

# INDIVIDUAL AND STATUS RECOGNITION IN THE CRAYFISH, *ORCONECTES RUSTICUS*: THE EFFECTS OF URINE RELEASE ON FIGHT DYNAMICS

by

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## Summary

This study examined individual and status recognition in dyadic interactions between crayfish and determines how blocking the release of urine, a known source of chemical cues, may influence recognition. Behavioral characteristics of agonistic interactions were compared between crayfish pairs that fought each other previously (familiar) and pairs derived from individuals with past status history but no previous experience with one another (unfamiliar). To address the role of urine born chemical cues in recognition, fight dynamics were examined in urine blocked and non-blocked familiar and unfamiliar pairs.

Our results indicate the existence of status recognition in crayfish as first fights were longer than second fights and the statistical interaction between fight number and familiar/unfamiliar treatment was similar. Urine cues play a role in social recognition in that fights are longer and more intense when urine cues are absent than when urine cues are present. Communication of behavioral state through urine appears to play an important role in the agonistic interactions of crayfish.

*Keywords:* chemical communication, dominance hierarchy, crustacean, urine, social behavior.

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## Introduction

Aggressive or agonistic interactions are common in many species (Wilson, 1975; Dingle, 1983), and have been shown to play an important role in competition for space, shelter, and access to mates and food. American lobsters, *Homarus americanus*, acquire access to shelters through agonistic contests. Winners gain possession of the shelter, while losers are left to search for a new residence (Cromarty *et al.*, 1999). In vervet monkeys (*Cercopithecus aethiops sabaues*) (Raleigh & McGuire, 1989) and cockroaches (*Nauphoeta cinera*) (Breed *et al.*, 1980), males who are successful in successive agonistic encounters have higher reproductive success than those who lose encounters. In rainbow trout (*Oncorhynchus mykiss*) (Johnsson, 1997) and spotted hyenas (*Crocuta crocuta*) (Tilson & Hamilton, 1984) males with high success in agonistic encounters have preferential access to limited food resources.

Success in agonistic interactions may be due to several factors ranging from physical attributes of an organism to past events in which the organism has participated. Factors such as physical size (Beaugrand *et al.*, 1991; Huntingford *et al.*, 1995; Pavey & Fielder, 1996), weapon size (Barki *et al.*, 1991; Rutherford *et al.*, 1996; Vye *et al.*, 1997), and body symmetry (Beaugrand *et al.*, 1991; Sneddon & Swaddle, 1999) all influence the outcome of agonistic contests. Prior fight experience (Franck & Ribowski, 1987; Moore *et al.*, 1995; Hsu & Wolf, 1999), prior residency (Beaugrand *et al.*, 1996; Cromarty *et al.*, 1999) and nearest neighbor distance (Moore *et al.*, 1995; Höjesjö *et al.*, 1998) are examples of events in the organism's history, which may alter agonistic success. Although any one of these can be important in agonistic success, usually a combination of these factors determines an organism's fighting capability and the dynamics during agonistic contests.

Typically, agonistic contests progress through several stages of intensity beginning with threat displays and progressing to periods of unrestrained combat. This behaviour has been documented in a wide range of taxa including the blue gourami (Frey & Miller, 1972), swordtail (Franck & Ribowski, 1987), grasshopper (Steinberg & Conant, 1974), crayfish (Bruski & Dunham, 1987), and crabs (Huber, 1987). Consequently, at the conclusion of an agonistic encounter a social relationship is formed resulting in a dominant and subordinate individual.

Once a dominance relationship has been established, the frequency and intensity of interactions between dominant and subordinate combatants

decreases over successive encounters (Höjesjö *et al.*, 1998; Issa *et al.*, 1999). Subordinates are less apt to engage dominants, and tend to avoid the approach of dominant individuals (Johnsson, 1997; Guiasu & Dunham, 1999a). Changes in dominant and subordinate behaviour may be due to some form of recognition. Generally, organisms may use two mechanisms of recognition: individual recognition of a prior opponent, or the detection of the opponents' relative dominance status (Winston & Jacobson, 1978; Francis, 1988).

Individual recognition is defined as recognition of a specific individual through previous contact with that individual (Grier, 1984; Caldwell, 1985). Individual recognition not only maintains a stable dominance relationship, but also has the potential to decrease the number and intensity of continual interactions between two individuals. This has been demonstrated in *H. americanus* where the subordinates back away from and avoid a second confrontation with a familiar opponent (Karavanich & Atema, 1998b). Lower aggression in successive fights is also seen in *O. mykiss* (Johnsson, 1997), and sea trout (*Salmo trutta*) (Höjesjö *et al.*, 1998) due to individual recognition.

