Chapter 3
To What Extent Can Freshwater Crayfish Recognise Other Crayfish?

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The ability for sophisticated and flexible recognition by vertebrates has been known for a very long time, probably because it features so strongly in human social behaviour and is therefore easily recognised in other species. As evidenced by the increasing number of studies and reports (Tibbets and Dale 2007), recent years have seen increased interest in the occurrence and properties of this response in non-vertebrates where it may not be so easily identified. Studies have now been undertaken on a wide range of organisms exemplified by the chapters of this review collection but our understanding of this phenomenon is still at an early stage and we can make few generalisations beyond its wide occurrence. In retrospect, its incidence should not be surprising. The advantages that it confers are apparent so that, all things being equal, it should be selected for. What characteristics of life history and interaction with con-specifics are likely to predict its presence and what factors predict the level of sophistication and flexibility? These questions remain to be answered but, based on what has already been discovered, we postulate here that it will evolve wherever there is a capacity for analysis of sensory signals that carry identifying information.

The focus of our chapter is to summarise the present state of knowledge concerning recognition in freshwater crayfish. When discussing this topic, it is not possible to consider crayfish alone because, at this stage, only limited data are available from crayfish species. So here we will refer to some findings from lobsters and other decapod species to provide a context for linking the known elements for crayfish. In the text we use the various degrees of "recognition" according to the definitions developed by Gherardi et al. (2005). We will deal with chemical recognition first, then with visual recognition and, even though there is a

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dearth of information, the intriguing matter of the relationship between the two—multimodal recognition. Along the way we will briefly mention some of the similarities to and differences from other invertebrates (reviewed more fully elsewhere e.g. Tibbetts and Dale 2007; Breithaupt and Thiel 2011) and will finish with some speculation about the evolution of recognition in crayfish and strategies for testing such hypotheses.

Social Behaviour and Hierarchies—A Valuable Paradigm for Crayfish Recognition Research

Investigations of recognition between crayfish conspecifics has predominantly involved dominance pairs or hierarchies established during competition for mates, shelter and food. It is by experimental manipulation of these encounters that the mechanisms and quality of recognition can be elucidated. The literature on staged encounters is extensive and has spanned more than half a century so we only consider here the key elements for recognition in the present context. It has been used, for example, to investigate the separation of class recognition (e.g. gender and dominance) from individual recognition (Gherardi et al. 2005).

Like many decapods, social crayfish establish dominance hierarchies of some complexity (e.g. Bovbjerg 1953, 1956; Daws et al. 2011) but the durability of these are not as well understood as those in lobsters, although there is some evidence that they are not as long-lasting (Bergman et al. 2003). The hierarchies are established on the basis of success in physical encounters—contest encounters—apparently made up of relatively common, stereotyped sequences across species (Moore 2007). These typically involve meral-expansion threat displays which, if they do not deter the contest partner, may be followed by claw grasping, wrestling and claw ripping leading to damage to the body and limbs. Eventually one contestant, the loser, retreats. None of this requires recognition by the contestants. The evidence for recognition comes from the interaction between individuals when they meet subsequently (e.g. Fig. 3.1). It would, in principle, be possible for contestants to test their standing against other crayfish by engaging in a series of short fights. As in most animal social systems, however, the value of avoiding potentially damaging physical encounters by both winners and losers is such that mechanisms evolve to render a rematch unnecessary or of reduced intensity to avoid physical harm to the protagonists.

Research with staged encounters has provided the foundation for the majority of recognition studies because it relates critical factors to controls for testing when recognition is occurring. Winner-loser effects, for example, aggression, isolation and hierarchy formation are known to alter crayfish behaviour and need to be considered in good experimental design (e.g. Bovbjerg 1953; Issa et al. 1999; Goessmann et al. 2000; Daws et al. 2002; Bergman et al. 2003; Baird et al. 2006; Hemsworth et al. 2007; Patullo et al. 2009). Most of our discussion here comes from research that considered these factors.

