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The soft red patch of the Australian freshwater crayfish (*Cherax quadricarinatus* (von Martens)): a review and prospects for future research

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Abstract

The red patch located on the propodus of *Cherax quadricarinatus* males is a sexually dimorphic structure. This patch presents an enigma because it is soft and uncalcified, consisting of a thin red to whitish-orange membrane. It presents an impairment of the fighting capability of the males, which, like many other clawed crustaceans, use these appendages in intra- and interspecific aggressive interactions. Present knowledge on patch structure and colour, development and their endocrine control by the androgenic gland is reviewed. The function of the red patch as a possible sensory organ or social signal is discussed. The red patch may transmit information concerning the gender, size and quality of its owner. Several hypotheses concerning the signal function of the patch are suggested and evaluated in the light of our present knowledge of the social behaviour of *C. quadicarinatus*.

Key words: crayfish, *Cherax quadricarinatus*, red patch, honest signal, androgenic gland

THE ENIGMA

The common name of the Australian freshwater crayfish *Cherax quadricarinatus* (von Martens) is 'redclaw', because of the red patch on the claw of the male (Fig. 1). This sexually dimorphic patch is found only on the outer surface of the propodus of the male. It is soft and uncalcified, consisting of a thin red to whitish-orange membrane. *Cherax quadricarinatus* is one of the few crayfish and clawed decapod crustaceans with a permanent soft area on their claw; in most species of clawed crustaceans the entire claw is covered by a hard exoskeleton. Moreover, in several species, higher levels of calcium concentration and a more rapid mineralization process following ecdysis have been reported in the claws than in several other body appendages (Hayes & Armstrong, 1961; Aiken, 1980). A similar area of soft exoskeleton on the chelipeds is found in two additional species, *C. lorentzi* and *C. albertsii* (Riek, 1951) but no function has been suggested for the patch in these species either. All these three species with a soft patch are very closely related and may in fact be part of a single polytypic species (C. M. Austin, pers. comm.). In a recent revision of the systematics of the freshwater genus *Cherax*, the most closely related species to *C. quadricarinatus* on the basis of allozyme data was *C. rhynchotus*, which has an intermediate patch condition that is of a white colour and only partly uncalcified (Austin, 1996).

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The location of the soft red patch on the outer surface of the claw presents an intriguing enigma because of the impairment of the fighting ability of the males, which like many other clawed crustaceans use these appendages in intra- and interspecific aggressive interactions. The soft membrane of the patch can be easily ruptured, resulting in excessive loss of haemolymph and damage to the soft tissue underneath it.

In this paper, the present state of knowledge of various aspects of the red patch structure, development and endocrine control is reviewed. Based on this knowledge, possible proximate and ultimate functions are suggested for this sexually dimorphic structure, as well as future directions for exploring this enigma.

RED PATCH DEVELOPMENT AND ITS ENDOCRINE CONTROL

Cherax quadricarinatus males in communal culture in Queensland have been reported to develop red patches while at a small size of 20–30 mm orbital carapace length, concomitantly with the allometric growth of the claw (Thorne, Fielder & Hansford, 1989). Populations of redclaw originating from separate river systems in northern Queensland differed with regard to the size at which the red patch first appeared in males (Jones & Rusco, 1996).

The development of the red patch, like that of other male sex characters in crustaceans, is under the endocrine

