



Sex, size and colour in a semi-terrestrial crab, *Heloecius cordiformis* (H. Milne Edwards, 1837)

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Abstract

We investigated the relationship between sex, size and colour in the little studied Australian endemic semaphore crab, *Heloecius cordiformis*, and related it to the crabs' social system with the aim of identifying the potential signalling function of claw colour.

Equal sampling of crabs from all size classes revealed a strong relationship between sex, size and claw colour. Purple-clawed males were larger and had larger claws than pink-, orange- or green-clawed males. Male claws showed positive allometric growth: relative to body size, purple-clawed males had larger claws. The largest females had pink claws; the few with purple claws were no larger than immature green-clawed crabs. Female claws grow isometrically with the body so the relative claw size did not differ among the female colour classes. Quantitative measurements of claw colour revealed spectral differences between these subjectively described colours. The purple claws typical of large males also contrasted more strongly against the mudflat background than the other colours.

Heloecius copulate outside female-owned burrows and probably within male-owned burrows. The male's waving display, in which both claws are raised and lowered, may feature in both mating strategies: as a territorial display and to attract wandering females. Large males are competitively superior so size, and potentially colour, are important in territorial disputes and may also feature in mate choice.

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1. Introduction

Ocypodid crabs, particularly fiddler crabs (genus *Uca*), exhibit vivid colours on their carapaces, chelae and walking legs (Crane, 1975), including red, yellow, orange, purple, blue, green, white, brown and black (Crane, 1975; von Hagen and Jones, 1989). These colours are based on the hormonally driven movements of pigments within at least four kinds of cuticular chromatophores (Thurman, 1988; Rao, 1985). Changes in colour due to endogenous rhythms and in response to stress are well known (see Warner, 1977). However, little work has been done on their role as a visual signal.

Animals with poor visual acuity may find colour (and motion) useful as a signal because the perception of hue is less affected by distance than the perception of spatial patterns (Rowland, 1979). This is particularly relevant to arthropods like crabs, whose compound eyes have relatively poor visual acuity (Land and Nilsson, 2002) and who may be pressed to signal over comparatively long distances. A fiddler crab communicating with other crabs over 0.5 m is like a human doing so over 70 m (Hyatt, 1975).

Colour is often associated with the parts of a crab used in social interactions. The claws of many male fiddler crabs are brightly coloured and are used in aggressive interactions with other males and waving displays to attract females (Crane, 1975; Christy and Salmon, 1984; Salmon, 1987). Colour signals may also be linked to movement on the walking legs, which are raised and lowered during the waving display (Crane, 1975).

That colour is likely to play a role in communication is further supported by the fact that the colours change depending on the state of the individual. Many male fiddler crabs change colour during displays: brightening existing colours or bleaching to a brilliant white. These display colours are lost within minutes when handled (Zeil and Hofmann, 2001) or after losing a fight (Crane, 1975; Thurman, 1988).

Recent evidence suggests ocypodid crabs may at least be dichromats (Horch et al., 2002), allowing them to distinguish between colours on the basis of wavelength. However, despite the variety of colours exhibited by ocypodids and their apparent role in social displays, little is known about the role that colour plays in their social systems.

As with the closely related fiddler crabs (Turkay, 1983; Fielder and Greenwood, 1985), the functional significance of the bright colouration in *Heloecius cordiformis* has not been thoroughly examined, although it is widely held that juvenile crabs are orange, while purple is an indication of maturity (Davey, 1998; MacFarlane et al., 2000). *H. cordiformis* is a common semi-terrestrial crab endemic to Australia, attaining a maximum carapace width of 25 mm (Davey, 1998). Their waving display, in which both equal-sized claws are raised and lowered, is believed to function in courtship (Griffin, 1968) and emphasises their orange or purple claw colouration. This study aims to confirm the relationship between sex, size and claw colour and relate this to the crabs' social system, thoroughly described by Griffin (1968), in an attempt to determine the potential social functions of body colours.

2. Materials and methods

2.1. Study site

Observations were conducted from July 2001 to March 2002, on an intertidal mudflat (10 × 20 m) on the banks of the Moruya River, New South Wales, Australia (150°09' E, 35°54' S). *H. cordiformis* was the most common inhabitant of the area.

