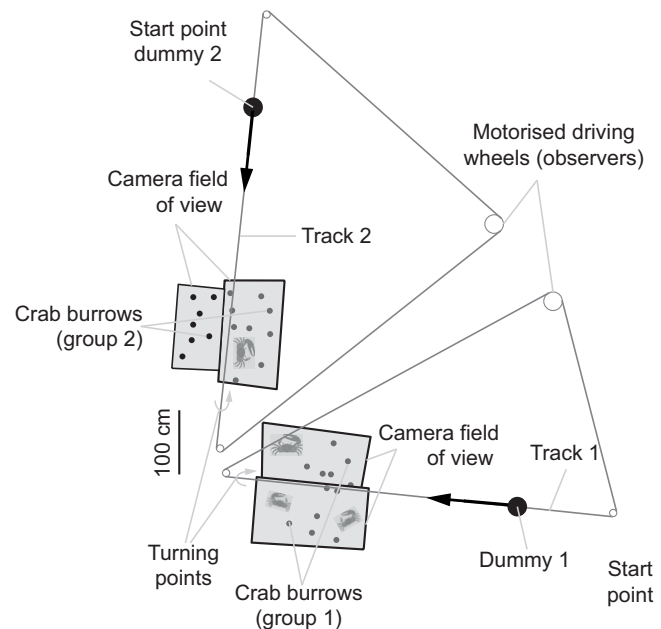

Fig. 1. Experimental setup. A top view of a typical setup showing the field of view of four cameras, dummy tracks, crab burrows, the dummies and the location of the observer. During a run, the dummies moved to the end of the track, where they turned around to go back to the starting position. We tested the responses of the crabs to single versus paired predators by running either a single dummy (in track 1 or track 2) or the two dummies simultaneously.

tangential. In our setup, the two dummy lines were positioned at right angles (Fig. 2B) such that dummy 1 was the 'direct' dummy for group 1 and the 'tangential' dummy for group 2 and vice versa for dummy 2 (Fig. 1). A directly approaching dummy more closely follows a direct collision course, whereas a tangential dummy passes the crabs at a distance (Fig. 2A). Previous research has shown that tangentially approaching dummies elicit earlier responses, but presumably because they are less dangerous, ultimately provoke fewer responses than directly approaching dummies (Hemmi, 2005a). In other words, a directly approaching dummy appears less threatening at the early stages of the approach, but becomes more threatening later as it comes closer. This response is irrespective of where the dummy appears in the field of view of the crabs as previous studies showed that whether the dummy approaches the crabs from the side, the front or the back has only a small effect on their response distances (Hemmi, 2005a).

Once the experimental setup was completed, crabs were given at least 10 min to resume their normal foraging activities before the experiment started. The responses of the crabs to single versus

Fig. 2. Definition of approach trajectory and response measures. (A) Direct dummies approach crabs in a trajectory that is closer to a collision course than that for tangential dummies. Direct dummies can ultimately approach the crabs more closely and therefore trigger more responses (Hemmi, 2005a). The approach trajectory is defined independently of the crab's own orientation. (B) In our experiment, direct and tangential dummies were moving at right angles to each other; however, 'direct' and 'tangential' still indicate how directly the crabs were approached by the dummy. (C) The geometry of various measurements used in the analysis. Crab–track distance was measured at the onset of dummy motion, and crab–dummy distance at the time of response. Please note that the figure only shows the top view and does not depict the height of the dummy above the ground.

paired predators were tested by running either one dummy (on track 1 or track 2) or the two dummies simultaneously. The order of presentation followed a Latin square design, leading to an approximately balanced experimental design. During each 'run', one or two dummies approached the recording areas from a distance of 6–7 m, moved past the visual field of the two cameras mounted along their perspective tracks, before returning to its/their starting position/s (Fig. 1). The runs were initiated every 2–3 min. The experiment was repeated on three different days at different locations. A total of 86 crabs from six groups of crabs (between 12 and 17 crabs from each group) and three independent setups (2 groups in each setup) contributed to the data. On average, each condition was tested 3 times for each crab.

Video analysis and response measures

Video footage was converted to AVI format, and down-sampled to 6.25 frames s^{-1} (160 ms intervals) using ffmpeg (ffmpeg.org) and temporally synchronised between the cameras. The Matlab (R2018a, MathWorks®) camera calibration toolbox (http://www.vision.caltech.edu/bouguetj/calib_doc/) was used to analyse a checkerboard pattern to calibrate the videos for lens distortions and other optical parameters. With the assumption that the ground is flat, the same toolbox was also used to determine the position of the cameras relative to each other and to the ground. Custom-written Matlab software (J.M.H.) was used to analyse the videos and extract the accurate 3D position of the crabs, burrows and dummies at 160 ms intervals for the full duration of each run. For frames where the dummy was not visible in the video, dummy positions were reconstructed from the movements of two patterned wheels, which were rotated by the pulling lines. Analysing the wheels' rotation, which was visible to at least one camera for each track, allowed us to calculate the exact 3D position of the dummy relative to the crabs for the entire duration of the experiment.

Crab escape responses were scored using the same criteria as in previous studies (e.g. Hemmi and Pfeil, 2010, Hemmi and Tomsic, 2015). A 'run home' was scored whenever a crab was at least 5 cm away from its burrow and moved at least 3 cm towards the burrow during a 3-frame period (480 ms). The start of the run home was assumed to occur in the first frame in which the crab moved at least 1 cm during one frame interval (160 ms). The decision to run home was assumed to have occurred one frame before a run. This assumption allowed for the crab's reaction time (Hemmi and Pfeil, 2010; Hemmi and Tomsic, 2015). Responses were only counted if they occurred while the dummy was still approaching the crab, i.e. before the dummy had passed the closest point to the crab (Fig. 2C). All crabs that left the cameras' field of view at any stage before the dummy had reached the closest point to the crab, or crabs that were involved in an interaction with other crabs (e.g. fighting), were excluded from the analyses. For each valid response, we determined the 3D crab–dummy distance, the 3D crab–track distance, and the crab–burrow distance (Fig. 2C). Previous studies have found no evidence for an effect of neighbouring crabs on the escape response in this experimental design (e.g. Hemmi and Tomsic, 2015).