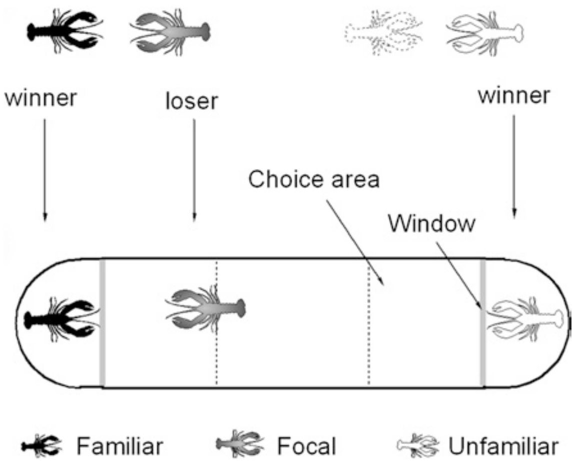

Fig. 3.1 Social encounters can be combined in test paradigms to demonstrate recognition. In this example, pairs of crayfish (*top*) meet and establish social rank or winning ability. A focal animal is placed in a test arena (*bottom*), in this case the losing crayfish from one of the previous encounters. Recognition is then tested by offering a choice between crayfish at either ends of the arena, which are visible to the focal crayfish through transparent windows. Status is controlled in the process by careful selection of the right combinations of crayfish in the ends, between winners and losers and familiar versus unfamiliar animals from the first encounter. Further detail Van der Velden et al. (2008)

Chemical Communication and Recognition in Crayfish

Like all aquatic crustaceans, crayfish possess many chemoreceptors (Bullock and Horridge 1965; Atwood and Sandeman 1982; Breithaupt and Thiel 2011). These may be found on all areas of the body but are concentrated on the antennules, antennae, mouthparts and at the tips of the pereiopods. Numerous studies indicate that they are used in social communication and are responsible, although not necessarily exclusively, for recognition (e.g. Breithaupt 2011, research summarised in Hemsworth et al. 2007 and more widely in other crustaceans Breithaupt and Thiel 2011).

The most effective systems permit recognition to occur at a distance without need for physical contact. The main source of chemical information available between conspecifics is broadcast in urine expelled from a small, anterior nephropore opening near the base of the antennae. Lobsters and other decapods can control the timing and direction of the urine stream (Aggio and Derby 2011) and there is increasing evidence that crayfish do the same, from incidental behavioural observations and the anatomical structures to facilitate it (Breithaupt and Eger 2002; Berry and Breithaupt 2010 and others cited in Breithaupt 2011). Information on the nature of the substances within the urine that are responsible for the communication between decapods is fragmentary and almost non-existent for crayfish. Discovering how species- and function-specific these are is an important objective for future research.

In clawed lobsters, where the most extensive studies have taken place, the most important receivers of urine signals are the aesthetasc hairs on the antennules (Hallberg and Skog 2011), although similar receptors are found elsewhere, particularly on the mouthparts and periopods (Johnson et al. 1984). Interference by amputation or mechanical blocking of the hairs to reduce or remove the signals appear to reduce or even abolish transfer of sexual information (*Homarus americanus*, Bushman and Atema 1997) although there may be some gender differences in the other homarid species (*H. gammarus*—Skog 2009a, b). Dominance information is also eliminated by similar experiments (Karavanich and Atema 1998a, b; Johnson and Atema 2005).

Those social crayfish studied thus far most commonly establish dominance hierarchies, but there is evidence of differences in the way the information for them is received and the way they are established and maintained. The situation in crayfish is similar to that found in lobsters in some aspects. *Procambarus clarkii* formed enduring hierarchical structures which ensure that fights with former winning opponents were either avoided or were shorter in duration than those between previously known animals (Horner et al. 2008). Shorter duration of subsequent encounters also occurred in *Astacus leptodactylus* (Breithaupt and Eger 2002). Furthermore, interference with the aesthetascs after an initial encounter resulted in behaviour more similar in duration and intensity to initial encounters than if the aesthetascs were not manipulated. A similar outcome was observed in fights between *Orconectes rusticus* with the important exception that the memory of opponents appeared to last for only about 60 min (Bergman et al. 2003). Recognition in this species is probably less sensitive or situation-specific than in *P. clarkii* because "winner" odour in the surrounding water influenced the outcome of encounters even if it was not from a former opponent and the outcome of choices in Y-mazes (Zulandt Schneider et al. 1999, 2001; Bergman and Moore 2005). This type of "status" recognition mechanism appears to be even more evident in *A. leptodactylus* and *Procambarus acutus* which show clear "former winner" and "former loser" behaviour whether or not they have previously encountered the opponent (Breithaupt and Eger 2002; Gherardi and Daniels 2003).

Examples mentioned throughout the reviews in this collection and in that of Breithaupt and Thiel (2011) reveal many more details of a rich diversity in signalling mechanisms and outcomes. We have barely scratched the surface of this variation in crayfish but, given the range of ecological situations in which crayfish live, diversity rather than conformity must be expected. Following a study of communication in *A. pallipes* which did not appear to match the then known commonalities of sexual communication in crayfish, Acquistapace and colleagues proposed that the diverse natural history of crayfish species would be found to mediate multiple variations in communication systems (Acquistapace et al. 2002).