2.2. Sampling and measurements

A population survey was conducted from 15 to 17 November 2001. The spatial distribution of crabs was very heterogenous. We therefore decided to position 10 plots (0.5 × 0.5 m) on two parallel transect lines, perpendicular to the water line, separated by 30 cm. One plot contained no crabs, resulting in a total of 19. All burrows were marked and the 103 resident crabs were caught by blocking their burrows as they surfaced. The crabs were sexed and the length of both claws (propodus) was measured, as was the carapace width at its widest point. Their claw colour was determined subjectively and objectively (see below). From 21 September 2001 until 28 March 2002, a further 855 crabs with carapace widths greater than 8.3 mm were caught, making a total of: 447 females and 511 males. The sample consisted of burrowless wanderers and resident crabs from all size classes. These crabs were also measured and their claw colour determined subjectively. Measurements were made to the nearest 0.1 mm with dial callipers. All crabs were released once measured.

The growth of male and female claws, relative to their carapaces, was determined by plotting the log of the length of the largest claw against the log of carapace width. Outlying crabs with unusually small claws, which may indicate regeneration, were removed to normalise the distribution of residuals. The slopes were compared for males and females and tested for their departure from a slope of 1.

To test whether their claws were symmetrical in length, the mean absolute differences between the claws, standardised against the largest claw, was tested for their departure from zero, treating males and females separately. To determine whether asymmetry increases with age, the relationship between carapace width and the relative absolute difference in the length of the two claws was compared.

2.3. Claw colour

Claw colour was subjectively assigned as 'purple', 'orange', 'pink' or 'green' by comparison to a colour chart made of paint samples. Individual claws could exhibit more than one colour, but 'claw colour' was taken to be the colour of the outer manus near the pollex and dactyl. Males and females were grouped into 1 mm size classes based on carapace width: 8 to >18 mm in males, and 8 to >16 mm in females. A sample of approximately 20 crabs was randomly chosen from each size class and the mean size of each colour class in terms of claw length, carapace width and the ratio of claw length to carapace width (relative claw length) was calculated for males and females separately. The crabs' biggest and smallest claws (if asymmetrical) were

treated separately to allow for the possibility that regenerating claws grow back as a different colour.

Claw colour was measured quantitatively for the subset of 103 crabs caught in the population survey. The reflectance spectra of the living crabs were recorded using a USB2000 UV–VIS portable spectrophotometer (Ocean Optics, Dunedin, USA), controlled by OOIBase32 software and attached to a unidirectional UV–VIS reflectance probe (Ocean Optics). A PX2 Xenon strobe (Ocean Optics) provided full spectral illumination of sampling areas approximately 1 mm in diameter. Reflectance was calculated relative to a white Spectralon standard. The probe was held at 90° to the surface of the dry claw and readings were taken from six areas in the same order on each claw (Fig. 4, inset). As there is some colour variation between the areas on a single claw (see Fig. 4), each was subjectively assigned to a colour class. Both claws were measured if present, but the side measured first alternated between the crabs to account for the possibility that the colour changes in the 1–2 min it took to measure each crab. 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 to 700 nm.

The reflectance values for all areas on all crabs were grouped, based on the subjective colours, and averaged treating males and females separately. The mean reflectances were plotted against wavelength, with 95% confidence intervals, yielding an approximation of the spectral differences between the subjective colours.

Readings were taken of the mud from five random areas in two of the plots. The normalised contrast (Pelli, 1990) was calculated using the average spectra of the subjective colour classes, where C is the normalised contrast for each wavelength from 300 and 700 nm, \bar{R}_c is the average claw reflectance (for each colour class) at each wavelength, and \bar{R}_m is the average mud reflectance at the same wavelengths.

$$C = \bar{R}_c / \bar{R}_m - 1$$

2.4. Behaviour

Behavioural observations were made to ensure that the crabs' behaviour did not differ from that reported by Griffin (1968). Two 0.7 × 0.7 m plots were established in areas with relatively high numbers of crabs (20 and 25 burrows per plot) and all but the smallest crabs were caught. They were measured, numbered with yellow enamel paint and returned to their original burrows within 5 min. Crabs that moved into the plot were caught and marked at the end of the observation period, or identified by distinguishing features. Intruders were sexed by the shape of their claws (see Fig. 1), and their relative size determined by comparison to a numbered crab.