Statistics
Cox proportional-hazards analysis
The 'run home' decisions were analysed in the context of a survival analysis using a Cox model (Collett, 2015). The Cox proportional-hazards model allows an integrated analysis of response probability and response timing. Separating response probability and response timing would lead to a strong bias towards sensitive crabs in the analysis of response timing. Survival analysis focuses on the
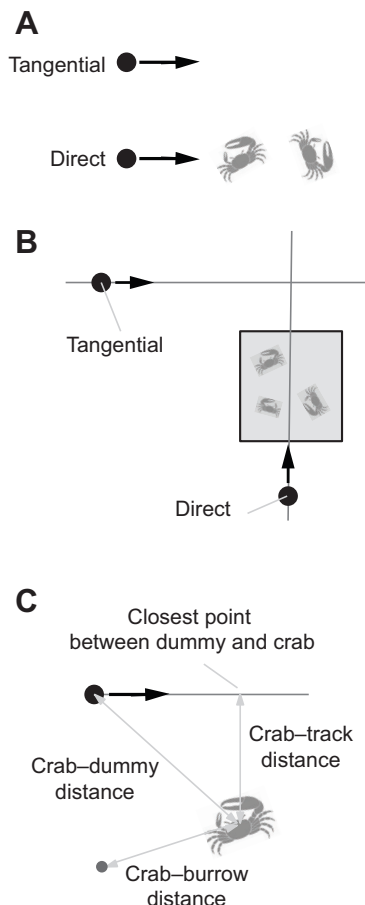
cumulative response probability as a function of the dummy's distance to the crabs. As the dummy is not always on a direct collision course, there is a limit as to how closely it can approach each crab (Fig. 2C). After reaching the closest point to a crab, the dummy always starts to move away again and is unlikely to elicit a response after that (Hemmi, 2005a). Consequently, individual crabs cannot meaningfully contribute to the dataset after the closest point of approach and are therefore removed from the data for calculations of response probabilities at closer crab–dummy distances. The removal point was marked by a cross on the survival curve and is known as the censor value.

Statistical analyses were performed in Matlab R2018a (MathWorks®) and statistical significance was calculated using a permutation test applied to the full Cox model (Collett, 2015). The experimental variable, 'dummy type', was treated as a factor with three levels: 'single direct', 'single tangential' and 'paired'. The effect of dummy type was tested by randomly permuting 5000 times across conditions (e.g. dummy type) for each individual crab – not across crabs, which accounted for the experimental and repeated measures design. Crabs were unique across cameras, setups and days. This also eliminates crab-to-crab variability from the statistical analysis. The log-likelihood estimate of the Cox model on the original un-permuted dataset was calculated and compared with the scores of the permuted datasets. Significance was calculated as the percentage of permutations that resulted in a score higher than or equal to the score calculated from the un-permuted data set. Therefore, P-values indicate the probability that the measured effect was only due to chance.

Expected response probability to the paired dummy

When crabs are confronted with both direct and tangential dummies simultaneously, three different cases are possible. (1) Crabs only respond to the direct dummy and ignore the tangential one. In this case, the response curve for the paired runs should look the same as the response curve for the single direct dummy. (2) Crabs respond to either the direct or the tangential dummy, whichever triggers the response first. In this case, the survival curve should be positioned in between the two curves for the single dummies. The expected survival curve can be calculate based on probabilities obtained from the single dummy runs and the actual observed positions of the dummy (see below). (3) Crabs take into account both dummies in their risk assessment. In this case, we would expect a higher response probability at further distances. In other words, the survival curve should be left shifted against the expected survival curve in case 2.

In order to identify which of these scenarios most likely describes the crabs' responses to the paired dummies, we calculated the expected survival curves based on the assumption that the crabs' overall response probability P is a function of responding to either of the two dummies independently ($P(P_d \cup P_t)$; case 2). This probability is given by:

$$P(P_d \cup P_t) = P_d + P_t - P(P_d \cap P_t),\qquad(1)$$

where P_d and P_t are the probability of response to the single direct and tangential dummy, respectively. $P(P_d \cap P_t)$ is the probability that a crab responds to both the direct and the tangential dummy in the same run. This term needs to be subtracted from the joint probability to avoid it being counted twice (Fig. S1).

In practice, we calculated the final survival curve using the following procedure. In the paired dummy runs, we had to consider two crab–dummy distances that varied slightly through the
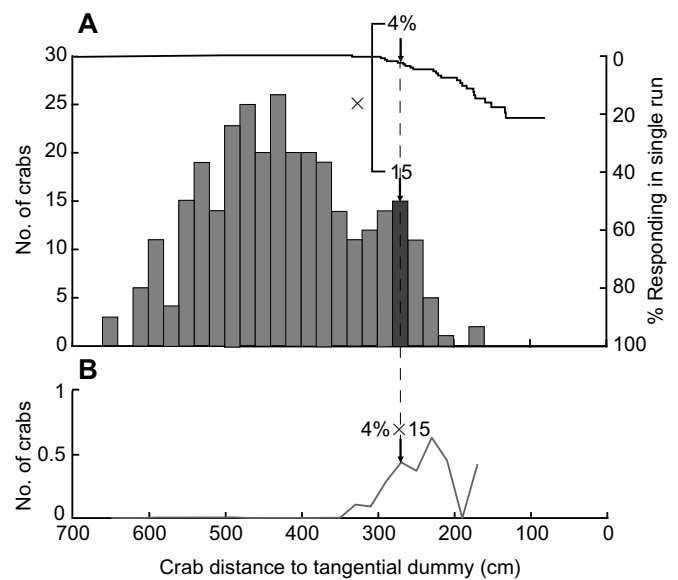

Fig. 3. Example calculation of the number of crabs expected to respond to the tangential dummy in the paired runs. (A) The histogram shows the distance of the crab to the tangential dummy when the crab's distance to the direct dummy was 226 cm. The 15 crabs that were between 260 and 280 cm away from the tangential dummy (dark grey bar) had an average response probability of 4% in the single tangential run (black line). (B) The number of crabs that were expected to respond to the tangential dummy at various distances to the tangential dummy. The area under the curve indicates the total number of expected responses to the tangential dummy (based on the single runs) that should have happened by the time the direct dummy approached the crab to within 226 cm. Note, this is in order to calculate the cumulative response probability as displayed in the survival curve.

experiments, depending on crab position and relative start of dummy movements. However, the distance to the directly approaching dummy d_d was always the closer distance and was used as the baseline. In order to calculate the probability of responding to the tangential dummy, we calculated the actual crab–dummy distance to the tangential dummy (d_t) for every crab–dummy distance to the direct dummy (d_d). Using these distances and the crabs' response probability profile to a single tangential dummy as estimated by the survival curves (see Results), we calculated the number of crabs that were expected to respond to the tangential dummy in the paired dummy runs before they respond to the direct dummy.

