

SIGNALS FROM ‘CRABWORLD’: CUTICULAR REFLECTIONS IN A FIDDLER CRAB COLONY

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Summary

Fiddler crabs inhabit intertidal sand- and mudflats, where they live in dense colonies and are active on the surface during low tide. They exhibit a rich behavioural repertoire, with frequent interactions between animals in the context of territorial and mating activities. Male fiddler crabs have one massively enlarged and conspicuously coloured claw, which they use in waving displays and in fights with other males. The crabs carry their eyes on long, vertically oriented stalks high above the body and, as a consequence, see the bodies of conspecifics in the ventral visual field, below the local visual horizon, and against the mudflat surface as background. We filmed events in a colony of *Uca vomeris* with a normal video camera and an ultraviolet-sensitive camera placed at the eye height of an average crab, approximately 2–3 cm above ground. We also used a spectrographic imager and linear polarized filters to analyse the cues potentially available to the animals for detecting, monitoring and possibly identifying each other. Areas of high contrast in

mudflat scenes include specular reflections on the wet cuticle of crabs that are horizontally polarised. Besides specular reflections, some parts of the cuticle generate high-contrast signals against the mudflat background, both at wavelengths between 400 and 700 nm, and in the ultraviolet region between 300 and 400 nm. *Uca vomeris* can be very colourful: the different parts of the large claw of the male are white, orange or red. The carapace colours of both males and females can range from a mottled yellowish green brown, to a brilliant light blue. White and blue colours contrast starkly with the mudflat background, especially in the ultraviolet wavelengths. Under stress, the blue and white colours can change within minutes to a duller and darker blue or to a dull white.

Key words: Fiddler crab, *Uca vomeris*, specular reflection, polarization reflection, cuticle colour, colour change.

Introduction

Fiddler crabs live in a highly structured visual world: they operate on the mudflat surface during low tide and carry their eyes on long vertical stalks, so that the local visual horizon becomes a reliable and simple discriminator between objects higher (larger) and objects lower (smaller) than the crabs' own eye height. For social interactions, the geometry of vision in a flat world ensures that for most crabs – with the exception of very small and young ones – the bodies of other crabs are always seen below the line of the horizon (see Fig. 1). The crabs can thus rely on a predictable topography of vision and discriminate predators from conspecifics by simply determining whether something appears above or below the local visual horizon (Zeil et al., 1986; Zeil et al., 1989; Land and Layne, 1995a; Layne et al., 1997; Layne, 1998). Interestingly, as has been pointed out (Christy, 1995; Land and Layne, 1995a), the waving displays of males, which involve vertical movements of the males' massively enlarged claw, violate this neat distinction between the ventral visual field,

concerned with social information, and the dorsal visual field, concerned with information on orientation (Altevogt and von Hagen, 1964; Korte, 1965), on optic flow (Kunze, 1963; Nalbach and Nalbach, 1987), and on predators (Layne, 1998). In both hemispheres, fiddler crabs are known to, or are likely to, use image motion (von Hagen, 1962; Land and Layne, 1995b; Zeil and Zanker, 1997), retinal size and position (von Hagen, 1962; Land and Layne, 1995a; Land and Layne, 1995b; Backwell and Passmore, 1996; Jennions and Backwell, 1996), object shape (von Hagen, 1962; Langdon and Herrnkind, 1985) and possibly also colour (von Hagen, 1970; Hyatt, 1975; but, for a contrasting view, see Altevogt, 1959) to detect and identify both predators and conspecifics and to decide whether they need attending to or not.

In this paper, we ask what visual cues are available to a crab in a fiddler crab colony to detect and identify other crabs on the mudflat surface. The question arises because the crabs live in dense colonies in which they interact in surprisingly

complex ways (e.g. Land and Layne, 1995b; Zeil and Layne, 2001), and in which there are many situations when crabs may or may not want to be seen by conspecifics. As a first attempt to establish an inventory of social visual tasks, there are at least three situations in the life of a fiddler crab in which detecting, identifying, monitoring or assessing other crabs would seem to be crucial.

First, in mating and territorial interactions, males need to be able to detect either resident or wandering females, and males that are too close to their sphere of influence. Fiddler crabs are known to have two basic mating systems (Christy and Salmon, 1984; Christy and Salmon, 1991). In the first type, which is prevalent in our study animal, *Uca vomeris*, males need to detect resident females and to track them back to their burrows, where courtship and mating take place (Salmon, 1984). In the second principal mating system, receptive females wander through the colony and males need to attract them to their own burrows for mating. At present, we have no idea whether there is any pressure on males to maximise the distance at which they can detect females or discriminate them from males. In both mating systems, this will depend on the activity range of males, which in both situations is likely to be limited by constraints imposed by the homing system, which has been shown to rely exclusively on path integration (Zeil, 1998; Zeil and Layne, 2001). We are equally ignorant about what visual tasks female fiddler crabs are confronted with in the context of mating interactions. We do not know, for instance, to what degree females attract males by signalling in those mating systems in which courtship and mating occurs at the surface in the entrance of the female burrow. In the mating systems in which mating occurs underground in male burrows, wandering females do react to waving males and possibly choose by size and/or other cues which male to follow (Backwell and Passmore, 1996; Jennions and Backwell, 1996). It would seem that, in both mating systems, both males and females need to distinguish between the sexes, possibly by noting the presence or absence of an enlarged claw (von Hagen, 1962; von Hagen, 1970; Salmon and Stout, 1962; Land and Layne, 1995a).

