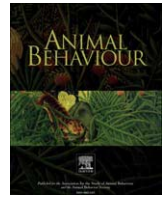




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Animal Behaviour

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The fiddler crab *Uca mjoebergi* uses ultraviolet cues in mate choice but not aggressive interactions

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ARTICLE INFO

Article history:

Received 5 January 2009
 Initial acceptance 6 March 2009
 Final acceptance 25 May 2009
 Published online 21 June 2009
 MS. number: 09-00008R

Keywords:

competitive ability
 Crustacea
 fiddler crab
 mate choice
Uca mjoebergi
 Ultraviolet
 UV

The perception of ultraviolet light and its role in communication has received a great deal of attention in recent years. Although ultraviolet light is no different to other wavelengths in many respects, its role as a signal does deserve special consideration, if only because it is frequently overlooked by human observers who are unable to see it. Studies on the role of ultraviolet cues in inter- and intrasexual interactions are still rare, and generally focused on vertebrates with relatively complex visual systems. Here we show for the first time that crustaceans, with a relatively simple, probably dichromatic, visual system, also use ultraviolet cues in mate choice. We found that the enlarged claws of male *Uca mjoebergi* reflect ultraviolet wavelengths of light. Mate-searching females preferred ultraviolet-reflecting males over those whose reflectance was blocked with sunscreen. Conspecific males showed no such preference when deciding which rival to attack, suggesting that ultraviolet cues are not involved in signalling competitive ability.

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Ultraviolet-sensitive photoreceptors are found in every major group of animals including invertebrates, fish, amphibians, reptiles, birds and mammals (Tovée 1995). Animals with ultraviolet-sensitive photoreceptors cannot necessarily see ultraviolet light. Some, like humans, have ultraviolet-blocking lenses or other ocular media that prevent the damaging, high-energy ultraviolet wavelengths from reaching their photoreceptors (Tovée 1995). It is the very fact that humans are unable to see them that makes ultraviolet signals so intriguing and means their importance is often overlooked. It is only in the last decade or so, with the advent of cheap, portable spectrophotometers, that the ubiquity of ultraviolet reflectance in nature has become apparent. Ultraviolet reflectance has been found in many potential visual signals from flowers and fruits to fish scales and bird plumages, exposing unexpected patterns and differences in organisms previously considered dull or monochromatic (Burkhardt & Finger 1991; Cuthill et al. 1999). As with colour patterns visible to humans, it is not enough to say that an animal is highly coloured and theoretically capable of perceiving colour. Experimental manipulations are required to show that

colour patterns, whether visible to humans or not, are adaptive signals involved in communication.

Ultraviolet wavelengths are no different to human-visible wavelengths with respect to their role in communication. They have been implicated in foraging and predator–prey interactions (Honkavaara et al. 2002), parent–offspring interactions (Bize et al. 2006; de Ayala et al. 2007; Tanner & Richner 2008) and most notably agonistic and mate choice behaviour. Ultraviolet ornamentation is involved in the mate choice decisions of at least eight birds (Maier 1993; Bennett et al. 1996, 1997; Andersson & Amundsen 1997; Johnsen et al. 1998; Hunt et al. 1999; Pearn et al. 2001, 2003; Siitari et al. 2002; Zampiga et al. 2008), four fish (Garcia & de Perera 2002; Kodric-Brown & Johnson 2002; Smith et al. 2002; Cummings et al. 2003; White et al. 2003; Boulcott et al. 2005; Rick et al. 2006; Rick & Bakker 2008a), six butterflies (Obara 1970; Rutowski 1977; Silberglied & Taylor 1978; Robertson & Monteiro 2005; Kemp 2007, 2008) and two spiders (Lim et al. 2007, 2008; Li et al. 2008). Ultraviolet cues are also involved in signalling competitive ability in four bird species (Alonso-Alvarez et al. 2004; Siefferman & Hill 2005; Woodcock et al. 2005; Pryke & Griffith 2006; Poesel et al. 2007), the Augrabies flat lizard, *Platysaurus broadleyi* (Whiting et al. 2006; Stapley & Whiting 2006) and the damselfish, *Pomacentrus amboinensis* (Siebeck 2004).