The histogram in Fig. 3A shows an example distribution of crab–dummy distance for the tangential dummy in the paired runs when the crabs' distance to the direct dummy was 226 cm. In this instance, there were 15 crabs that were between 260 and 280 cm from the tangential dummy (dark grey bar). Assuming the crabs' response probability to the tangential dummy is the same as that measured during the single run (Fig. 3A), 4% of crabs are expected to respond before the tangential dummy approaches to 270 cm. Therefore, we expected that 4%×15 crabs would respond to the tangential dummy in the paired dummy runs. Applying the same calculation to all the observed distances to the tangential dummy (for every bin in Fig. 3A) we get Fig. 3B. The area under the curve in Fig. 3B indicates the number of crabs that we expected would respond to the tangential dummy in the paired dummy runs N_t when the direct dummy was 226 cm away:

$$N_t|_{d_d=226} = 4\% \times 15 + 4.5\% \times 11 + \cdots \qquad(2)$$

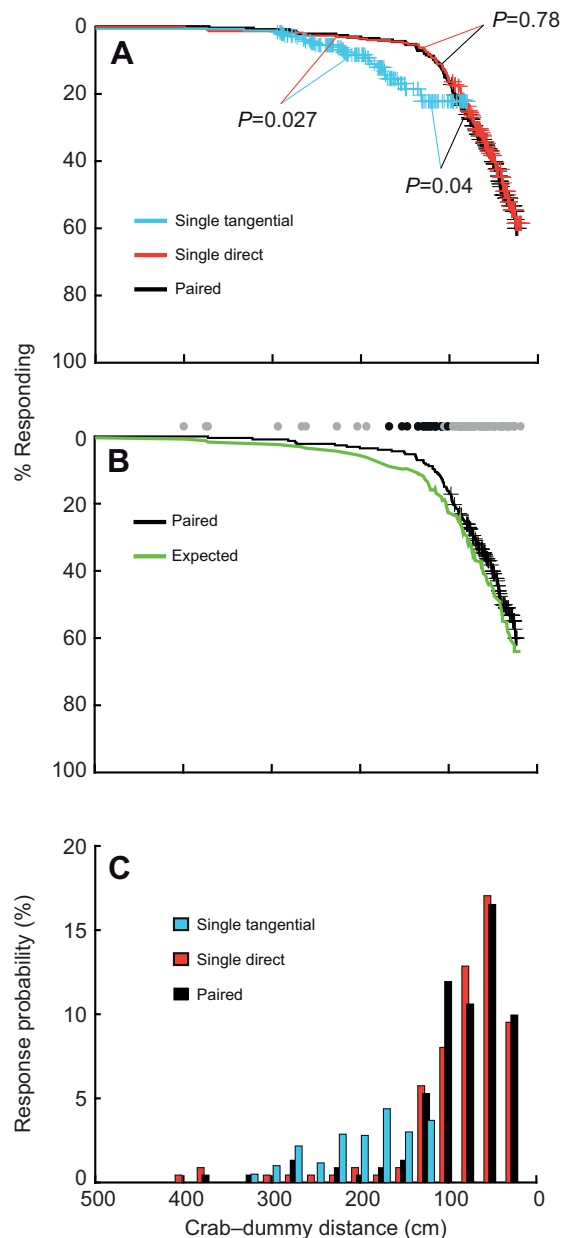By repeating this calculation for all crab distances to the direct

Fig. 4. Run home response. (A) Fiddler crabs respond earlier to tangentially approaching dummies, compared with directly approaching or paired dummies. Lines show the response curves analysed in the context of a survival analysis using a Cox model. The response curves show the percentage of crabs that responded before the dummy reached a certain distance to the crab (please note that the y-axis is reversed and lower points on the y-axis represent higher cumulative response probability). Crosses show censor points where a dummy reached its closest possible distance to the crab without eliciting a response and therefore could not contribute to the overall estimate of response probability at shorter crab–dummy distances (please note that the censor points do not have a real y-value and they are only plotted on the relevant curve at the dummy's closest distance to the crab; see Materials and Methods). The crabs' responses to paired dummies are plotted against the distance between the crab and the closer of the two dummies. (B) The expected survival curve was calculated based on the response distances of the two dummies during the paired approach and response probabilities of the crabs to single dummies (see Materials and Methods for details). The black and grey dots above the graph indicate at which crab–dummy distances the difference between the paired dummy and the expected combined response is significant and non-significant, respectively. (C) The probability of response plotted against crab–dummy distance.

dummy (at 10 cm intervals) and knowing the number of crabs, we therefore can calculate the probability P_t of the crabs that were expected to have responded to the tangential dummy in the paired dummy runs. Crabs that responded to either the direct or tangential dummy were removed from the pool of potential respondents.

Generalised linear mixed model
In addition to the survival analysis, which provides an integrated analysis of response probability and response timing, response probabilities were also analysed in the form of a generalised linear mixed model (GLMM) with logit as the link function (Matlab R2018a). The tested experiment types (single direct, single tangential and paired) were treated as categorical variables. We took into account individual variance between crabs by treating them as random factors. The final model was selected by sequentially fitting parameters and including only those parameters that reached significance at a 5% level when compared with the final model.

RESULTS
Crabs that responded to the approaching dummy predators always ran home towards their burrows. At the entrance of the burrow, they often paused before retreating underground or resuming other activities. However, as fiddler crabs retreat underground only if the predator comes close, the tangential dummies evoked very few underground responses, limiting our analysis to the run home response. To test how two simultaneously approaching dummies affected the crabs' escape responses, we examined how the response timing and response probability varied between single and paired dummy approaches.

Run home
When presented with only a single dummy, crabs clearly differentiated between the directly and tangentially approaching dummies (Fig. 4A,C, Table 1 permutation test: P=0.027, Table 2 GLMM: P<0.001, n=78 crabs, N=455 crab–dummy interactions). The crabs responded more often to the direct dummy (Fig. 4A,C, n=72 crabs, N=229), but when they responded to the tangentially approaching dummy, they tended to respond earlier, indicated by a clear early dip in the survival curve (Fig. 4A,C, n=78 crabs, N=226).