A second context in which both male and female fiddler crabs need to be sensitive to the presence of other crabs is in burrow surveillance (Zeil and Layne, 2001). The burrow is a valuable resource for fiddler crabs and they have to worry continuously about defending it against burrow snatchers. Depending on their size, the crabs cease to see the entrance to their burrows after having moved away from it by approximately 10–20 cm during a foraging excursion, as corrective manoeuvres during homing and burrow closure experiments show (Zeil, 1998; Zeil and Layne, 2001). Burrow owners, nevertheless, are very sensitive to other crabs approaching their burrow even if their foraging excursions have led them away from home for quite large distances (possibly up to 1 m). In response to other crabs approaching their (not visible) burrow, the crabs rush back to defend it. In this particular context there indeed appears to be pressure on maximising the distance at which other crabs can be detected, but not necessarily discriminated.

Third, fiddler crab colonies are dynamic societies. Burrow ownership is hotly contested and male crabs especially are repeatedly challenged by neighbours or immigrants and may lose the resulting contests. Crabs that have been evicted from their burrows or that have decided to leave their burrow for other reasons wander through the colony in search of a new home. Wandering crabs are more vulnerable to bird predation and are probably the main target for predatory birds (e.g. Ens et al., 1993; Land, 1999). Wanderers protect themselves by approaching burrow owners, which react by retreating to their burrows. Wanderers track retreating burrow owners back to their burrows and, despite being chased away, attach themselves to these foreign burrows by starting path integration at some point during the interaction when they have come sufficiently close to the foreign burrow. The rationale behind this behaviour is that, in moments of danger, both burrow owner and wanderer take cover in the same burrow (Zeil and Layne, 2001). As in burrow surveillance, there appears to be pressure on wandering crabs to maximise the distance at which they can detect burrow owners. It may also pay them to be able to judge whether another crab is relatively larger or smaller than themselves. Since burrow owners always try to chase a wanderer away, interactions with equally sized or smaller crabs may be safer, although approaching very much smaller crabs may also be dangerous because their narrow burrows do not offer protection.

What then, in the visual world of a fiddler crab, identifies another crab? On the most elementary level, the answer is: anything that moves in the ventral visual field and that has a minimum angular size of 2–4° (Land and Layne, 1995a). Although feeding crabs on the surface are slowly moving or still, they do produce a variety of motion signals by the movements of their feeding claws, by locomotion and by the waving displays of both males and females (e.g. von Hagen, 1993; Zeil and Zanker, 1997). Since motion detection relies on correlated changes in light intensity in neighbouring photoreceptors, a prerequisite for detecting image motion is the ability to detect differences in luminance. Image motion may not always allow a crab to distinguish conspecifics from other sympatric animal species, such as the much larger *Macrophthalmus* sp. crabs or mudskippers. Beside luminance contrast and motion patterns, colour and polarisation contrast may provide important cues for the presence of a conspecific crab. To explore these possibilities, we provide here a first survey of cuticular reflections as they occur in colonies of *Uca vomeris* and examine what relevance they may have both for intra-specific detection, monitoring and signalling and in the context of predation.

Materials and methods

The study was carried out during September/October in several colonies of *Uca vomeris* (McNeill) (Ocypodidae, Brachyura, Decapoda) in the mudflats off Cunggulla, a small settlement at the shores of Bowling Green Bay, south of Townsville, Queensland, Australia (approximately 19° 25.6' latitude, 147° 6.9' longitude).

Video footage was recorded with a Sony DCR-TRV110E digital camcorder and a Hamamatsu ultraviolet-sensitive camera (Beam Finder III, C5332 series), the latter being equipped with a filter combination that passed ultraviolet from 300–400 nm only (Oriel No. 51720 and No. 51124). See Fig. 3D for the spectral sensitivity of the camera, with and without filters. To determine, when required, the angular size of the camera image and to ensure that the cameras were placed at crab eye height, we filmed a vertical scale bar at a defined distance away from the camera that carried a marker at a defined height above the ground. The height of the camera was then adjusted such that the marker was aligned with the visual horizon line, indicating that the height of the camera lens corresponded exactly to the height of the marker.

To determine spectral and polarization reflectances, we scanned crabs with a spectrographic imager (CASI, ITRES Canada), equipped with lenses with either 13.9° or 37.5° field of view, which could be fitted with a polariser. The CASI (compact airborne spectrographic imager) is a CCD-based, push-broom imager in which the image of a scene is focused by the objective lens onto a slit. Light exiting from the slit is collimated and meets a reflection diffraction grating. The spectrally dispersed light is refocused onto a CCD, such that consecutive 2 nm wide spectral bands are imaged onto neighbouring rows. The CASI is calibrated in several steps, using a luminance standard (model LS-65-8D Rev. B; Hofmann Engineering Corporation, Stamford, USA), and a suite of spectrum lamps (helium, hydrogen, mercury and oxygen). The calibration involves tests for accurate alignment and positions of spectral bands on the CCD, the determination of noise floor and system gain, the correction for pixel-to-pixel variations in the CCD, for vignetting, for slit irregularities, for spectral transmittance and for entrance port reflections. The calibration results in radiant sensitivity coefficient matrices, which contain the calibration values for each CCD pixel.

The raw data were stored on tape and resulted, after radiometrical calibration, in a series of single-waveband images with pixel values in units of $\mu\text{W s}^{-1}\text{sr}^{-1}\text{cm}^{-2}\text{nm}^{-1}$. For most purposes, we transformed the images to units of photons $\text{degrees}^{-2}\text{s}^{-1}\text{nm}^{-1}$. Downstream processing was performed using ENVI software, the IDL programming language (Research Systems, Colorado, USA) or Matlab (Mathworks, Natick, USA).