From 30 September until 4 October 2001, each plot was observed for the entire low tide (approximately 6 h/day) except for the last 2 days, when rain reduced observation time to approximately 2 h/day. Observations spanned the entire day, from 08:00 to 17:00. Due to the limited plot size, all crabs could be observed simultaneously, so the circumstances and sex, size and colour of the crabs involved in waving displays, fights and copulations could

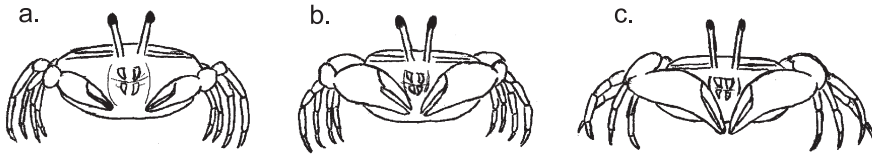


Fig. 1. Appearance of male and female *H. cordiformis*. (a) Female claws appear more delicate than those of males (b, c). Mature male chelae (c) appear more curved than juveniles' (b).

be recorded. Observations were made while sitting motionless, 1–2 m from the plots. Details of more infrequent activities, such as copulations, were revealed by general observations of the mud flat. MacFarlane and King (2002) found that the presence of human observers increases the time spent waving and standing motionless in *Heloecius*. However, our main aim was to identify the social context in which colour may be used, not to conduct a quantitative analysis of behaviour.

2.5. Statistical analysis

Parametric tests were used where the assumptions of normality were met; otherwise nonparametric tests were employed. Unless stated otherwise, results are presented with means \pm standard errors.

3. Results

3.1. Morphometrics

Although males attained a larger maximum size, 22.3 mm compared to 17.7 mm for females, on average males and females were the same size: females were 13.2 ± 1.9 mm and males were 13.9 ± 3.2 mm (ANOVA, $F_{1,88} = 1.7$, $p = 0.2$).

Both males and females had slightly asymmetrical claws (Wilcoxon signed-rank test mean different from 0, male $p = 0$, $n = 39$; female $p = 0$, $n = 48$); on average, female claws differed by 1%, while male claws differed by 4%, although the median difference was 0 for both sexes. However, neither sex became more asymmetrical as they aged (Spearman rank-order correlation, male correlation between carapace width and relative absolute difference in claw length equals 0.03, $p = 0.9$, $n = 39$; female correlation equals -0.09 , $p = 0.5$, $n = 48$). An average of $4 \pm 5\%$ of the males in each plot were missing a claw, which is not significantly different from the $7 \pm 5\%$ of females missing a claw (paired t -test, $t_{1,18} = -0.63$, $p = 0.53$).

Male claws appeared more bulky, with a wider manus, than those of females (Fig. 1), and were longer at all carapace widths (Fig. 2). An indirect measure of growth based on a survey of claw sizes across a range of carapace sizes suggests that male claws show

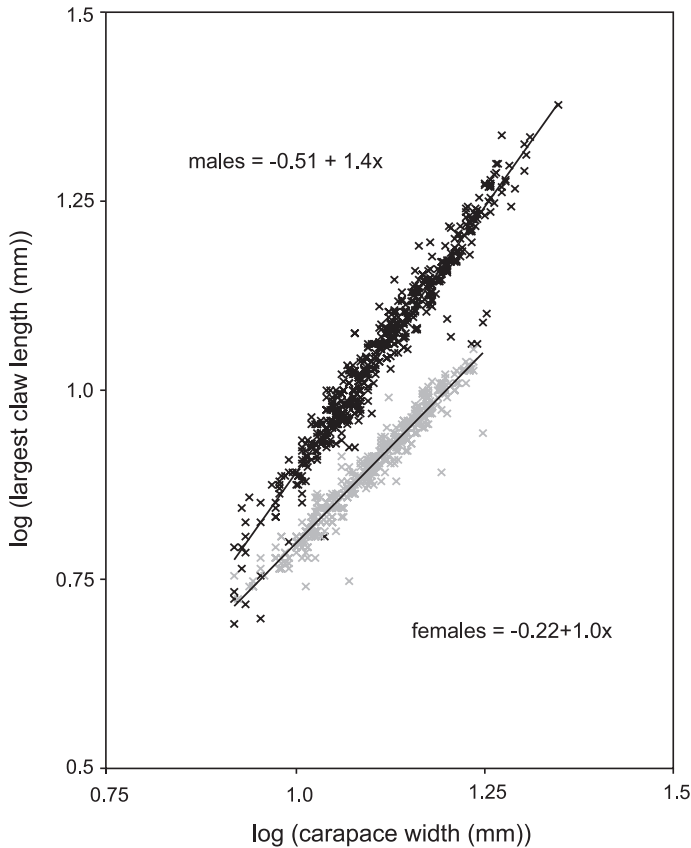


Fig. 2. Allometric claw growth in *H. cordiformis*. Males (black), females (grey). Male and female claws grow at different rates (ANCOVA, regression $F_{3,944}=18564$, $p=0$; sex effect $F_{1,946}=241$, $p<0.0001$; interaction $F_{1,946}=498$, $p<0.0001$).

positive allometric growth relative to their carapace, while female claws grow isometrically (see Fig. 2).