There is a profound bias towards the study of vertebrates with respect to the role of ultraviolet signals in communication. Studies

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of invertebrates are generally limited to butterflies. This is surprising given the ubiquity of ultraviolet sensitivity and ultraviolet reflectance in invertebrates, especially among the arthropods (Silberglied 1979; Tovée 1995). With the possible exception of jumping spiders, whose spectral sensitivities are still under debate (DeVoe 1975; Yamashita & Tateda 1976; Peaslee & Wilson 1989), studies on the use of ultraviolet signals are also restricted to organisms with relatively complex visual systems, composed of three or more types of photoreceptors and various filters and oil droplets. Invertebrates, with their often brilliant coloration in the ultraviolet and human-visible wavelengths, short generations, ease of manipulation, varied social systems and relatively simple visual systems represent ideal and unappreciated models for the study of colour signalling.

Fiddler crabs (genus *Uca*) are particularly well suited for studies on the adaptive significance of colour ornaments. They are brilliantly coloured (at least to human eyes), visually oriented animals (Layne et al. 1997; Hemmi & Zeil 2003) with complex social systems that have been the focus of numerous studies on mate choice and sexual selection (Backwell & Passmore 1996; Jennions & Backwell 1998; Backwell et al. 2000; Pratt et al. 2003). Like many other crustaceans (Cronin et al. 1994; Tovée 1995; Johnson et al. 2002), fiddler crabs are probably dichromats with two types of photoreceptors in their compound eyes: one type maximally sensitive to wavelengths between 510 and 540 nm in the main reticular cells (R1–7), and the other maximally sensitive to shorter wavelengths around 430 nm, probably located in the eighth reticular cell (R8) of the rhabdom (Scott & Mote 1974; Horch et al. 2002; Jordão et al. 2007). Behavioural experiments have also shown that fiddler crabs are capable of colour vision (Hyatt 1975; Detto 2007) and that colour is an important social signal (Detto et al. 2006; Detto 2007). However, as is often the case, none of these studies took ultraviolet wavelengths into account, despite the fact that the crabs are sensitive to ultraviolet light (see Fig. 1b) and reflect ultraviolet wavelengths (Zeil & Hofmann 2001) which probably make them more conspicuous to bird predators as well as conspecifics (Hemmi et al. 2006).

Uca mjoebergi are endemic to Australia and are characterized by mottled brown carapaces and the male's uniformly yellow major claw. Both males and females construct and defend burrows in clearings within the upper mangrove forests. Around neap tides, females leave their burrows and wander through the colony visiting a number of males before choosing one and remaining in his burrow to mate. As in many other species, males wave their single enlarged claw to attract wandering females to their burrow, which the female assesses before selecting her mate (Backwell & Passmore 1996). The first, vital, step in successful reproduction is attracting a female, which is done, at least in part, through the colour of the male's claw. Females are attracted to the yellow of the male's claw, to the extent that they prefer heterospecifics with yellow-painted claws over conspecifics painted red and white to resemble a heterospecific (Detto et al. 2006). Females are also able to discriminate between unpainted males and those painted yellow (Detto et al. 2006), which to humans appear very similar. A possible explanation is that *U. mjoebergi* females are responding to the absence of ultraviolet reflectance in the yellow paint (Detto 2007).

Our aim in this study was to determine whether *U. mjoebergi* males possess ultraviolet ornamentation that females may use in mate assessment, and then to test whether its removal influences female choice in a seminatural situation. It has been suggested that sexually selected traits first evolved as signals of competitive ability, allowing males to assess the fighting ability of potential rivals from a distance without risking injury (Berglund et al. 1996). With this in mind, we also tested whether males are more likely to fight conspecifics whose claws do not reflect ultraviolet