Results

The mudflat background

At first glance, the mudflat background against which fiddler crabs see each other is

rather dull and simple compared with other natural scenes (see Fig. 1). There is little colour variation, and the surface can be as smooth as few other surfaces in nature. In most cases, however, the surface is corrugated, through wave action, through the digging activities of fish and large swimming crabs during high tide and through the excavation and feeding deposits that the crabs themselves produce during their activity on the surface. The mudflat background, as seen from the viewpoint of a fiddler crab, can thus be visually highly structured and quite 'noisy' with respect to the task of detecting the presence of other crabs. The problem of detecting other crabs becomes particularly severe at viewing directions towards the sun (e.g. between 250° and 360° azimuth in Fig. 1), since it is here that the appearance of the wet and corrugated surface is characterised by specular reflections and shadows.

The signals

The most conspicuous signals we can identify in images taken from the viewpoint of a fiddler crab are the specular reflections returned by the smooth and wet cuticles of other crabs. The contrast of the signals generated by these specular reflections is enhanced by the fact that the ventral side of crabs

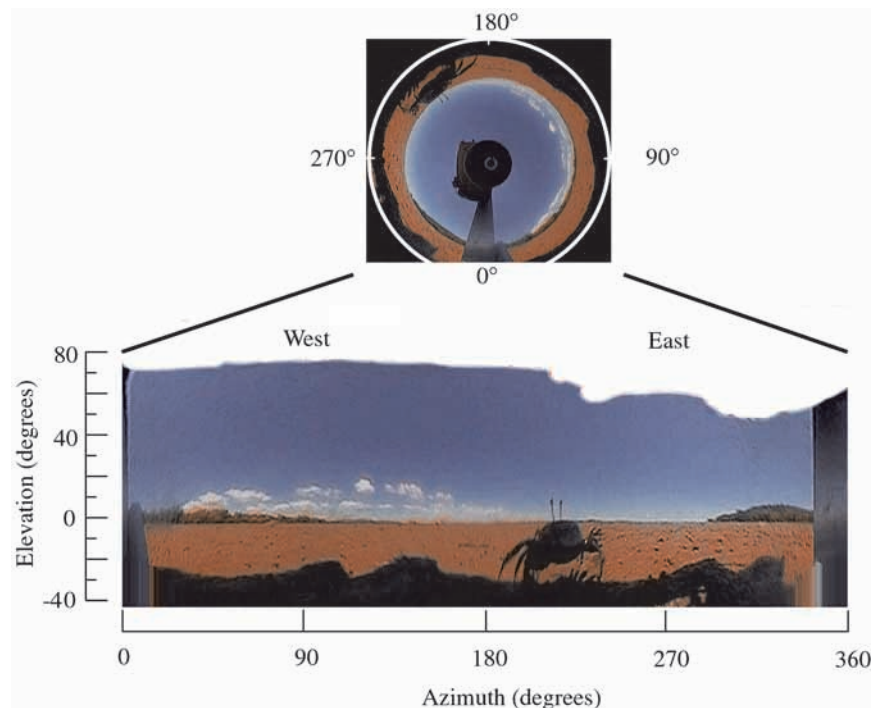


Fig. 1. A panoramic view of a mudflat scene. The image was recorded by pointing a video camera downwards onto a panoramic imaging surface (top; Chahl and Srinivasan, 1997) and by subsequently unwarping the image to generate a 360° flattened representation of the scene, which covers approximately 120° in elevation (bottom). The visual axis of the panoramic camera image was approximately 2 cm above ground. Note the distinct topography of 'crabworld', with the line of the horizon dividing the visual field into two hemispheres, and that the bodies of other crabs appear exclusively in the ventral visual field. The image was taken at 10.00 h and the mudflat surface appears more corrugated at viewing directions towards East because specular reflections and shadows are more prevalent when viewed against the sun.

is always in shadow and that the crabs themselves throw shadows onto the substratum. Viewed from the 'cockpit' of a crab observer, other crabs appear as strong biphasic signals, with a dorsal component brighter than the background and a ventral component darker than the background (see transects on the right in Fig. 2). Depending on the distance at which a crab is seen, these effects can become irrelevant to a crab observer as a result of the low-pass-filtering properties of the crab eye optics (compare left-hand transects in Fig. 2).

The mudflat background is rather dark and uniform in the ultraviolet wavelengths. Specular reflections and the bright parts of the cuticle of the crabs are thus particularly pronounced in the short-wavelength part of the spectrum, as can be seen from the horizontal and vertical transects through a series of ultraviolet images in Fig. 3. The coloured lines in Fig. 3B,C show the transects for the image shown in Fig. 3A, in which the transect locations are indicated by equivalently coloured lines. Transects are expressed as normalized contrast, which is defined as $c(x,y)=(L(x,y)/L_{av})-1$, where $L(x,y)$ is the luminance at image position xy and L_{av} the mean luminance of the whole ensemble of transects (see Pelli, 1990). Specular reflections and the brightly coloured patches on the carapace and the claws of crabs generate contrast values of 1 to 1.5 in the ultraviolet region of the spectrum.

Since specular reflections are horizontally polarized, they are much more conspicuous when seen through a horizontal (Fig. 4 left), than through a vertical (Fig. 4 right) polarizer. The panels below the images in Fig. 4 show the spectral reflectances of three selected points on the crab's cuticle (labelled 1–3) as measured through the horizontal (red) and the vertical (green) polarizer. The ratios of horizontal to vertical reflectances are given in the bottom panels (blue lines). Specular reflections can be distinguished from surfaces that are simply bright by virtue of the fact that they are polarized: the reflectance of the posterior surface of the male's dactyl (the upper part of his enlarged claw) is virtually the same when measured through a horizontal or a vertical polarizer (grey and black lines in the centre panel in Fig. 4; the locations of measurements are indicated by circles in the images). The degree of polarization reflection depends on the wetness of the surface, so that reflections are reduced in intensity when the cuticle is dry. As a consequence, crabs that have recently emerged from their burrows where they have had access to ground water, such as the crab on the right in the images shown in Fig. 2, are much more conspicuous than crabs that have been operating on the surface for some time. Specular reflections are likely to be weaker when the sky is overcast. At the moment, we are not in the position to decide whether the fiddler crab cuticle itself has polarizing properties, as has been shown for

some parts of the bodies of crayfish and mantis shrimps (Neville and Luke, 1971; Marshall et al., 1999).