3.2. Claw colours

The claws of *Heloecius* ranged from orange, through to pink, purple, and olive green to brown with the occasional white individuals. Most had white-tipped claws, which sometimes extended to the base of the chelae, or onto the manus. The merus of the ambulatory legs and claws may also be bright orange/red or purple. The carapace varied from black to olive green or dark purple, with pale or cream mottling.

Orange was the most common claw colour; $55 \pm 4\%$ of the crabs in the population survey were orange, $16 \pm 4\%$ green, $15 \pm 4\%$ pink, and $14 \pm 4\%$ purple (ANOVA, colour classes per m^2 , $F_{3,77}=24.6$, $p<0.0001$).

The claws of crabs observed in the wild and those held in captivity for 2 weeks, or during measurements, did not change between the colour classes. However, the dorsal region of the manus did appear to darken and become dark greenish when held during measurements.

Males showed an increase in claw length through the various colour classes; from green through to orange, pink and finally purple claws, which were the largest. Females showed a similar relationship between claw colour and size, except the average sizes were smaller for all colour classes and their purple claws were no larger than green claws, resulting in largest female claws being pink (Fig. 3a). Males and females both showed the same relationship between claw colour and carapace size (Fig. 3b) as they did with claw size (Fig. 3a).

Purple-clawed males had larger claws than pink-, orange- or green-clawed males, relative to their carapace widths. There was no difference in the relative claw size of any of the colour classes in females (Fig. 3c).

The relationships between size and colour are the same when using the smallest or largest claws in both sexes. It was not uncommon to see a male with one purple claw and a smaller, regenerating, orange or pink claw.

Although classified as the same subjective colour, the reflectance spectra varied between different claws and different areas on the same claw. Fig. 4 shows photographs of a representative male from each subjective colour class and the associated reflectance spectra from the six sampling areas on the claws, illustrating the spectral differences between the colour classes and some of the variability between the different areas of the claw. In general, it appears that the proximal regions of the claw are more saturated than the distal regions. Nevertheless, there are clear objective differences in the spectral shapes of the subjective categories of 'green', 'orange', 'pink' and 'purple' (Fig. 5a).

The colour of the mangrove mud, against which the crabs view others of their species, reflects highly at long wavelengths. Claw colours with low reflectance at the shorter wavelengths, such as pink, orange and green, contrast poorly against the mud or appear darker than the background. Purple and white, which reflect at short wavelengths, contrast strongly against the mud (Fig. 5b). The result is that males, and larger males in particular, are more conspicuous than females against the mudflat background.

3.3. Behaviour

Males and females were active on the surface in equal numbers: 10.5 ± 1.5 females and 8.0 ± 1.5 males per m^2 (paired *t*-test, $t_{1,18} = -0.77$, $p = 0.45$). The overall density, including unsexed crabs smaller than 8.3 mm, was 21 ± 1.9 crabs per m^2 .

Each day 28% of the crabs were forcibly evicted from their burrows, usually by wandering males. Both sexes were equally likely to be evicted, as females made up 31% of the marked crabs and 34% of the evictees. Only males were observed forcibly evicting other crabs.

The larger crab was victorious in all but 1 of 33 observed fights in which the relative carapace widths of the combatants was known. The size difference ranged from 0.2 to 5.6 mm with an average of 1.5 ± 1.5 mm (standard deviation, $n = 22$).

Copulations were observed as early as August until at least April. The crabs appear to utilise two distinct mating strategies. Five instances of surface copulation, outside the