The crabs' responses to paired dummies (Fig. 4A,C, n=69 crabs, N=227) were not significantly different from those to the single, direct dummy (Table 1 permutation test: P=0.235, Table 2 GLMM: P=0.187, n=76 crabs, N=456), but were significantly different to the single, tangentially approaching dummy (Table 1 permutation test: P=0.023, Table 2 GLMM: P<0.001, n=76 crabs, N=448). In the case of the paired dummies, both Fig. 4 and our analysis used the distance of the closest dummy as a measure of escape distance. Given our experimental setup, this was always the 'direct' dummy.

Table 1. Results of the permutation test applied to the full Cox model

Comparison	N (n)	Model term	P
Direct versus tangential	455 (78)	**Experiment type**	0.027
		Crab–burrow distance	0.066
Direct versus paired	456 (76)	Experiment type	0.235
		Crab–burrow distance	0.208
Paired versus tangential	448 (76)	**Experiment type**	0.023
		Crab–burrow distance	0.130

Permutations were restricted to within crab to account for the repeated measures per crab. N, crab–dummy interactions; n, crabs. Terms included in the final model are shown in bold.

Table 2. Results of the generalized linear mixed model analyses for response probability (random model: crab identity)

Comparison	N (n)	Fixed effects (x_i)	Estimate	d.f.	logLik	P
Direct versus tangential	455 (78)	Intercept	−1.474	1	–	–
		Experiment type	1.23 (direct)	1	41.45	<0.001
		Crab–burrow distance	–	1	0.760	0.217
Direct versus paired	456 (76)	Intercept	−0.654	1	–	–
		Experiment type	–	1	0.870	0.187
		Crab–burrow distance	0.005	1	2.240	0.0345
Paired versus tangential	448 (76)	Intercept	−0.929	1	–	–
		Experiment type	1.98 (paired)	1	45.43	<0.001
		Crab–burrow distance	–	1	1.16	0.128

Terms included in the final model are shown in bold.

Our results suggest that the presence of a second, slightly more distant dummy did not influence the crabs' escape responses at all. This was surprising, because Fig. 4A,C clearly shows a significant number of early responses to a tangentially approaching dummy compared with a directly approaching one. Therefore, if the crabs were responding to both dummies, these early responses should have been visible in the response curve for the paired dummy, as an early downward deflection of the survival curve (Fig. 4A).

One explanation for this result is that the tangential dummy during the paired treatment was still too far away when the crabs made their decision to respond to the direct dummy. To check whether this was the case, we calculated the expected survival curve (Fig. 4B) based on the crabs' actual distances to both of the dummies under the assumption that the crabs responded independently to the two dummies according to their response probabilities displayed in the single dummy runs (Fig. 4A; see Materials and Methods, 'Expected response probability to the paired dummy', for details). We compared this expected survival curve with the crabs' actually measured curves to paired dummies using Fisher's exact test at each crab–dummy distance (Fig. 4B; the black dots represent the statistical comparisons that were significant at the 5% level). This analysis therefore suggests that the response probabilities at crab–dummy distances between 167 and 103 cm were significantly lower than expected had the crabs been responding to the two dummies independently.

Effect of track distance on run home responses

As highlighted by previous studies (Hemmi, 2005a; Hemmi and Pfeil, 2010; Hemmi and Tomsic, 2015), the distance of the crab to the dummy track (crab–track distance, Fig. 2C), a measure of the directness of the dummy's approach, strongly influences response probability and timing. In our experiments, by definition, direct and tangential dummies had on average very different crab–track distances. This difference between direct and tangential was much stronger for crabs that were close to the direct dummy track (crab–track distance <38 cm; Fig. 5) as opposed to crabs that were further away (crab–track distance ≥38 cm; Fig. 5).

The pattern of responses of the 'close' crabs, which showed a very strong difference between the direct and the tangential dummy (the crabs in the dark grey region of Fig. 5) to our three treatments was very similar to the pattern we saw in the overall results (Fig. 6A, B versus Fig. 4A,B; see also Tables 1 and 2 versus Table 3; Table S1). However, this was not the case for the crabs that were far from the direct track (Fig. 6C). The crabs that were far from the direct track (the crabs in the light grey region of Fig. 5) did not suppress their responses to the tangential dummy. Their responses to the single direct dummy were also significantly different from those to the tangentially approaching dummy (Fig. 6C and Table 4, P=0.011, n=49 crabs, N=196; see Table S2 for the results of GLMM

analysis). However, their response to the paired dummy (unlike the group of 'close' crabs) was between those to the single direct and single tangential dummy (Fig. 6C). The responses of the 'far' crabs to the paired dummy were not significantly different from those to either the single direct (Fig. 6C and Table 4, P=0.505, n=47 crabs, N=207) or the tangential dummy (Fig. 6C and Table 4, P=0.274, n=46 crabs, N=202). Similarly, when tested at each crab–dummy distance, there was no difference between the predicted and measured survival curves as indicated by Fisher's exact test (Fig. 6D).

DISCUSSION

We examined escape responses of fiddler crabs when the crabs were faced with two simultaneously approaching predators under naturalistic conditions in the field. The aim was to find out how crabs integrate the information from two unequal but simultaneous threats in order to decide whether and when to escape.

The results from single dummy approaches showed that both tangentially and directly approaching dummies were visible to the crabs and elicited escape responses (Fig. 4). The crabs responded earlier to the tangentially approaching dummy than to the directly approaching one. This is in agreement with several previous studies (e.g. Hemmi, 2005a, Hemmi and Pfeil, 2010). We have previously argued that this is because stimuli that directly approach the crabs produce less retinal motion initially, but eventually become more threatening because they approach closer and therefore appear bigger (Hemmi, 2005a; Hemmi, 2005b; Hemmi and Pfeil, 2010).