Specular and polarization reflections are properties of any wet and smooth surface, and would not therefore serve to distinguish different sympatric species of crabs (or fish) that are active on the mudflat surface. It is significant, therefore, that fiddler crabs are very colourful. Although the colours are highly variable within a given species, they are routinely used as taxonomic features (e.g. von Hagen, 1968; Crane, 1975; George and Jones, 1982). In *Uca vomeris*, the large claw of males is pink to brilliantly white on top, i.e. on the dorsal side of the manus and throughout the dactyl, while the ventral part, including the manus and the pollex, is orange to deep red (Fig. 5). The front of both males and females can become white, depending on the territorial and mating status and on the time in the activity cycle (e.g. Crane, 1975). As shown by the ultraviolet images on the right in Fig. 5, the white and blue parts of fiddler crab cuticle are highly reflective in the ultraviolet region of the spectrum.

The most noticeable differences between individuals, between crabs in neighbouring colonies and from one time to another in the same individual crab are, however, seen in the colours of the posterior carapace (Fig. 6). In *Uca vomeris*, the colours of the carapace can vary in both males and females between a mottled green-yellowish colour, through some dark blue spots, to brilliant light blue or white patches of various shapes and sizes on a dark brown-black carapace. To the human eye, the mottled carapace contains small spots of blue, green, yellow and red (see spectra in Fig. 6C), which when averaged (thick grey line in Fig. 6C) appear to be designed to

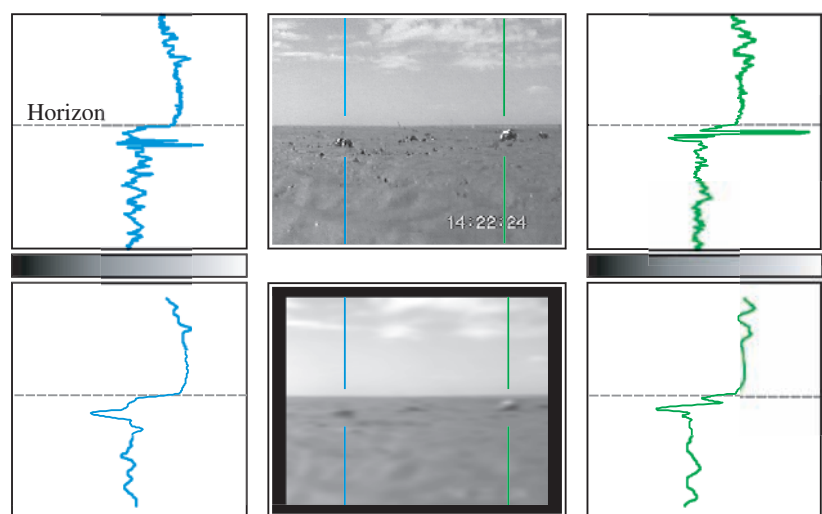


Fig. 2. A view into 'crabworld' at normal video resolution (top) and at the spatial resolution of a fiddler crab eye (bottom). Diagrams on the left and right show transects through the images in the centre at the image positions marked by blue and green lines, demonstrating the signals generated by specular reflections from the crabs' wet cuticle and by the shadows associated with the ventral sides of crabs on the mudflat surface. The position of the horizon is marked by grey dashed lines. Note that the low-pass filtering of the crabs' optics and sampling array can eliminate the strong signals generated by small specular reflections through local averaging (bottom left). For technical details of filtering, see Zeil and Zanker, 1997.