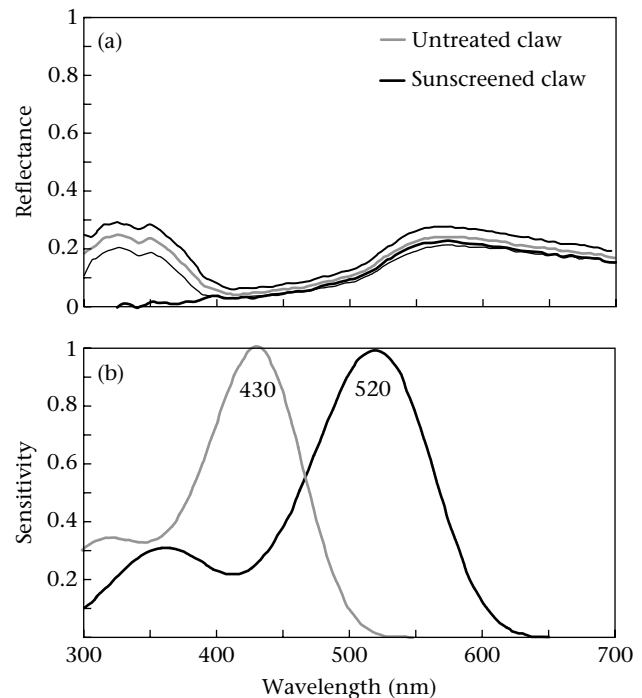


Figure 1. Average claw reflectance \pm SD and hypothetical spectral sensitivities of *Uca mjoebergi*. (a) Reflectance when sunscreen was applied to the males' claws and reflectance of untreated claws. Standard deviations of only untreated claws are presented as thin solid lines for clarity. (b) The hypothetical spectral sensitivities of *U. mjoebergi* (Govardovskii et al. 2000) based on the λ_{\max} values of the fiddler crab *U. thayeri* (see Horch et al. 2002).

wavelengths as would be expected if they act as a signal of competitive ability. This is the first time ultraviolet cues have been tested for mate choice in a dichromat and the first time they have been examined as signals of competitive ability in an invertebrate.

METHODS

To determine whether *U. mjoebergi* use ultraviolet cues in their decision to approach potential mates or competitors, we gave males and females a choice between males whose claws naturally reflected ultraviolet light and those treated to remove the ultraviolet reflectance. Experiments were conducted in September and December 2007 and 2008 on an intertidal mudflat in the East Point Reserve, Darwin, Australia (12°24'35"S, 130°50'00"E).

During the mating period we tethered two males with 1 cm of thread glued to their carapace and tied to a nail stuck in the ground 30 cm apart in an area cleared of existing crabs and burrows (as per Detto et al. 2006). The males were matched for size (within 1 mm claw length), handedness and colour based on human vision. Tethered males had an average claw size of 18 mm (range 13.3–22 mm). Sunscreen was randomly applied to either the front of their major claw, reducing the ultraviolet reflectance visible to other crabs, or the back of their claw as a control. Once applied, human observers were unable to discriminate between these treatments. We alternated the positions of the males throughout the experiment.

Males and actively mate-searching females were caught and placed individually under a transparent plastic container half way between the tethered males. The container was lifted remotely after 1 min to release the focal crab who was observed for 5 min or until it made a choice by approaching a tethered male to within approximately 2 cm. Crabs that had not chosen after 5 min or that

left the area without approaching either male were considered not to have made a choice and the trial was repeated with new individuals until a successful choice was made. Although some tethered pairs were used twice, for males and females, each pair was never used in more than one successful choice from each sex so both sexes were tested against a total of 20 different pairs of tethered males. After each successful trial, we cut the tethers and released the males and any focal animals back into the population. None of the crabs appeared to suffer any negative effects from their short captivity. We used exact binomial tests to determine whether their choices were significantly different from random.

We used a USB4000 ultraviolet-VIS spectrophotometer (Ocean Optics Inc, Dunedin, FL, U.S.A.) with a PX-2 Pulsed Xenon lamp (Ocean Optics Inc) to quantify the effect of the sunscreen on the spectral reflectance of the males' claws. An area of approximately 1 mm² on the claw was illuminated at 90° to the surface and the reflected light was collected at 45° to reduce specular reflections. A single measurement was taken from the manus of five autotomized claws (within 12 h of removal) before and after the application of sunscreen within a darkened room. Reflectance was calculated relative to a white Spectralon standard. A new reference and the dark current (i.e. the output of the spectrophotometer when no light reaches the sensor) were recorded before each crab was measured. The raw reflectance values were averaged to 3 nm intervals, from 300 nm to 700 nm.

RESULTS

We found that the males' major claws have a reflectance peak around 550 nm, responsible for their yellow appearance to humans. However, they have an equally large second peak at approximately 325 nm, invisible to humans (Fig. 1a). This ultraviolet peak was virtually eliminated by the application of sunscreen. The sunscreen also slightly reduced the reflectance over the rest of the spectrum, although well within the levels of natural variation (Fig. 1a).

Females preferentially approached males with ultraviolet-reflecting claws over males lacking ultraviolet reflectance; 16 approached the control male and four approached the male treated with sunscreen (binomial: $N = 20$, $P = 0.01$). Choosing females behaved as typical mate-searching females, approaching the tethered males and stroking or tapping them with their legs.