Individual recognition is more difficult, and quite laborious to establish experimentally than class or group recognition. To date, the only convincing method for establishing the presence of individual recognition is to test for evidence following staged encounters using devices such as choice experiments or a second round of fighting. Examples of assessment in choice experiments include those in which losers of contests are given options between the winner of one of their earlier contests and a matched (size, colour, gender etc.) unfamiliar winner of a contest in which the focal loser was not involved. The focal animal then demonstrates that it can recognise the familiar animal by a non-random preference for the winner or loser (e.g. Crook et al. 2004, Fig. 3.1). Paradigms to test individual recognition by successive fights were applied to chemical recognition of urine in the lobsters before crayfish (Karavanich and Atema 1998a, b). A number of studies suggest that the ability for individual chemical recognition is also present in some crayfish species but it has not yet been definitively demonstrated. There is evidence that *C. destructor*, which can use visual information for individual recognition of previous opponents (see below and Fig. 3.1), can also use chemical information for this purpose but the design of the experiment did not entirely preclude familiar recognition (Crook et al. 2004). Similarly, conclusions from outcomes of second rounds of fights between *C. dispar* (Seebacher and Wilson 2007) and those following observation of contests in *P. clarkii* (Aquiloni et al. 2012) suggest that individual recognition could exist, although the experiments do not preclude the possibility of explaining the result by status recognition or experience. Given the intensity of research across several genera of crayfish we predict that this will be confirmed experimentally for additional species shortly.

Visual Communication and Recognition in Crayfish

Studies of crustacean eyesight reveal that stomatopods have the most advanced vision in the Class Crustacea (e.g. Marshall et al. 1996; Chiao et al. 2000; Cronin et al. 2001). Crayfish vision is not thought to be as advanced, but vision is important in many behavioural situations. Crayfish change behaviour in response to visual cues of various shape, size and colour (wavelength) indicating that sight is a valuable sense in their world.

Crayfish have at least one photosensitive pigment and receptor system (Kennedy and Bruno 1961). There is also conflicting evidence that supports the presence of a second pigment and receptor system (Wald 1967). In agreement, is that crayfish can detect different wavelengths of light throughout most of the colour spectrum that is visible to humans. The peak sensitivity of the main system is at about 570 nm, yellow, and this decreases as wavelengths approach 650 nm, red (Kennedy and Bruno 1961).

What does this visual ability mean to a crayfish? At the simplest level, objects and shadows will cause behavioural change. Waving a human hand over the body can cause the animal to react and adopt a posture known as the defence response where the abdomen extends, the animal arches its back and spreads its chelae (Kelly and Chapple 1990). Other threatening shadows and looming objects also induce defensive reactions in *P. clarkii* (Glantz 1974a, b, 1978; Beall et al. 1990). Further to this, fights between individuals of the crayfish *O. rusticus* last longer and occur at a more intense level in dim light compared with the same behaviour

Fig. 3.2 Greebling on a crayfish. Different coloured patches added to a crayfish body are used to determine focus areas of visual recognition in *Cherax destructor*. Further detail in Van der Velden et al. (2008)

observed in bright light (Bruski and Dunham 1987). Female *P. clarkii* also need visual cues before they can distinguish a male mate (Aquiloni et al. 2009). The last two examples indicate that crayfish pay attention to visual cues beyond shadows so that recognising another crayfish may reveal the importance of this sense.

From shadows to shapes, greebles were the main method used to demonstrate that this visual acuity was sophisticated enough to recognise body parts and thus vision could be a modality used to recognise another individual. The art of greebling involved modifying the appearance of an animal with controlled artificial forms to test hypotheses (Gauthier and Tarr 1997, Fig. 3.2). So just as a human could distinguish two similar people by looking at hats on their heads, for example a magician's cylindrical top hat from a Mexican's conical wide-brimmed sombrero, research showed crabs could distinguish one another based on objects attached to their backs (Hazlett 1972). The addition of other greebles, such as artificial markings, has demonstrated similar results in a range of invertebrates (Dunham 1978; Vannini and Gherardi 1981; Detto et al. 2006). This raises the question of whether or not crayfish can also analyse body features of an individual to recognise it later and, if so, what parts of the body are important to remember. Evidence in two species suggests crayfish can do this.