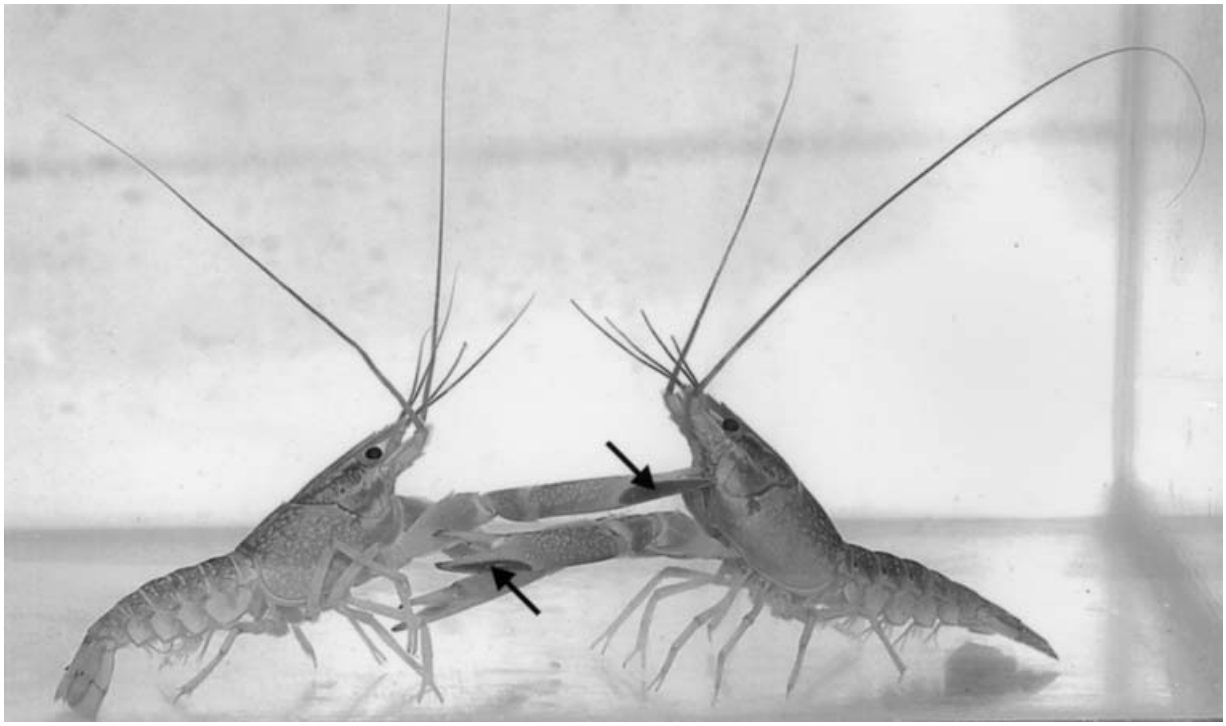

Fig. 1. Two *Cherax quadricarinatus* males during escalated fighting. Note their elevated position while facing one another; their carapaces and antennae are directed upwards and their claws are in close contact with the soft red patch (arrowed) visible.

control of the androgenic gland (AG). In decapods, this gland is responsible for sexual differentiation, gonad function, development of sex characters and somatic growth rate (Charniaux-Cotton & Payen, 1988; Sagi, Snir & Khalaila, 1997; Sagi & Khalaila, 2001). The AG has recently been localized adjacent to the proximal portion of the sperm duct in Parastacidae; in *C. destructor* (Fowler & Leonard, 1999) and in *C. quadricarinatus* (Khalaila *et al.*, 2001). The AG of *C. quadricarinatus* has been identified as a long thin cord-like tissue situated underneath the articular membrane of the last thoracic sternum, connected to the proximal (ejaculatory) portion of the sperm duct on one side and to the cuticle of the last thoracic sternum of the fifth walking leg on the other side. The first evidence showing a regulatory effect of the AG over the development of the red patch was provided by experiments conducted in *C. quadricarinatus* intersex individuals. Intersex individuals in this crayfish are phenotypic and functional males having both male and female openings, an active testis and an arrested ovary (Sagi *et al.*, 1996). Removal of the AG from mature intersex individuals (30–50 mm orbital carapace length) caused a shift in the balance between male and female components of the reproductive system (Khalaila, Weil & Sagi, 1999). After 1 year the red patch of andrectomized intersex individuals was significantly smaller than that of intact ones. Moreover, implantation of the AG in juvenile females (*c*. 3 months old) caused development of male-like sexual characters in the implanted female. Most of the implanted females (91.6%) developed a red patch on their propodus, while none of the control females developed such a male sexual character (Khalaila *et al.*, 2001). The implantation of the AG also resulted in the development of additional male secondary characteristics such as the size and shape of the propodus, the pleopods and the brood chamber. These morphological changes were also accompanied by increased aggressiveness of the implanted females (Karplus *et al.*, 2002).

RED PATCH STRUCTURE: A POSSIBLE SENSORY ORGAN?

A morphological study of the red patch with the aid of light microscopy demonstrated that the patch cuticle lacks an outer layer of endocuticle and the layers present are about half the width of those in adjacent hard cuticle regions (Thorne, Fielder & Hansford, 1989; Thorne & Fielder, 1991). The density of sensillae on the red patch cuticle was found to be similar to that on the hard cuticle of the claw. However, these comprised only simple sensillae, whereas the adjacent cuticle contained both simple and feathery sensillae. There was no difference between the sensilla density on the red patch and that on the corresponding area in females. The lack of special sensory organs on the patch and beneath it, and the similarity between the distribution of the general sensory sensillae on it and that on the adjacent area of hard cuticle of the claw, suggest that the patch is not a specialized sensory organ. However, further studies with the aid of electron microscopy should be carried out to validate this point.