Focal males behaved very differently to females, showing no ultraviolet-based preference and choosing to fight the males they approached. Of the 20 males, 10 approached the control male and 10 approached the sunscreen-treated male (binomial: $N = 20$, $P = 1$).

DISCUSSION

Female *U. mjobergi* were more likely to approach males whose claw reflected ultraviolet wavelengths than those whose ultraviolet reflectance was removed with sunscreen. This is the first time that a dichromatic crustacean has been shown to use ultraviolet cues in mate choice. Males, however, did not base their decision to fight on the presence or absence of ultraviolet reflectance on their potential rival's claw. The ultraviolet component of claw colour was therefore not a signal of competitive ability. This casts doubt on the idea that mate choice traits evolve from honest signals of competitive ability (Berglund et al. 1996).

It could be argued that females were not making normal mate choice decisions because of the stress of being handled and the seminatural conditions of the experimental arena. It is possible that they were responding to the most conspicuous crab rather than selecting a mate. However, we would then expect males to

be influenced in the same way, which they were not. Furthermore, female behaviour during the trials was remarkably similar to natural mate-searching behaviour in this species: females paused before walking in a straight line towards a particular male, sometimes even starting towards one male before changing their minds and turning to approach the other male. The female responses were not rushed or erratic. Females appeared to be searching for mates and were using ultraviolet cues in this process.

It is also unlikely that females were avoiding the males that completely lacked ultraviolet signals because they looked unnatural. Females are able to discriminate between conspecific and *U. signata* males in the absence of ultraviolet wavelengths and will even approach heterospecific males on the basis of yellow paint that does not reflect ultraviolet light (Detto et al. 2006; Detto 2007). So, while ultraviolet cues may play a role in species recognition, they are clearly not essential for successful recognition, as the crabs are able to rely on longer wavelengths in the absence of ultraviolet cues.

The expression of ultraviolet reflectance on male claws may be correlated with some aspect of male quality. Ultraviolet ornamentation in other species can be linked to a male's physical condition and size (Keyser & Hill 2000; Mougeot & Arroyo 2006; Dobson et al. 2008), developmental conditions (Knüttel & Fiedler 2001; Kemp et al. 2006; Kemp & Rutowski 2007), parasite load (Doucet & Montgomerie 2003; Mougeot et al. 2005), reproductive success (Doucet et al. 2005; Siefferman & Hill 2005), territory quality (Keyser & Hill 2000; Whiting et al. 2006), competitive ability (Siefferman & Hill 2005; Stapley & Whiting 2006) and even genetic quality (Sheldon et al. 1999). Any number of these could be of interest to a potential mate. However, another possibility is that ultraviolet reflectance does not signal anything about the male, but increases the male's conspicuousness to mate-searching females. *Uca mjobergi* live in clearings in mangrove forests so males are seen against a background of mud and trees, which tend to absorb ultraviolet light (Zeil & Hofmann 2001; Honkavaara et al. 2002). Male claws would therefore contrast strongly against the background.

It has been proposed that ultraviolet signals represent a private channel of communication, particularly in birds and fish (Burkhardt & Finger 1991; Cummings et al. 2003; Stevens & Cuthill 2007). The theory suggests that individuals are well camouflaged in the human-visible wavelengths but conspicuous in the ultraviolet region, to which their predators are blind. Fiddler crabs like *U. mjobergi* are unlikely to use ultraviolet as hidden signals because their main predators are birds and other crabs (personal observation) which are likely to be sensitive to ultraviolet light. In fact Cummings et al. (2008) found that the colour patterns that were most conspicuous to other fiddler crabs were equally visible to birds. One advantage that fiddler crabs may gain from using ultraviolet wavelengths is that they are scattered more than long wavelengths and so are difficult to detect from a distance (Hunt et al. 2001; Hausmann et al. 2003; Rick & Bakker 2008b), especially by vertebrates because of chromatic aberration (Bowmaker 1980). Ultraviolet signals may thus be well suited for signalling over short distances which is ideal for fiddler crabs whose social interactions are generally limited to within approximately 1 m of their burrow and which can only detect other crabs up to 2 m away (Zeil et al. 2006).

Acknowledgments

This work was supported by an Australian Research Council grant (to P.R.Y.B.). We thank I. Booksmythe for assistance in the field, and J. Zeil and J. Hemmi for access to the spectrophotometer.

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