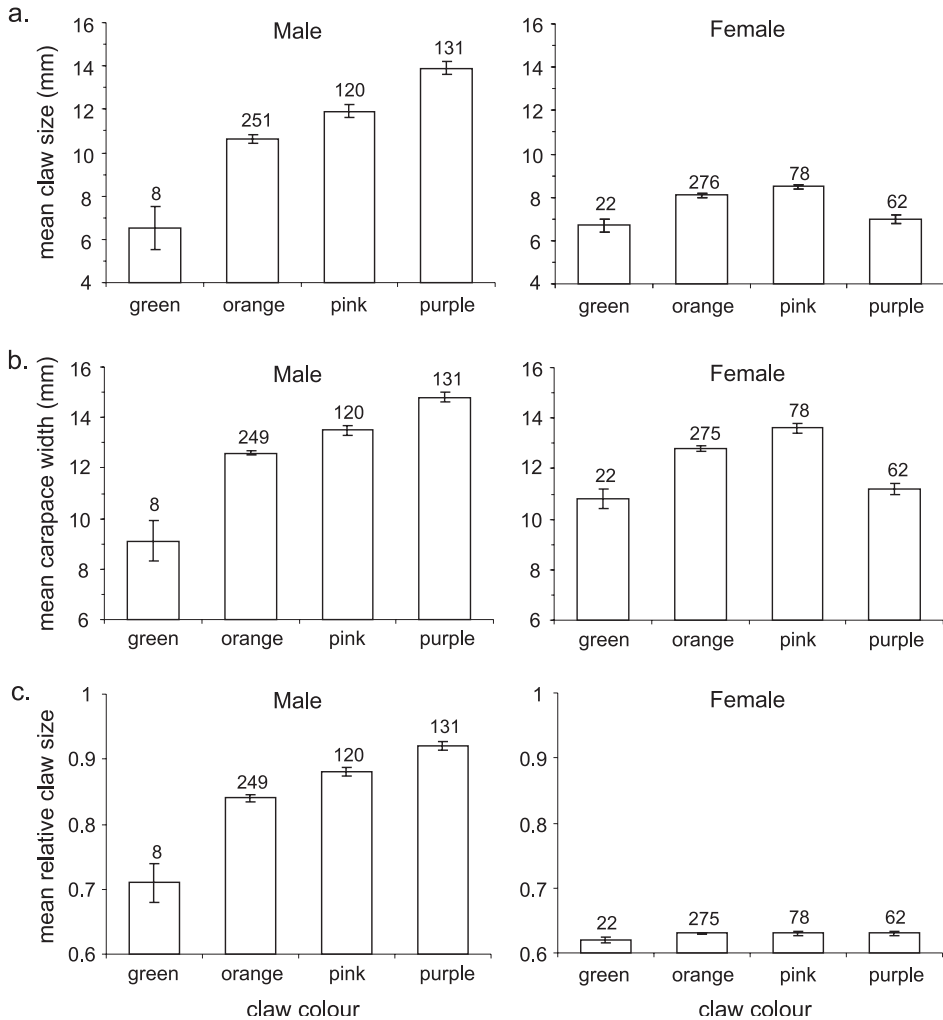


Fig. 3. Mean (\pm S.E.) size of subjective claw colour classes (described by comparison to a colour chart) in *H. cordiformis*. (a) Male purple claws are larger than pink, orange or green claws (ANOVA, $F_{3,507}=45.9$, $p<0.0001$). Purple female claws are no larger than their green claws (ANOVA, $F_{3,435}=25.4$, $p<0.0001$). (b) The same relationship is seen between carapace width and colour (males ANOVA, $F_{3,505}=35.5$, $p<0.0001$; females, ANOVA, $F_{3,434}=26.8$, $p<0.0001$). (c) Purple-clawed males have relatively larger claws than any other males (ANOVA, $F_{3,505}=42.4$, $p<0.0001$). All female colour classes have the same relative claw size (ANOVA, $F_{3,431}=1.7$, $p=0.16$). Sample sizes presented above.

female burrow, were observed in the plots over 2 weeks, and more than 20 during casual observations. Males enticed females out of their burrows by stroking and tapping her with their legs. Afterwards, the crabs returned to their own burrows, or the male wandered off.