Surprisingly, however, we found that crabs that faced multiple predators simultaneously behaved as if they only faced the single, directly approaching predator and suppressed the normally earlier occurring response to the less threatening tangential one. This suggests that the crabs do not perceive, or do not respond to the increased risk of predation posed by two simultaneous predators. We found no indication that the crabs
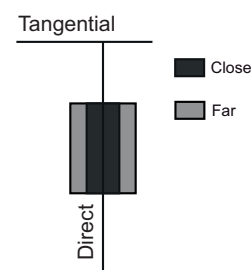
Fig. 5. Direct dummy track distances. Schematic diagram of how the crabs were divided into 'close' and 'far' groups based on their distance to the direct track (please note that this is only for illustration purposes and does not show real scaled distances).
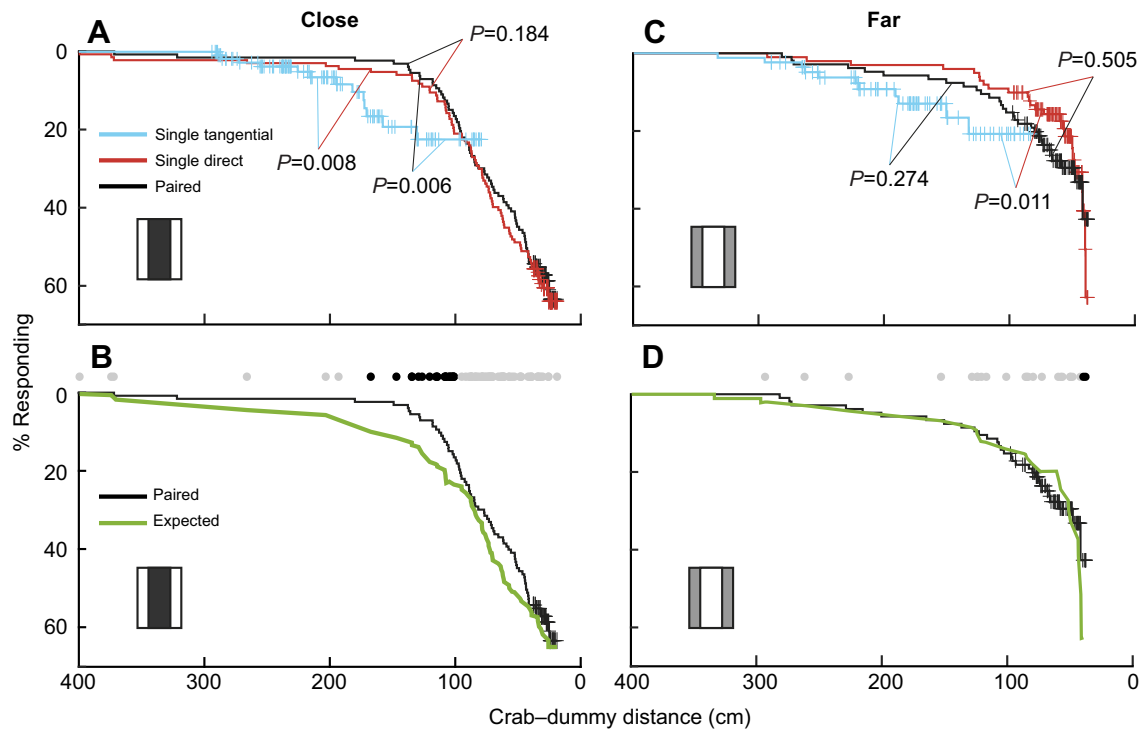
Fig. 6. Response to different treatments and expected response. (A) Responses of the crabs that were close to the direct track to different treatments were similar to responses of all crabs observed in Fig. 4A. (B) The calculated expected response to the paired dummy was significantly different from the actual response at crab–dummy distances between 170 and 100 cm. (C) Unlike the responses of the 'close' crabs to the paired dummy, those of the 'far' crabs were between the responses to the single direct and the single tangential dummies. (D) The calculated expected response to the paired dummies for the 'far' crabs provided a very close estimation of their actual response to the paired dummy. The black and grey dots above the graphs in B and D indicate at which crab–dummy distances the difference between the paired dummy and the expected response probability is significant and non-significant, respectively.

responded earlier or more often to two approaching dummies than to one (Fig. 4). This suggests there is no summation of the risk posed by multiple events.

A more in-depth analysis of our results suggests that when one dummy is perceived as being significantly more dangerous than the other, rather than summing the risks posed by the two dummies, the combined response probability is actually even less than expected had the crabs responded independently to the two dummies. Our calculation of the expected escape response (Figs 4B and 6B) showed that the crabs suppressed the early responses to the tangential dummy (Fig. 4B at 167–103 cm distance) and only responded to the more dangerous, directly approaching dummy. This suggests that when the crabs are presented with two threatening stimuli with different threat levels, they identify and respond to the more dangerous stimulus and suppress the response to the less threatening one. Interestingly, this was only true for those crabs that saw a clear difference between the direct and indirect dummies (Fig. 6). Crabs that were farther from

the direct dummy track did not suppress their response to the tangential dummy and responded independently to the two dummies (Fig. 6C,D). This suggests that these crabs were not able to clearly distinguish between the two dummies or assign the two dummies to different risk groups.

Our results indicate that fiddler crabs are capable of selective attention, which is the ability to respond selectively to only one stimulus among multiple alternatives (Treue, 2001; Yorzinski et al., 2013; Wiederman and O'Carroll, 2013; De Bivort and Van Swinderen, 2016; Lancer et al., 2019). Selective attention has been observed in a range of animal groups, including humans and other primates (Treue, 2001), birds (Yorzinski et al., 2013; Sridharan et al., 2014) and insects (Pollack, 1988; Rossel, 1996; Nityananda and Pattrick, 2013; Wiederman and O'Carroll, 2013; Paulk et al., 2014; De Bivort and Van Swinderen, 2016; Lancer et al., 2019) across a diversity of tasks such as mating, feeding and predation (Nityananda, 2016). A female cricket choosing between two male conspecifics (Pollack, 1988), a bee selecting among

Table 3. Results of the permutation test applied to the full Cox model for crabs that are close (<38 cm) to their direct dummy track

Comparison	N (n)	Model term	P
Direct versus tangential	259 (46)	**Experiment type**	0.008
		Crab-burrow distance	0.254
Direct versus paired	249 (45)	Experiment type	0.184
		Crab-burrow distance	0.654
Paired versus tangential	246 (46)	**Experiment type**	0.006
		Crab–burrow distance	0.465

Permutations were restricted to within crab to account for the repeated measures per crab. Terms included in the final model are shown in bold.