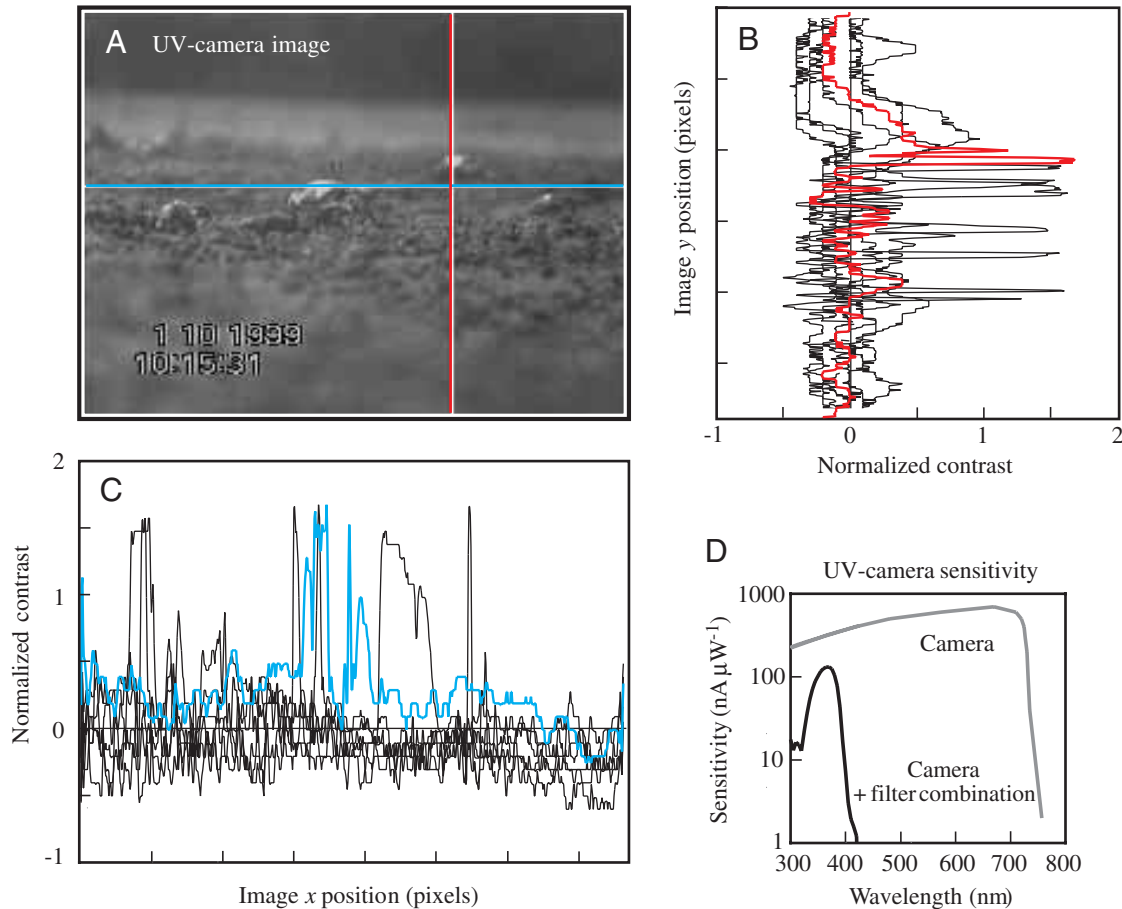


Fig. 3. The appearance of specular reflections in ultraviolet images. Video images were recorded with an ultraviolet-sensitive camera equipped with a filter combination that eliminated the long-wavelength sensitivity of the camera (see D for the sensitivity of the camera with and without the filter combination). The blue line (C) and the red line (B) show the horizontal and the vertical transects, respectively, which are indicated by a blue and a red line in the ultraviolet camera image (A). Horizontal and vertical transects through a number of similar ultraviolet images are shown as black lines in B and C, respectively. The transect values are in units of normalized contrast, which is defined as $c(x,y) = (L(x,y)/L_{av}) - 1$, where $L(x,y)$ is the luminance at image position xy and L_{av} the mean luminance of the whole ensemble of transects (e.g. Pelli, 1990).

match the colour of the mudflat background (thick black line in Fig. 6C, Fig. 7E). The blue and white patches, in contrast, provide strong signals, as shown in the form of the spectrum in Fig. 6D for the blue patches of a male crab and in the form of the normalized spectral contrast with the average mudflat background for the white front, the blue back and the orange claw for a female in Fig. 7C. The properties of the blue and white carapace colours therefore indicate a function in signalling, a conjecture that is further supported by the observation that these bright patches can change their colour rapidly. When a crab is being caught and handled, for instance, the bright blue colours on the back of the carapace, and also the white fronts, can change to dull dark blue or dull white within minutes. These rapid colour changes are shown in Fig. 7A from the approximate viewpoint of a conspecific, for different locations on the anterior (left) and posterior (right) carapace of a female *U. vomeris*. In Fig. 7B, thick lines show the reflectance shortly after capture and thin lines the reflectance 15 min later for four locations (marked by equivalently coloured circles in Fig. 7A) on the anterior

(Fig. 7Bi,iii) and posterior (Fig. 7Bii,iv) carapace. The colour changes markedly reduce the contrast with the mudflat background (compare the normalized contrast characteristics in Fig. 7C,D), the average spectrum of which is shown in Fig. 7E. These effects cannot be explained by changes in illumination, since the colour changes occurring within 15 min were much larger than the changes in incident luminance during the same period. This is documented for the scans of the posterior carapace in Fig. 7F, which show the ratio of the light reflected from the crab's blue patches together with the ratio of incident illumination during the first and the second scan.

Discussion

We have shown that the cuticle of crabs presents quite a strong contrast against the mudflat background, by being wet, smooth and coloured. In addition, the crabs can vary their cuticular colours over a surprisingly short time scale. Even some of the physical properties of fiddler crab cuticle may be manipulated by the crabs. Crabs appear from their burrows wet

and shiny, but quickly lose water when operating on the surface through evaporation and through its use in filter-feeding. The water is regularly replenished during returns to the burrow and by sucking up interstitial water, indicating that the crabs can, in principle, control how shiny they will appear to other crabs, since the state of wetness will affect the level of specular reflections and the polarization characteristics of the crabs' cuticle. Despite the access they have to interstitial water, individuals that wander through a colony of fiddler crabs in search of a new home or that have been on the surface for some time are very often rather dry, and consequently appear dull, because they have not had the opportunity to enter a burrow, or to collect interstitial water to replenish their water supply. Therefore, specular reflections not only signify the presence of a crab but may be much more informative: they may indicate that a crab has access to ground water and is therefore a resident and not a wanderer.

The second property of their cuticle that fiddler crabs are able to control is the state of their chromophores, and with this the colour they present to an observer. There are several time scales over which these changes can occur. It has long been noted that the colours of crabs wax and wane following an endogenous rhythm that tracks the local tidal movements in their habitat (for reviews, see Thurman, 1988; Palmer, 1995). There are also indications that cuticle colours in fiddlers change depending on the mating status of crabs, on the level of stress and possibly on local diet (e.g. Crane, 1975; Wolfrath, 1993; Shih et al., 1999). We have shown here that, in *Uca vomeris*, these changes can occur within minutes (Fig. 7), suggesting that they are subtle indicators of a crab's general state, but also that the crabs may be able to adjust their visibility to predatory birds or conspecifics.