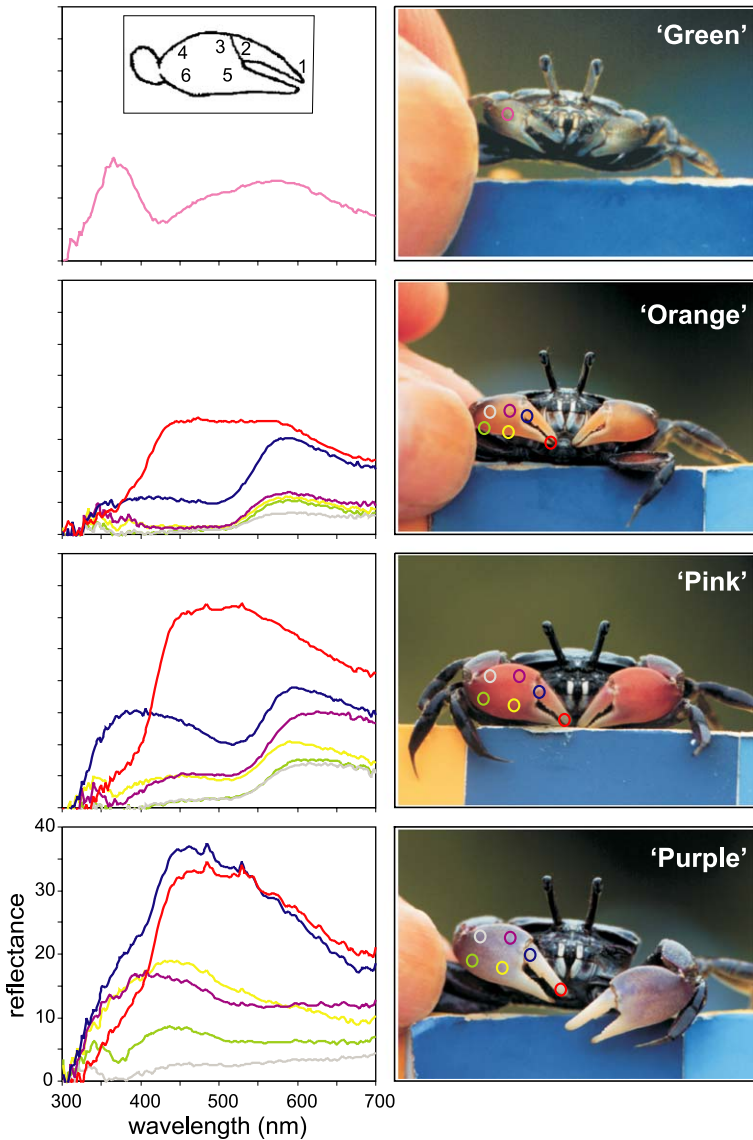
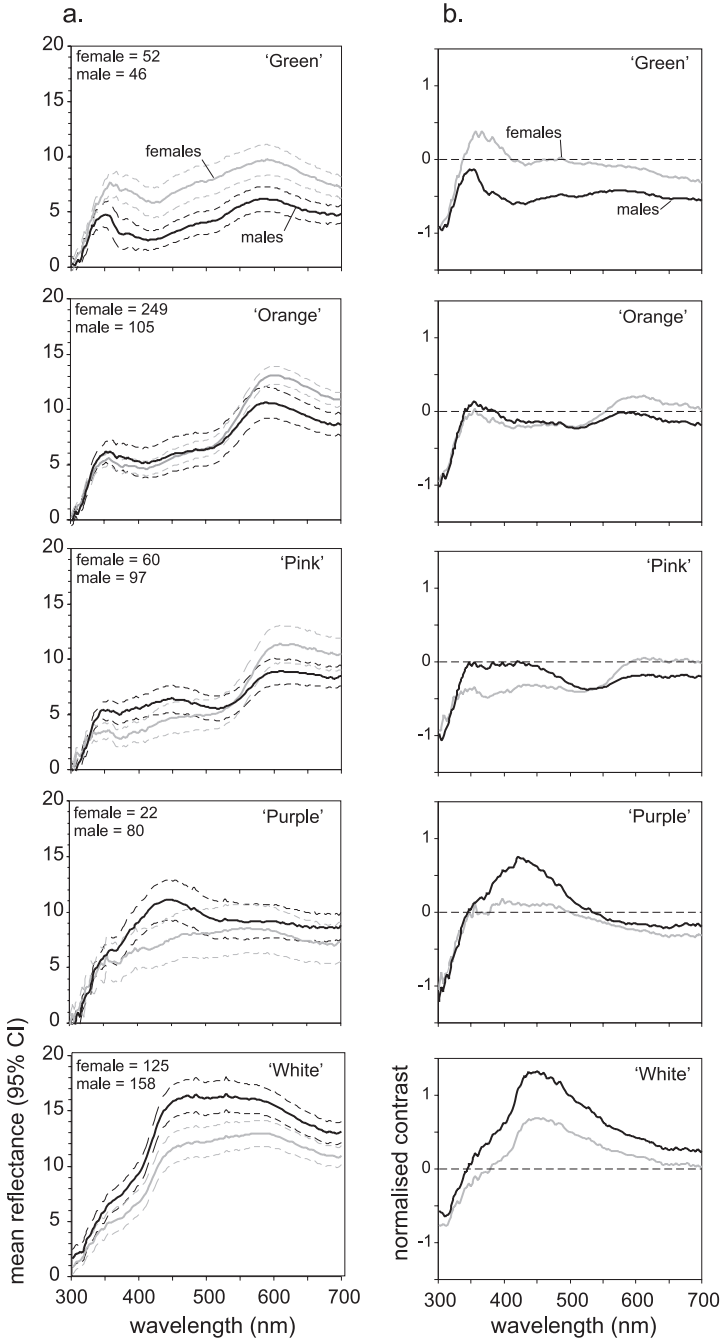


Fig. 4. Claw reflectance spectra of representative males from each subjective colour class. The spectra correspond, by colour, to the six measurement areas circled on the claws (see inset). There are clear differences between the subjective colours, and between the same subjective colours on the one claw. Only one measurement was taken of the green crab due to its small size (claw < 7 mm).