Table 4. Results of the permutation test applied to the full Cox model for crabs that are far (≥38 cm) from their direct dummy track

Comparison	N (n)	Model term	P
Direct versus tangential	196 (49)	**Experiment type**	0.011
		Crab–burrow distance	0.026
Direct versus paired	207 (47)	Experiment type	0.505
		Crab–burrow distance	0.029
Paired versus tangential	202 (46)	Experiment type	0.274
		Crab–burrow distance	0.031

Permutations were restricted to within crab to account for the repeated measures per crab. Terms included in the final model are shown in bold.

flowers (Nityananda and Pattrick, 2013) or dragonflies hunting a swarm of prey (Wiederman and O'Carroll, 2013) all use a selective attention mechanism to tackle similar problems.

Attention is a limited resource and even the most sophisticated neuronal systems have limited capacity to attend to multiple stimuli at a time (Alvarez and Franconeri, 2007). Animals, therefore, use a variety of cues including timing, depth, shape, colour, orientation or direction of movement of the stimuli to efficiently and effectively guide their attention.

Saliency, the quality of standing out from alternatives, is one of the strongest cues for guiding attention (Koch and Ullman, 1987; Li, 2002; Treue, 2003; Lancer et al., 2019). Our results suggest that fiddler crabs probably use a saliency-based attention mechanism, such as 'winner-takes-all' (Riesenhuber and Poggio, 1999; Yuille and Geiger, 1998; Maass, 2000a; Maass, 2000b) in their escape responses. However, if selective attention is solely based on saliency, then the animal might be distracted too frequently. In fact, if winner-takes-all was indeed the underlying mechanism, we would have expected the crabs to first respond to the dummy approaching tangentially before switching their attention to the direct one. The fact that this was not the case suggests that the crabs are perhaps capable of identifying the most dangerous dummy predator at the earliest stages of approach. The only physical difference between the two approaching dummies, however, is their approach trajectories. How the crabs are able to determine the approach trajectories and which visual cues they use to do so are still unclear. We have previously argued that the crabs should find this task really difficult (Hemmi, 2005b) because of their low spatial resolving power (Land and Layne, 1995; Zeil and Al-Mutairi, 1996; Smolka and Hemmi, 2009; Bagheri et al., 2020) and inability to gain distance information for objects that move above the horizon (Collett and Harkness, 1982; Zeil and Hemmi, 2006). The current experiments suggest that, if the movements are different enough, the crabs are able to distinguish between directly and tangentially approaching dummies very early on, when the direct and tangential dummies' angular sizes are only 1.15±0.33 and 0.78±0.10 deg (mean±s.d.), respectively. Further neuronal and behavioural experiments in more controlled experimental conditions will be required to identify how the crabs make this discrimination and what underlying mechanism guides selective attention in these animals.

Author Contributions
Conceptualization: Z.M.B., J.M.H.; Methodology: Z.M.B., J.M.H.; Formal analysis: Z.M.B., J.M.H.; Investigation: Z.M.B., C.G.D.; Writing - original draft: Z.M.B.; Writing - review & editing: Z.M.B., C.G.D., J.M.H.; Funding acquisition: J.M.H.

References
Alvarez, G. A. and Franconeri, S. L. (2007). How many objects can you track? Evidence for a resource-limited attentive tracking mechanism. *J. Vis.*, **7**, 14. doi:10.1167/7.13.14

Amo, L., López, P. and Martín, J. (2004). Multiple predators and conflicting refuge use in the wall lizard, Podarcis muralis. In *Annales Zoologici Fennici*, pp. 671-679. Finnish Zoological and Botanical Publishing Board.

Bagheri, Z. M., Jessop, A. L., Kato, S., Partridge, J. C., Shaw, J., Ogawa, Y. and Hemmi, J. M. (2020). A new method for mapping spatial resolution in compound eyes suggests two visual streaks in fiddler crabs. *J. Exp. Biol.* **223**, jeb210195. doi:10.1242/jeb.210195

Campbell, F. W. and Green, D. G. (1965). Optical and retinal factors affecting visual resolution. *J. Physiol.*, **181**, 576-593. doi:10.1113/jphysiol.1965.sp007784

Clinchy, M., Sheriff, M. J. and Zanette, L. Y. (2013). Predator–induced stress and the ecology of fear. *Funct. Ecol.*, **27**, 56-65. doi:10.1111/1365-2435.12007

Collett, D. (2015). *Modelling survival data in medical research*. Chapman and Hall/CRC.

Collett, T. S. and Harkness, L. I. K. (1982). Depth vision in animals. In *Analysis of Visual Behaviour* (ed. D. J. Ingle, M. A. Goodale and R. J. W. Mansfield), pp. 111-176. Cambridge, MA: MIT Press.

Cooper, W. E., Pérez-Mellado, V. and Hawlena, D. (2007). Number, speeds, and approach paths of predators affect escape behavior by the Balearic lizard, *Podarcis lilfordi*. *J. Herpetol.*, **41**, 197-205. doi:10.1670/0022-1511(2007)41[197:NSAAPO]2.0.CO;2

Creel, S. and Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends Ecol. Evol.*, **23**, 194-201. doi:10.1016/j.tree.2007.12.004

De Bivort, B. L. and Van Swinderen, B. (2016). Evidence for selective attention in the insect brain. *Curr. Opin. Insect Sci.*, **15**, 9-15. doi:10.1016/j.cois.2016.02.007

Dill, L. M. and Fraser, A. H. (1997). The worm re-turns: hiding behavior of a tube-dwelling marine polychaete, *Serpula vermicularis*. *Behav. Ecol.*, **8**, 186-193. doi:10.1093/beheco/8.2.186

Ens, B. J., Klaassen, M. and Zwarts, L. (1993). Flocking and feeding in the fiddler crab (*Uca tangeri*): prey availability as risk-taking behaviour. *Netherlands Journal of Sea Research*, **31**, 477-494. doi:10.1016/0077-7579(93)90060-6

Ferrari, M. C., Wisenden, B. D. and Chivers, D. P. (2010). Chemical ecology of predator–prey interactions in aquatic ecosystems: a review and prospectus. *Can. J. Zool.*, **88**, 698-724. doi:10.1139/Z10-029

Geist, C., Liao, J., Libby, S. and Blumstein, D. T. (2005). Does intruder group size and orientation affect flight initiation distance in birds?. *Anim. Biodivers. Conserv.*, **28**, 69-73.