WHAT KIND OF INFORMATION MAY THE RED PATCH CONVEY?

Communication modalities

The red patch may transmit information through two modalities: visual and tactual. Thorne *et al.* (1989) argued that the red patch is unlikely to be a visual signal, since crayfish are active mainly at night, and several species of crustaceans have been reported to be relatively insensitive to red light (Goldsmith & Fernandez, 1968; Shaw & Stowe, 1982; Cummins, Chen & Goldsmith, 1984). Nevertheless, the red patch may function as a visual signal, since red-claw crayfish are also active during the day, as observed in the laboratory (Barki & Karplus, 1999; Levi *et al.*, 1999). Often during the day, only part of the crayfish claw including its red patch is exposed, while the rest of its body is concealed inside a shelter. Because the patch bears a wide range of colours, some hues are likely to be visible to the crayfish. Red claw occur in their natural environment both in turbid water bodies and clear water streams and creeks; thus there are certainly places where the red patch is visible (C. M. Austin, pers. comm.).

The red patch may also provide tactile stimuli, since the softness of its cuticle is clearly different from that of the surrounding hard cuticle of the claw.

Possible types of information

The red patch of *C. quadricarinatus* may transmit three messages concerning the gender, size and quality of its owner.

(1) *Gender*. The occurrence of females with a red patch is rare. Thorne *et al.* (1989) reported on a low occurrence of *c*. 1% of females with patches, and suggested that these females possess an androgenic gland. A much lower frequency of females with patches was observed in Israel among pond-raised females at harvest ($< 0.1\%$) and in the laboratory. Furthermore, examination of several thousand pond-raised males revealed that only a few individuals lacked a red patch and these were relatively small, while large individuals invariably possessed a red patch. Thus, the presence of a patch is a reliable indicator that its owner is a male.

(2) *Size*. The morphometric relationship between the lengths of the red patch, the propodus and the carapace were analysed in a pond-raised population. Linear regression of the red patch length *vs* propodus length was highly significant ($r = 0.904$) and so was the regression of propodus length *vs* carapace length ($r = 0.945$) (Sagi *et al.*, 1996). The length of the red patch is thus a highly reliable indicator of its owner's size. However, size can be also derived from the length of the whole propodus.

(3) *Male quality*. The colour of the patch varies from bright red to a pale orange. Individuals collected from earthen ponds, rich in plant materials and other natural foods, invariably possess brownish claws with bright red patches. Males raised in captivity and fed strictly on commercial pellets lacking carotenoids possess bluish claws and pale orange patches. This observation was carried out on thousands of specimens raised either in earthen ponds or in intensive systems. Since crayfish cannot synthesize carotenoids, variation in patch colour reflects variation in the level of ingested carotenoids. Different types of carotenoids (free astaxanthin, astaxanthin bound to mono- and di-esters and β-carotene) may accumulate in the bodies of *C. quadricarinatus* fed different types of plants and algae (Harpaz *et al.*, 1998). The reduced hue and saturation of the patch when carotenoid-rich food is limited probably reflects a reduced nutritional state, which in natural environments depends on the foraging efficiency of the male. A comparison of haemocyte counts and exoskeleton pigmentation in the related crayfish *Cherax tenuimanus* reared in semi-intensive earthen ponds and intensive systems revealed a reduced pigmentation and physiological state in the intensive system which was attributed to nutritional deficiency (Jusila, 1997). Thus, the patch colour is a condition-dependent character, honestly reflecting the physiological health of a crayfish, as affected by nutrition. Astaxanthin added to the juvenile redclaw diet resulted in an increase in survival and growth by $> 20\%$ compared with controls lacking this supplement (Rouse & Rash, 1999). However, in another study (Harpaz *et al.*, 1998), growth and survival of redclaw were not affected by the addition of carotenoids to their diet. We have no explanation for these contradictory results. Irrespective of the direct effects of carotenoids *per se* on *Cherax quadricarinatus*, the enhanced effects of carotenoid extracts on growth and survival reported for crustaceans (Bordner *et al.*, 1986; Sommer, Morrissy & Potts, 1991) may be the result of increased levels of essential growth factors such as polyunsaturated fatty acids and or sterols in these extracts (Omara-Alwala *et al.*, 1985). Thus the pigment (e.g. astaxanthin) indicates the presence of growth stimulating factors.