Copulation probably also occurred underground, within the male burrow. On one occasion in the plots, and less than 10 times during casual observations, wandering females followed or led a male down his burrow and remained there while the male sealed



it behind them. Although copulation was not actually observed, the burrow remained sealed for at least the remaining low tide, and the crabs never shared their burrows for extended periods on any other occasion. On many other occasions, the female emerged a few minutes after entering the burrow, and wandered off.

Instances of possible underground copulation were preceded by the male's waving display, in which he raised his body and both claws, until reaching a peak, at which point the claws and body are rapidly dropped to the starting position. Displays consisted of a single wave or up to a wave a second for several minutes. The claws may be barely lifted above the starting position, or to a point slightly above the eyes, accompanied by the elevation of one or two pairs of legs. The claws were lifted directly in front of the body or extended laterally. Crabs of all colours were observed waving, so there is no evidence that a particular colour is associated with a display phase.

Males waved at any wandering crabs that passed within 30 cm of their burrows, after successfully taking over a burrow or after fighting off an intruder. In general, when wandering females approached, males waved while slowly retreating to their burrows. When approached by wandering males, resident males ran back to their burrows and stood at the entrance waving until the wanderer moved off. They increased the frequency and height of the display as wanderers of either sex approached. However, there was no obvious relationship between the sex of the wandering crab and the form of the wave.

Resident females were also observed waving on three occasions, with no lateral extension. Two females followed to their burrows after waving at approaching males, proceeded to kick at the males until they wandered off. One female came out of her burrow and waved at a courting male who then wandered off.

4. Discussion

There was a strong relationship between size and colour in *H. cordiformis*: purple-clawed males were larger and had larger claws than pink-, orange- or green-clawed males, and due to the positive allometric growth of male claws, they also had relatively larger claws. Females showed a similar pattern, although purple-clawed females were rare and were no bigger than juvenile green-clawed females. As female claws grow at the same rate as their bodies, there was also no difference in the relative claw length of any of the colour classes. MacFarlane et al. (2000) reported that the ratio of purple- to orange-clawed females was site-specific. Thus the population at our study site may be lacking mature, purple-clawed, females, biasing our results towards relatively small females whose 'purple' is also spectrally different from that of males. Nevertheless, the relationship between size and the spectrally distinct claw colours does suggest that claw colour could be an important visual signal.

Fig. 5. Average reflectance spectra ($\pm 95\%$ confidence intervals) of subjective claw colours and normalised contrast against the mud (see Materials and methods for definition). Males (black), females (grey), sample sizes presented in top-left corner. (a) Orange, pink, and green reflect at long wavelengths. Pink and green have additional peaks at 450 and 350 nm, respectively. Male purple is characterised by a peak at 450 nm, absent in females. (b) Females generally contrast poorly against the mud, while male colours, particularly white and purple, which reflect highly at short wavelengths, contrast strongly.

Signals must be adapted to the sensory and neural mechanisms of receivers (Rowland, 1979; Johnstone, 1997). Consequently, when studying animal signals it is important to consider how the animals perceive the signals, which is undoubtedly very different from human perception. Recent evidence shows that *Uca thayeri* are likely to have two visual pigments with peak sensitivities near 430 nm and between 500 and 540 nm (Horch et al., 2002). This suggests that fiddler crabs may at least be dichromats, with the ability to discriminate colours and thus use them in communication. However, until the presence of colour vision in *Heloeccius* is confirmed, the role of colour as a visual signal remains speculative.

Heloeccius have slightly asymmetrical claws on average, although the majority exhibited no difference in the length of their claws. Both sexes were equally likely to be missing a claw and as asymmetry did not increase with age, it is probably due to the loss and subsequent regeneration of one of their claws. The fact that the smaller, regenerating, claws assume the colour appropriate to their size, rather than immediately assuming the colour of the original claw or the colour appropriate to the size of the crab, suggests that colour is related to the growth of the claws.