Gursky-Doyen, S. and Nekaris, K. A. I. (eds.) (2007). *Primate Anti-Predator Strategies*. Springer Science and Business Media.

Hemmi, J. M. (2005a). Predator avoidance in fiddler crabs: 1. Escape decisions in relation to the risk of predation. *Anim. Behav.*, **69**, 603-614. doi:10.1016/j.anbehav.2004.06.018

Hemmi, J. M. (2005b). Predator avoidance in fiddler crabs: 2. The visual cues. *Anim. Behav.*, **69**, 615-625. doi:10.1016/j.anbehav.2004.06.019

Hemmi, J. M. and Pfeil, A. (2010). A multi-stage anti-predator response increases information on predation risk. *J. Exp. Biol.*, **213**, 1484-1489. doi:10.1242/jeb.039925

Hemmi, J. M. and Tomsic, D. (2015). Differences in the escape response of a grapsid crab in the field and in the laboratory. *J. Exp. Biol.*, **218**, 3499-3507. doi:10.1242/jeb.129072

Hugie, D. M. (2004). A waiting game between the black-bellied plover and its fiddler crab prey. *Anim. Behav.* **67**, 823-831. doi:10.1016/j.anbehav.2003.03.023

Humphreys, R. K. and Ruxton, G. D. (2018). A review of thanatosis (death feigning) as an anti-predator behaviour. *Behav. Ecol. Sociobiol.*, **72**, 22. doi:10.1007/s00265-017-2436-8

Iribarne, O. O. and Martinez, M. M. (1999). Predation on the southwestern Atlantic fiddler crab (*Uca uruguayensis*) by migratory shorebirds (*Pluvialis dominica*, *P. squatarola*, *Arenaria interpres*, and *Numenius phaeopus*). *Estuaries*, **22**, 47-54. doi:10.2307/1352926

Jennions, M.D., Backwell, P.R., Murai, M. and Christy, J. H. (2003). Hiding behaviour in fiddler crabs: how long should prey hide in response to a potential predator?. *Anim. Behav.* **66**, 251-257. doi:10.2307/1352926

Koch, C. and Ullman, S. (1987). Shifts in selective visual attention: towards the underlying neural circuitry. In *Matters of intelligence*, pp. 115-141. Dordrecht: Springer.

Kramer, D. L. and Bonenfant, M. (1997). Direction of predator approach and the decision to flee to a refuge. *Anim. Behav.*, **54**, 289-295. doi:10.1006/anbe.1996.0360

Lancer, B. H., Evans, B. J., Fabian, J. M., O'Carroll, D. C. and Wiederman, S. D. (2019). A Target-Detecting Visual Neuron in the Dragonfly Locks on to Selectively Attended Targets. *J. Neurosci.*, **39**, 8497-8509. doi:10.1523/JNEUROSCI.1431-19.2019

Land, M. F. and Layne, J. E. (1995). The visual control of behaviour in fiddler crabs. I. Resolution, thresholds and the role of the horizon. *J. Comp. Physiol. A*, **177**, 81-90. doi:10.1007/BF00243400

Layne, J. E. (1998). Retinal location is the key to identifying predators in fiddler crabs (*Uca pugilator*). *J. Exp. Biol.*, **201**, 2253-2261.

Layne, J., Land, M. and Zeil, J. (1997). Fiddler crabs use the visual horizon to distinguish predators from conspecifics: a review of the evidence. *J. Mar. Biol. Assoc. U. K.*, **77**, 43-54. doi:10.1017/S0025315400033774

Li, Z. (2002). A saliency map in primary visual cortex. *Trends Cogn. Sci.*, **6**, 9-16. doi:10.1016/S1364-6613(00)01817-9

Lima, S. L. (1998). Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*, **48**, 25-34. doi:10.2307/1313225

Lima, S. L. and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**, 619-640. doi:10.1139/z90-092

Maass, W. (2000a). On the computational power of winner-take-all. *Neural Comput.*, **12**, 2519-2535. doi:10.1162/089976600300014827

Maass, W. (2000b). Neural computation with winner-take-all as the only nonlinear operation. In *Advances in Neural Information Processing Systems*, pp. 293-299. MIT Press.

Martín, J. and López, P. (1999). When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. *Behav. Ecol.*, **10**, 487-492. doi:10.1093/beheco/10.5.487

McIntosh, A. R. and Peckarsky, B. L. (1999). Criteria determining behavioural responses to multiple predators by a stream mayfly. *Oikos*, **85**, 554-564. doi:10.2307/3546705

Nalbach, H. O. (1990). Visually elicited escape in crabs. In *Frontiers in crustacean neurobiology*, pp. 165-172. Basel: Birkhäuser.

Nityananda, V. (2016). Attention-like processes in insects. *Proc. R. Soc. B*, **283**, 20161986. doi:10.1098/rspb.2016.1986

Nityananda, V. and Pattrick, J. G. (2013). Bumblebee visual search for multiple learned target types. *J. Exp. Biol.*, **216**, 4154-4160. doi:10.1242/jeb.085456

Paulk, A. C., Stacey, J. A., Pearson, T. W., Taylor, G. J., Moore, R. J., Srinivasan, M. V. and Van Swinderen, B. (2014). Selective attention in the honeybee optic lobes precedes behavioral choices. *Proc. Natl Acad. Sci. USA*, **111**, 5006-5011. doi:10.1073/pnas.1323297111

Pollack, G. S. (1988). Selective attention in an insect auditory neuron. *J. Neurosci.*, **8**, 2635-2639. doi:10.1523/JNEUROSCI.08-07-02635.1988

Preisser, E. L., Bolnick, D. I. and Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, **86**, 501-509. doi:10.1890/04-0719

Riesenhuber, M. and Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nat. Neurosci.*, **2**, 1019-1025. doi:10.1038/14819

Rossel, S. (1996). Binocular vision in insects: How mantids solve the correspondence problem. *Proc. Natl Acad. Sci. USA*, **93**, 13229-13232. doi:10.1073/pnas.93.23.13229

Sih, A. (1987). Predators and prey lifestyles: an evolutionary and ecological overview. In *Predation: Direct and Indirect Impacts on Aquatic Communities* (ed. W. C. Kerfoot and A. Sih). Wiley.