The functional significance of these variable cuticle colours in fiddler crabs is largely unresolved, but must be influenced both by their role as intraspecific signalling and by the effect they have in making the crabs more detectable to predatory birds. Cuticle colours are likely to serve a multitude of functions, ranging from temperature control, through camouflage directed at predators and/or conspecifics, species recognition to intraspecific signalling for detectability, identity, status in the mating cycle, territorial status and, possibly, also for the state of fitness or quality. Despite the fact that fiddler crab

colour changes have attracted scientific attention for over 100 years (for reviews, see Rao, 1985; Thurman, 1988), surprisingly little is known about their functional roles in the natural habitat and in the social life of these crabs (e.g. von Hagen, 1962; von Hagen, 1970; Crane, 1975; Wolfrath, 1993; Shih et al., 1999).

For *Uca vomeris*, it is striking to note that the colours differ depending on whether they are presented frontally or on the posterior part of the carapace: in the front, the colours are predominantly white and red, while on the back they are blue or white in the most colourful state an animal can reach (Fig. 7). Compared with its appearance at long wavelengths, the mudflat is rather dark and homogeneous at short wavelengths, so that a blue signal will be quite conspicuous when seen by birds or by conspecifics against this background (Fig. 7C). It will also predominantly stimulate a hypothetical short wavelength pigment of the crab eye (see below). The white colours that the crabs present with their claws and their

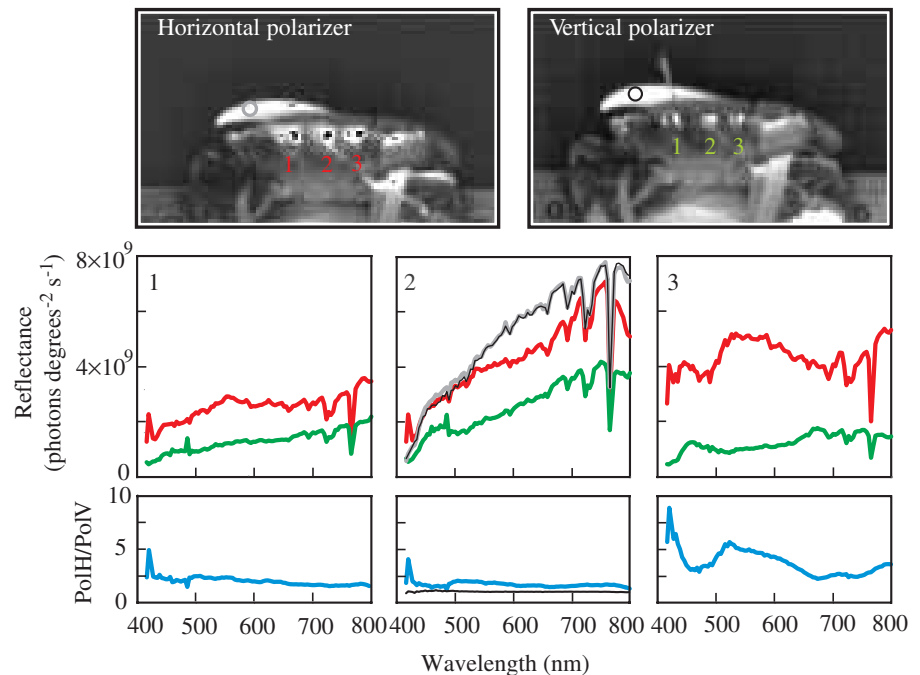


Fig. 4. The polarization and spectral characteristics of specular reflections from fiddler crab cuticle. The false colour images (top) were generated from hyperspectral scans with a spectrographic imager by assigning the scans at wavelengths of 453 nm, 569 nm and 683 nm to the blue, green and red channels of the image, respectively. The left image was recorded through a horizontal polarizer and the right-hand image through a vertical polarizer. The middle diagrams show the reflectance of three specular spots (labelled 1–3) on the carapace of the crab through the horizontal polarizer (red) and the vertical polarizer (green), in units of photons degrees⁻² s⁻¹, against wavelength. Included in panel 2 are the reflectance measurements of the posterior dactyl of the male's claw in grey (horizontal polarizer) and in black (vertical polarizer). Points of measurement are indicated by circles in the top images. The bottom diagrams show the ratio between the spectral reflectances through the horizontal and vertical polarizers (PoH/PoV), demonstrating that horizontally polarized specular reflections are 2–8 times more intense than vertically polarized reflections. The spectral characteristics of the three areas with specular reflections are quite different because the measurements were taken slightly off centre from the spots to avoid the locations of strongest specular reflections where the sensor saturated (black spots in the left-hand image).