Cherax destructor prefers to spend more time closer to an individual it has met during a previous fight rather than with an unfamiliar crayfish when only visual cues of the opponent are available to make judgment (Crook et al. 2004). This confirms that *C. destructor* is capable of binary recognition between the familiar and the unfamiliar. This response is consistent with dear enemy theory where animals prefer to spend time with familiar individuals, even if they are stronger, rather than battle with the unknown and risk higher energetic cost (Fisher 1954).

In addition, *P. clarkii* is attracted to it's reflection in mirrors (Drozdz et al. 2006; May and Mercier 2006). This discovery could be evidence of a form of visual self-recognition similar to that of humans recognising their own reflection. It needs further testing, however, because the outcome was different depending on the social status of the crayfish (May and Mercier 2006). That is, *P. clarkii* may only recognise its reflection as a "crayfish", not as itself, or only be responding to movement of an object.

The familiar recognition and potential self-recognition experiments with *C. destructor* and *P. clarkii* demonstrate that a focal crayfish can recognise up to two individuals. Aquiloni and Gherardi (2010), Aquiloni et al. (2010) suggest the

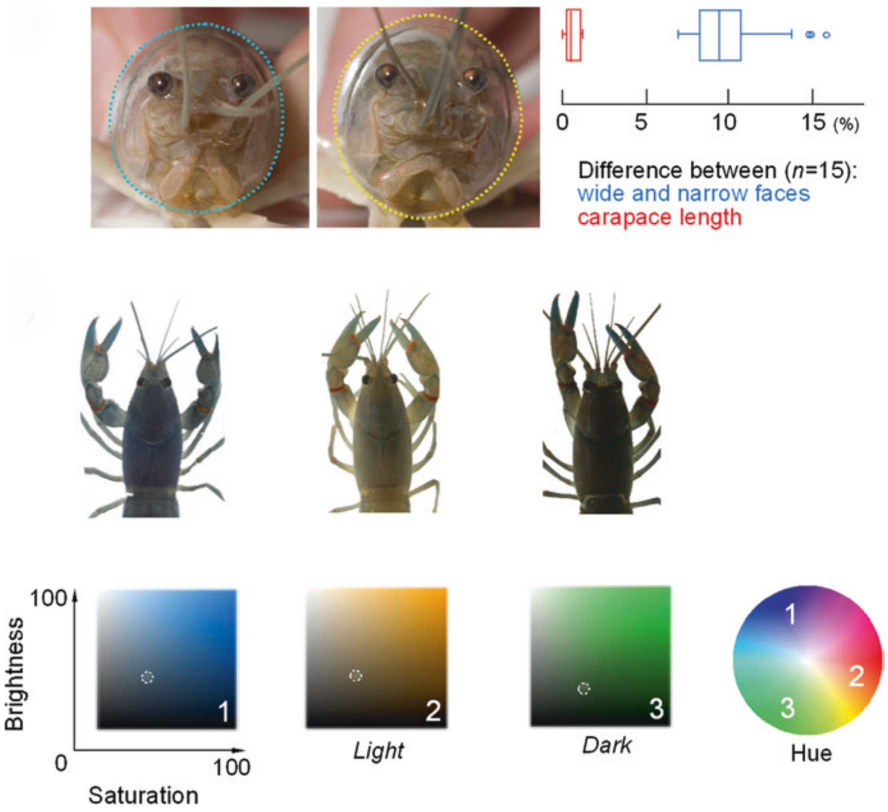

Fig. 3.3 Variation in visual features of *Cherax destructor*: facial width (*top*) and colour (*middle and bottom*). Further detail in Van der Velden et al. (2008)

ability is more advanced because they demonstrated that *P. clarkii* can distinguish between three crayfish. They allowed a female to watch two males fight and then gave the female a visual choice between one of those males and a third, unfamiliar male. The female spent more time in the vicinity of the familiar male. This outcome suggests that true individual recognition is present in some crayfish and provides another possible reason why crayfish might recognise one another—in sexual selection to identify optimal mates.

A combination of visual clues must be analysed for successful recognition of multiple individuals. Markings on the anterior carapace, natural colour of the carapace and facial width are three features that *C. destructor* can recognise (Van der Velden et al. 2008, Figs. 3.2 and 3.3). It is not possible to determine the exact physical features being analysed in the Van der Velden et al. (2008) study because facial width may, for example, be correlated to other physical attributes such as body size. Nonetheless, colour and facial width were not correlated so this species must be using at least a small matrix of cues to remember each animal it meets (Fig. 3.3).