Sih, A. (1994). Predation risk and the evolutionary ecology of reproductive behaviour. *J. Fish Biol.*, **45**, 111-130. doi:10.1111/j.1095-8649.1994.tb01087.x

Sih, A. (1997). To hide or not to hide? Refuge use in a fluctuating environment. *Trends Ecol. Evol.*, **12**, 375-376. doi:10.1016/S0169-5347(97)87376-4

Sih, A., Krupa, J. and Travers, S. (1990). An experimental study on the effects of predation risk and feeding regime on the mating behavior of the water strider. *Am. Nat.*, **135**, 284-290. doi:10.1086/285044

Smolka, J. and Hemmi, J. M. (2009). Topography of vision and behaviour. *J. Exp. Biol.*, **212**, 3522-3532. doi:10.1242/jeb.032359

Smolka, J., Zeil, J. and Hemmi, J. M. (2011). Natural visual cues eliciting predator avoidance in fiddler crabs. *Proc. R. Soc. B*, **278**, 3584-3592. doi:10.1098/rspb.2010.2746

Smolka, J., Raderschall, C. A. and Hemmi, J. M. (2013). Flicker is part of a multi-cue response criterion in fiddler crab predator avoidance. *J. Exp. Biol.*, **216**, 1219-1224. doi:10.1242/jeb.076133

Sridharan, D., Schwarz, J. S. and Knudsen, E. I. (2014). Selective attention in birds. *Curr. Biol.*, **24**, R510-R513. doi:10.1016/j.cub.2013.12.046

Treue, S. (2001). Neural correlates of attention in primate visual cortex. *Trends Neurosci.*, **24**, 295-300. doi:10.1016/S0166-2236(00)01814-2

Treue, S. (2003). Visual attention: the where, what, how and why of saliency. *Curr. Opin. Neurobiol.*, **13**, 428-432. doi:10.1016/S0959-4388(03)00105-3

Wiederman, S. D. and O'Carroll, D. C. (2013). Selective attention in an insect visual neuron. *Curr. Biol.*, **23**, 156-161. doi:10.1016/j.cub.2012.11.048

Yager, D. D. (2012). Predator detection and evasion by flying insects. *Curr. Opin. Neurobiol.*, **22**, 201-207. doi:10.1016/j.conb.2011.12.011

Ydenberg, R. C. and Dill, L. M. (1986). The economics of fleeing from predators. In *Advances in the Study of Behavior*, vol. 16, pp. 229-249. Academic Press.

Yorzinski, J. L., Patricelli, G. L., Babcock, J. S., Pearson, J. M. and Platt, M. L. (2013). Through their eyes: selective attention in peahens during courtship. *J. Exp. Biol.*, **216**, 3035-3046. doi:10.1242/jeb.087338

Yuille, A. L. and Geiger, D. (1998). Winner-take-all mechanisms. In *The Handbook of Brain Theory and Neural Networks*, pp. 1056-1060. MIT Press.

Zeil, J. and Al-Mutairi, M. (1996). The variation of resolution and of ommatidial dimensions in the compound eyes of the fiddler crab *Uca lactea annulipes* (Ocypodidae, Brachyura, Decapoda). *J. Exp. Biol.*, **199**, 1569-1577.

Zeil, J. and Hemmi, J. M. (2006). The visual ecology of fiddler crabs. *Journal of Comparative Physiology A*, **192**, 1-25. doi:10.1007/s00359-005-0048-7

Zwarts, L. (1985). The winter exploitation of fiddler crabs *Uca tangeri* by waders of Guinea Bissau. *Ardea*, **73**, 3-12.
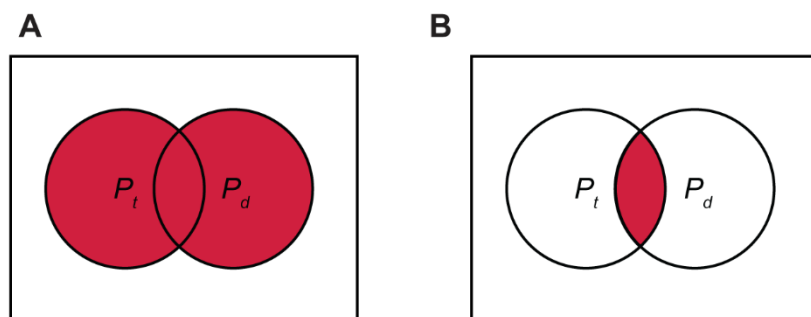
A   **B**

Figure S1. Venn diagrams. Venn diagrams illustrate A) probability of the expected combined response $P(P_d \cup P_t)$ and B) the probability of the crabs that responded to both the direct and the tangential dummy $P(D_d \cap D_t)$ which used in Eq. 1.

Table S1. Results of the generalized linear mixed model analyses for response probability for crabs that are close (< 38 cm) to their direct dummy track (random model: crab identity). Terms included in the final model are shown in bold.

Comparison	*N (n)*	Fixed effects (x_i)	Estimate	d.f	Loglik	*P*
Direct vs Tangential	259(46)	Intercept	-1.103	1	-	-
		Experiment Type	1.79 (direct)	1	45.26	<0.001
		Crab-burrow distance	-	1	1.47	0.186
Direct vs paired	249(45)	Intercept	0.927	1	-	-
		Experiment Type	-	1	0.13	0.613
		Crab-burrow distance	-	1	0.620	0.266
Paired vs Tangential	246(46)	Intercept	-0.929	1	-	-
		Experiment Type	1.98 (paired)	1	47.570	<0.001
		Crab-burrow distance	-	1	0.04	0.613

Table S2. Results of the generalized linear mixed model analyses for response probability for crabs that are far (≥38 cm) from their direct dummy track. Random model: crab identity. Terms included in the final model are shown in bold.

Comparison	*N (n)*	Fixed effects[b] (x_i)	Estimate	d.f	Loglik	*P*
Direct vs Tangential	196(49)	Intercept	-1.7665	1	-	-
		Experiment Type	0.56 (direct)	1	3.6480	0.007
		Crab-burrow distance	-	1	0.1130	0.0536
Direct vs paired	207(47)	Intercept	-1.33	1	-	-
		Experiment Type	-	1	0.660	0.248
		Crab-burrow distance	-	1	1.89	0.051
Paired vs Tangential	202(46)	Intercept	-2.40	1	-	-
		Experiment Type	0.68 (paired)	1	5.70	<0.001
		Crab-burrow distance	0.006	1	1.970	0.047