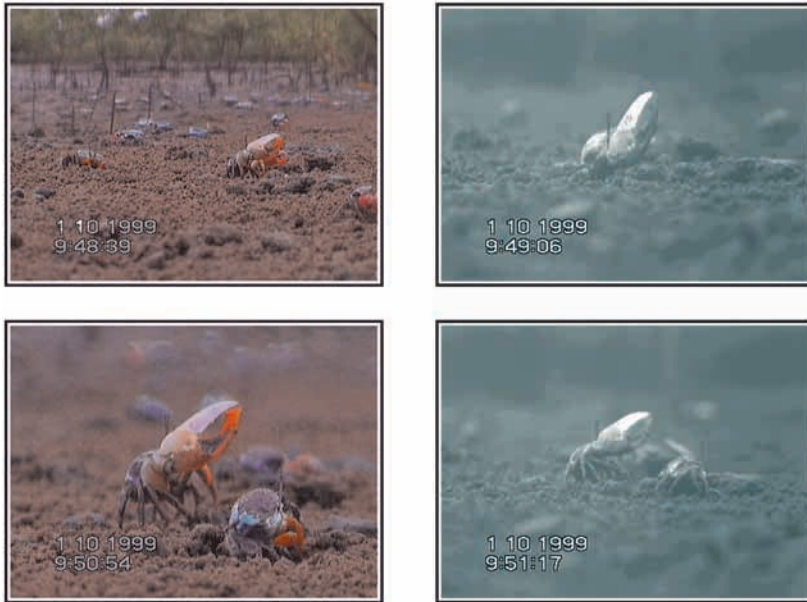


Fig. 5. Images of crabs in a fiddler crab colony as seen by a colour video camera (left) and the same scenes recorded from a slightly different position with a ultraviolet-sensitive camera (right). See Fig. 3D for the sensitivity of the camera and the filter combination. Note that specular reflections as well as the white parts of the male claw and the blue parts of the carapace of both males and females reflect in the ultraviolet, and contrast strongly with the mudflat background which appears dark in ultraviolet wavelengths.

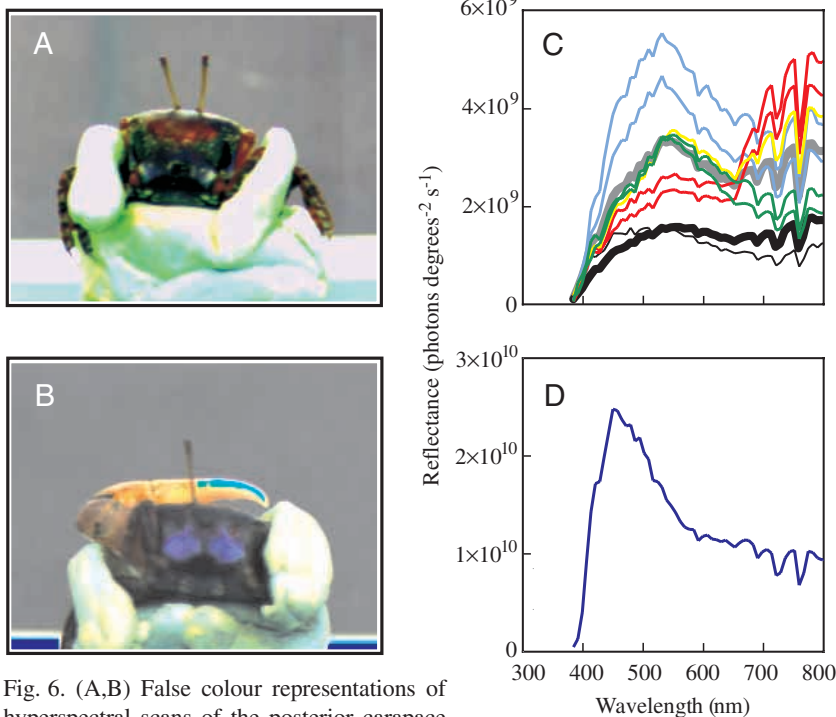


Fig. 6. (A,B) False colour representations of hyperspectral scans of the posterior carapace of a mottled female *Uca vomeris* (A) and a male *U. vomeris* exhibiting dark blue spots (B). The angular size of the images is about 6.5° in width and 5° in height. (C) Spectra measured at several locations on the mottled female carapace. The thick grey line is the average of all the spectra shown. The thick black line is the average spectrum of the mudflat background (see Fig. 7E). (D) Spectrum measured at the left-hand blue spot on the male carapace. The line colours approximately mimic the appearance of the cuticle colours to the human eye. Note the different scales.

display fronts will, in turn, be conspicuous across the human-visible spectrum and, thus, be stimulating short- and long-wavelength pigments to similar degrees. It may be significant that red colours dominate on those parts of the crabs that can be actively moved and are used in waving displays by both males and females (von Hagen, 1993): in *U. vomeris* at least, it is always the claws and the legs that are red, never the carapace (see Fig. 5 for males and Fig. 7 for females). Considering that in most animals the signals from only one receptor type, the green receptor, are fed into the motion-detection system, and that fiddler crabs may be dichromats (see below), this suggests that red colours and motion detection are linked, in the sense that they will exclusively stimulate only one of the two receptors.

The signals potentially available to a fiddler crab, as we have described them here, need at some stage be related to the spectral and polarization sensitivities of the crabs, which are at present unknown. Although we have a fair impression of the structure of the ommatidial sampling array in fiddler crabs (Zeil et al., 1986; Land and Layne, 1995a; Zeil and Al-Mutairi, 1996), we know little about their spectral and polarization sensitivities, let alone how they are distributed across the visual field. Electroretinograms (ERGs) suggest that fiddler crabs may possess only one pigment (Scott and Mote, 1974) with a peak sensitivity around 508 nm, although Hyatt (Hyatt, 1975) has presented electrophysiological evidence (by selective adaptation of the ERG amplitude with ultraviolet and long-wavelength light) and behavioural evidence indicating that they may be dichromats with an additional short-wavelength pigment. Fiddler crabs do possess an 8th retinula cell (*Uca coarctata*; Sally Stowe, personal communication) which, in crayfish, has been shown to be a short-wavelength receptor (Cummins and Goldsmith, 1981). However, attempts to characterize the spectral sensitivities of fiddler crabs in more detail using microspectrophotometry have unfortunately failed (Cronin and Forward, 1988). Equally, there is behavioural evidence that fiddler crabs are polarization-sensitive (Altevogt and von Hagen, 1964; Korte, 1965), but the detailed structure of their rhabdoms, the degree to which their photoreceptors are polarization-sensitive and how this sensitivity is distributed across the visual field are not known.