Although the pigments responsible for *Heloeccius*' colouration have yet to be characterised, claw colour is obviously related to growth. The isopod *Idotea montereyensis* incorporates carotenoids (derived from its algal food) into its exoskeleton, thus gradually assuming the colour of its algal substrate, in a process linked to growth and moulting (Rao, 1985). If a similar situation is involved in the determination of colour in *Heloeccius*, requiring the gradual accumulation of carotenoids or the development of specific enzymes, claw colour may be an honest signal of an individual's foraging ability or maturity, as is documented in many bird species (see Olson and Owens, 1998; Inouye et al., 2001; McGraw and Hill, 2001; Pryke et al., 2001).

Since nothing is known about the relative feeding efficiency of male and female claws in *Heloeccius* (for fiddler crabs see Weissburg, 1993), it remains to be seen whether the exaggeration of male claw size is the result of sexual selection or an adaptation to obtain more food, perhaps to sustain a more active lifestyle (Lee, 1995). Sexual selection would operate on the claws' functions in two ways: as weapons that give a male a competitive edge over rival males and thus increase his reproductive success, or as signals that enhance a male's attractiveness to females (Baker and Wilkinson, 2001).

Large *Heloeccius* males are competitively superior, as in other ocypodid crabs (Jennions and Backwell, 1996; Koga and Murai, 1997; Backwell et al., 2000). Opponents were generally well matched in terms of carapace size, with a mean difference of only 1.5 mm, so males seem to assess potential rivals and avoid fights with much larger males. As colour is more visible than specific details of shape, colour-coding weapon size reduces the need to approach rivals to determine the likely outcome of a fight, which would make colour a useful signal in territorial displays. Highlighting competitive ability means small wanderers are less likely to harass large residents, and are thus less likely to be injured. Small residents may also benefit because large males are unlikely to evict much smaller males, as their burrows are too small.

As with the fiddler crabs *Uca vocans* and *Uca vomeris*, the females of which are also brightly coloured (Christy and Salmon, 1984; Zeil and Hofmann, 2001), *Heloeccius* females defend their own burrows. In such situations, colour may help to stabilize the population,

keeping the crabs appropriately spaced and helping to delineate territories. Conversely, females that primarily wander through the colony searching for males are exposed to predators and should be well camouflaged, as in *Uca beebei* and *Uca musica* (Crane, 1975).

Like many ocypodids (Christy and Salmon, 1984; Salmon, 1987; Salmon and Zucker, 1988; Koga and Murai, 1997; Koga et al., 1998), *Heloeceus* appear to utilise two alternative mating strategies. Copulation occurred most frequently on the surface outside the female burrow and, judging from similarities in behaviours associated with underground copulation in *U. lactea* (Koga et al., 1998; Yamaguchi, 1998), copulation probably also occurs within the male burrow. The mating system may be density dependent: underground copulations are more common in high-density fiddler crab populations due to increased competition forcing females out of their burrows, or decreased costs associated with searching for males (Christy and Salmon, 1984; deRivera et al., 2003). Receptive *Heloeceus* females may resort to underground mating only after losing their own burrows, as in *U. beebei* (Christy and Schober, 1994). Griffin (1968) who observed only surface mating in *Heloeceus* did so, for instance, in a captive population of about 6 crabs m⁻², compared to 21 crabs m⁻² at out study site.

Independently of the mating system, colour and motion cues may interact during waving displays (Zeil and Zanker, 1997; Zeil and Hofmann, 2001). Waving displays, and consequently claw colour, may play a role in both mating systems. Unfortunately, too few copulations were observed to examine female mate choice in *Heloeceus* in relation to size (Hyatt, 1977; Backwell and Passmore, 1996) and colour. All we can say at the moment is that large purple males are highly conspicuous against the mudflat background, both to conspecifics and predators.

Conspicuous purple colouration is also more likely to incur a cost as it would be more visible to predators. Fiddler crab males, for instance, are more vulnerable to a certain form of predation in which birds run past the crabs, but then turn back and catch them, using their bright colour to track them (Koga et al., 2001).

5. Conclusions

H. cordiformis showed a strong relationship between crab size, claw size, claw growth and the colouration of their claws. In males, the largest crabs also contrasted most strongly against the mud while female colours were all relatively inconspicuous. Size determines the outcome of territorial disputes and may also be involved in mate choice. The existence of a relationship between colour and size supports the hypothesis that colour is an important signal for *H. cordiformis* during courtship or aggressive interactions. However, it is still unknown if *H. cordiformis* possess colour vision. The challenge thus remains to confirm the presence of colour vision, electrophysiologically and behaviourally, and to determine the functional significance of body colour through experimental manipulation.

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