The extent of the matrix of important visual clues to identity and the number of unique individuals able to be remembered may be increase by future investigation. To date however, crayfish recognition research has been limited to paradigms where opponents fight, whether it is to monitor behavior in that fight or a fight prior to an experimental test. This approach may not easily lend itself to testing interactions beyond those currently known and may require a new strategy to reveal the full complexity of crayfish visual recognition.

Multimodal Communication and Recognition in Crayfish

Crayfish are likely to benefit if they can use more than one sense to communicate because in the wild conditions vary. Water can range from being stagnant to high flowing and turbidity can fluctuate (Merrick 1991). A changing local environment means that not all modes of communication will be available all the time so survival should favour species with multiple information channels that permit them to apply the best sense for the presenting conditions. We are probably yet to know how flexible crayfish are in this respect, but the number of reports of evidence for multimodal communication in crayfish is on the increase. Callaghan et al. (2012) showed that chemical, tactile and visual information can be used by *O. rusticus* in the establishment of hierarchies. By interfering with each of these modalities in turn they showed that in this species under the test circumstances the effectiveness ranking is chemical > tactile > visual. Bouwma and Hazlett (2001) also investigated multiple modalities, but only investigated two sensory pathways. They revealed that both visual and chemical cues are used by *Orconectes propinquus* to detect fish predators.

There is also increasing evidence that one crayfish can use multiple senses to recognise another. Both visual and chemical information can be used in gender recognition between individuals of the species *A. pallipes* (Acquistapace et al. 2002). Gender recognition may also influence subsequent encounters in *P. clarkii,* along with mate choice and eavesdropping—one crayfish observing fights between others (Aquiloni and Gherardi 2008; Aquiloni et al. 2009). Both visual and chemical information are also important in communication between familiar *C. destructor* opponents as mentioned in previous sections here (Crook et al. 2004).

Crayfish have a very keen tactile sense with which to explore their environment (Sandeman and Varju 1988; Basil and Sandeman 2000; McMahon et al. 2005; Patullo and Macmillan 2006) and it is likely that this also plays a part in agonistic behaviour, particularly in nocturnal species or those living in turbid waters. There is, for example, some evidence that *C. destructor* combines chemical information and tensile force monitored by its claws in the establishment of dominance relationships (Seebacher and Wilson 2007). So it is likely that we have not yet revealed the full skill set of how crayfish use multiple senses, not only for recognition but also in other parts of their everyday lives.

Sorting out the use and extent of multimodal systems is challenging but the issues involved speak to some very interesting questions in behaviour and its evolution. For example, to what extent are their residual abilities for the availability of a parallel information channel if it is not used for a significant evolutionary period? What neural changes are likely to accompany this situation? What would this tell us about the cost of maintaining a disused channel? The variability of crayfish biology adds to the intrigue of how and why animals evolve their senses. Thus, they form a particularly attractive group for gaining insight into these kinds of behavioural evolutionary questions, adding to the other advantages already advocated by others (see reviews in Breithaupt and Thiel 2011).

Making Sense of Diversity

It is clear that the information on recognition in social crayfish is fragmentary and related only to a few popular study species so it is still too early to assemble the elements of the jigsaw into a coherent picture without extrapolation that includes evidence from other crustacean groups (Table 3.1). While it is tempting to use results from other crustacean species, particularly other decapods to fill in the gap, it should be clear from our brief survey here that this is likely to be a productive enterprise only insofar as it informs us about the range of described possibilities and so assist us when embarking on research with new species.

It appears to us that we will gain a better understanding of not only recognition in crayfish, but also of the biological role of their communication, if we seek to study crayfish with particular ecological niches or needs and to compare the differences in communication systems employed. We advocate, for example, comparisons between crayfish living in lotic versus lentic environments, those with nocturnal habits against those with diurnal ones, those from clear waters versus those from turbid ones and so forth, the list is extensive. In this way we might hope to build a matrix of recognition responses based on biological factors. This understanding of the biological reasons for the evolution of particular

Table 3.1 A summary of the different levels of recognition across crayfish species demonstrated so far. Six species across four genera have been the main focus of research. They have revealed evidence for at least five potential types, or levels, of recognition. Compiled from references included in the text

Level of recognition	Species
True individual	*P. clarkii, C. destructor*
Familiar	*P. clarkii, C. destructor*
Gender (class)	*P. clarkii, A. pallipes*
Status/social rank (class)	*P. clarkii, P. acutus, A. leptodactylus, C. dispar, C. destructor*
Self(class)*	*P. clarkii*

* May vary depending on interpretation of methods and results.

communication strategies should permit us to predict the likelihood that a particular species will exhibit certain characteristics of recognition in its communication.

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