At present we know too little about the physiology of their photoreceptors and the mechanisms of early visual processing in fiddler

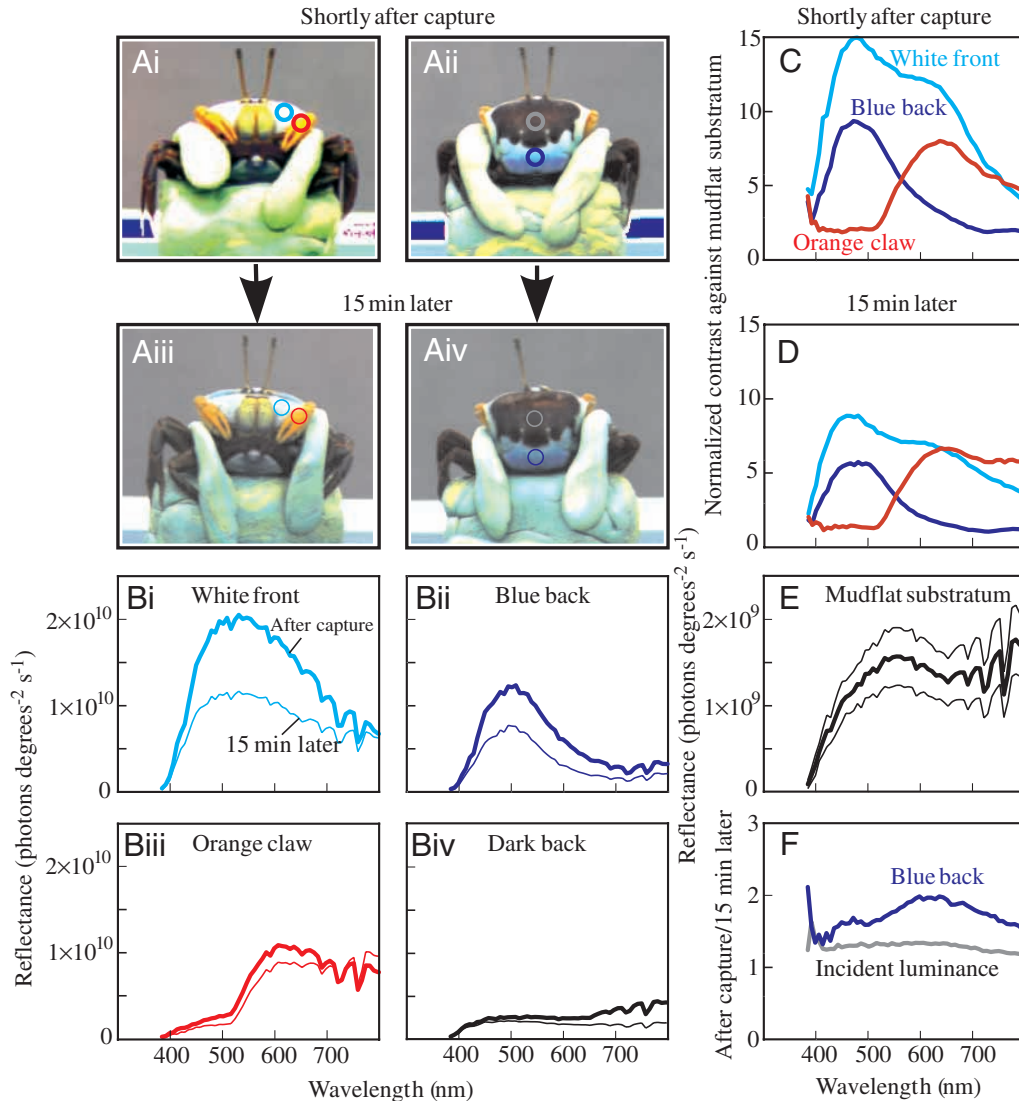


Fig. 7. The cuticular colours of *Uca vomeris* can change within minutes of handling the animals. The figure shows hyperspectral scans of a female *Uca vomeris* from the front (Ai) and from the back (Aii) within minutes of capture and 15 min afterwards (Aiii, iv). The angular size of the images is about 6° in width and 5° in height. For the scans, which took approximately 30 s each, the crab sat on a platform of soft yellow-green plastic (Blue Tag) and was immobilized by strips of the same plastic holding down its walking legs. The spectral reflectances (in units of photons degrees $^{-2}$ s $^{-1}$) of selected parts of the body (marked by equivalently coloured circles in A) are shown below the images (Bi–iv), as measured shortly after capture (thick lines) and 15 min later (thin lines). (C,D) Normalized contrast shortly after capture (C) and 15 min later (D) of the white front patch, the blue back patch and the orange claw of the female against the mudflat background, the average spectrum of which under the same recording conditions is shown in E (mean \pm s.d., $N=7$). Note the different scales for the mudflat spectrum and the cuticle spectra. The incident illumination (in relative units) changed slightly in the 15 min separating the two scans, but much less so than the colours of the crab. This is documented in F, in which we plotted the ratio of incident illumination during the initial scan to that 15 min later (grey line), together with the ratio of reflectances of the blue back spot during the first and the second scans (blue line). Crab and mudflat surface were scanned approximately 10 m away from the site of collection in the shade of a dark grey umbrella. Between scans, the crab was kept in the shade in a container, the floor of which was covered with approximately 0.5 cm of sea water.

crabs to assess fully the significance of the specular reflections, polarization reflections and spectral reflections that their cuticle presents to a conspecific observer. In addition to characterizing spectral and polarization sensitivities, it will be important to determine the angular acceptance functions of receptor cells, to enable us to assess the absolute light sensitivity, the contrast sensitivity and, with this, the efficacy of these signals at the level of the retina. It will also be

interesting to determine whether spectral and polarization sensitivities interact in fiddler crab eyes, as they do in butterflies (Kelber, 1999), and how adaptive this may be in processing the signals we have described here.

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