WHAT ARE THE POSSIBLE SIGNAL FUNCTIONS OF THE RED PATCH?

Being an honest character conveying reliable information on gender, size and quality, the red patch may function as a signal appropriate to several situations, depending on the context (e.g. sexual or agonistic). The following non-exclusive hypotheses concerning the signal function of the patch are evaluated in the light of our present knowledge of the social behaviour of *C. quadricarinatus*.

Stimulating females to copulate

Anecdotal reports indicated that the red patch of the male contacts the female during courtship when the male makes a series of short, sharp jabs at her (Thorne *et al.*, 1989; Thorne & Fiedler, 1991). However, in a study on female receptivity in *C. quadricarinatus* (Barki & Karplus, 1999),

eight mating events were recorded on video and revealed no actual contact. Rather, the male faced the female with the outer side of the propodi of the chelipeds including the red patch visible to the female, as also described by Sammy (1988). The male then performed short and rapid extensions of the chelipeds in the direction of the female (thrust) with no contact. This action and the prior exposure of the female to the patch may function to inhibit an escape response and stimulate co-operation in receptive females during mating.

Signalling male quality to females

In an earlier section the suitability of the red patch for conveying reliable information concerning male size and quality was discussed. However, the patch seems to be disadvantageous to its bearer because of the soft, vulnerable and easily ruptured membrane located on the claw, the male's major weapon. The evolution of such traits that are seemingly disadvantageous is explained by the handicap principle (Zahavi, 1975, 1977), according to which males that can manage in spite of a handicap send a message of their proven quality. The red patch has an important property, which is required by theory, namely it is resistant to cheating. Cheating with respect to size would be too costly, since a small male developing a relatively large soft patch would be left with claws unable to perform essential functions like feeding, fighting and deterring predators. Cheating with regard to colour is impossible since crayfish cannot synthesize carotenoids. Advertising male quality by the patch may be useful in the context of mate selection by females. In two groups of fishes, guppies and sticklebacks, females prefer to mate with males with well-developed carotenoid-based colours (Kodric-Brown, 1985; Baker, 1993). Two studies actually demonstrated that female guppies prefer males with bright orange spots over males with dull spots. In one case variation in brightness was the result of laboratory manipulation of diet (Kodric-Brown, 1989), in the other, it was due to laboratory manipulation of parasitic infection (Houde & Torio, 1992).

Signalling in aggressive interactions

The soft red patch may convey information on the size and quality of its bearer to potential male competitors and thus allow assessment of the resource holding potential (RHP) by the adversary. Higher levels of aggression were displayed between interacting males than between males and females (Karplus *et al.*, 2002). Thus, the absence of a patch may reduce aggression towards females. In a typical escalated fight two opponents face each other in the 'body up' position (Tierney, Godleski & Massanari, 2000), with the carapace elevated obliquely and antennae pointing upwards (Fig.1). In this position the red patch is clearly visible and the opponents perform 'chela contact' (Tierney *et al.*, 2000) usually with 'interlocked' chelae (Bruski & Dunham, 1987). During fighting the opponents engage in pushing against each other and grasping the antennae, pereiopods and other anterior body parts. The red patch was not targeted or accidentally ruptured during fights. The loser retreating (either walking or tail flipping) or turning aside and lowering the body against the substrate terminates the fight.

The importance of carotenoids in signalling during aggressive interactions between males was elegantly demonstrated in male firemouth cichlids by staging encounters under either white or green light. Only under white light did fish raised on a high-carotenoid diet have a significant advantage in contests, which was attributed to the visibility of the intense carotenoid pigmentation, which reflected a general quality with more energy available for fighting (Evans & Norris, 1996).

CONCLUSIONS

The red patch in *C. quadricarinatus* males has a combination of properties that make it most suitable for conveying reliable information on the characteristics and quality of the crayfish. This unique structure fits into criteria for traits with a signal function as predicted by theory (Zahavi, 1987). The suggested signal functions of the red patch are not mutually exclusive since it may play multifunctional roles in male–female and male–male interactions. Investigations are needed in controlled experiments in the laboratory as well as in the natural environment to validate the specific roles of the patch and to understand their evolution. Our knowledge of the endocrine control of the development of the patch and the ability to manipulate it may aid in achieving this goal.

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