The hypothesized mechanism for individual recognition is through the recognition of a phenotypic trait or combination of traits belonging to the previous opponent (Barnard & Burk, 1979; Grier, 1984; Beecher, 1989). For example *H. americanus* recognize prior opponents through chemicals released in urine. When urine cues are blocked, lobsters are unable to recognize prior opponents and no decrease in aggression is observed (Karavanich & Atema, 1998a). By altering the visual cues associated with individuals in groups of familiar crabs (*Potamon fluviatile*), Vannini & Gherardi (1981) increased the aggressiveness of encounters between familiar individuals, demonstrating that visual cues are important in the recognition of familiar opponents.

The second potential mechanism of recognition is the recognition of status. Status recognition can be defined as the recognition of a combatant's dominance level that has been established during one or several prior encounters (Copp, 1986; Karavanich & Atema, 1998b). Unlike individual recognition, this does not require prior experience with the combatant, but like individual recognition, status recognition can also lower the number of aggressive contacts between unfamiliar and familiar organisms. Hermit crabs (*Pagurus longicarpus*) show decreases in aggression when facing both

familiar and unfamiliar opponents due to status recognition (Winston & Jacobson, 1978).

The basis of status recognition is through the recognition of an opponent's aggressive state, which can be interpreted as an organism's willingness to engage in an aggressive encounter (Winston & Jacobson, 1978; Copp, 1986). Continual success in agonistic encounters heightens aggression while continual defeat lowers aggression (Karavanich & Atema, 1998b; Goessmann *et al.*, in press). It has been shown that the aggressive state of cockroaches (*N. cinera*) is transmitted through chemical cues. Cockroaches release pheromones during agonistic encounters and the blend of chemicals an organism releases depends upon its experience in previous encounters, and allows information on status to be transferred to their opponent (Moore *et al.*, 1995). Transmission of aggressive state through chemical cues has also been suggested but not demonstrated in crayfish (Copp, 1986). In crayfish, aggression is closely linked to serotonin levels in the body and these levels change depending upon the past fight history of an organism (Sneddon *et al.*, 2000). These levels can be reflected in released chemical signals and therefore conceivably communicated to opponents. Status recognition through chemical cues in crayfish is supported by a study showing that crayfish have the ability to recognize unfamiliar dominant and subordinate individuals through chemical cues (Zulandt Schneider *et al.*, 1999).

In Crustaceans, sensory information plays an important role in agonistic interactions and recognition. Karavanich & Atema (1998a) showed that chemical cues released in lobster urine were important in individual recognition. Elimination of chemical cues increased the duration and aggression in fights, essentially eliminating individual recognition. Snyder *et al.* (1992, 1993) examined mating behavior in lobsters and suggest that chemical cues are important in normal mating behavior. Lobsters deprived of visual cues still exhibited normal mating behavior (Snyder *et al.*, 1992)

Bruski & Dunham (1987) found that visual cues are important for efficient communication during crayfish agonistic encounters. At low light levels, behaviors that involve tactile information are performed at a higher rate and more time and energy is devoted to fighting as compared to variables measured at ambient light levels (Bruski & Dunham, 1987). The use of the antennules, crustacean chemosensory organs, in agonistic interactions has also been well documented (Rutherford *et al.*, 1996; Smith & Dunham, 1996). Dominant organisms exhibited an increased rate and

duration of antennule movement when compared to the rate and movement of a subordinate's antennules (Rutherford *et al.*, 1996). Zulandt Schneider *et al.* (1999) also showed that chemical signals are important for social recognition in crayfish in that both socially naïve and crayfish with social experience recognize the status of dominant and subordinate organisms solely through chemical cues.

The purpose of this study is twofold; to examine the existence of individual and status recognition in the crayfish, *Orconectes rusticus*, through agonistic interactions and the role of urine released odors in crayfish social recognition and agonistic interactions. We hypothesize that crayfish in agonistic encounters with conspecifics utilize individual and status recognition and that olfaction plays a role in this communication.

## Methods

### *Crayfish*

Adult male crayfish, *Orconectes rusticus*, were collected from the Portage River, Wood County, Ohio from March to August 1999. Carapace lengths of crayfish were measured with calipers to the nearest 0.01 millimeter. 150 male crayfish were used with an average carapace length of  $3.11 \pm 0.04$  cm. Crayfish were individually marked with Testors® paint in the center of the carapace, and housed singly in  $10 \times 10$  cm ventilated plastic containers in a flow through holding tank ( $48 \times 154 \times 31$  cm). Crayfish were kept on a 14 : 10 L : D cycle at 23°C. The crayfish were fed 0.01 g of rabbit chow three times a week.

### *Experiment 1: Social recognition*

#### Experimental design

Crayfish were isolated for one week prior to any experimental interactions. Unpublished previous work in our lab and published work in others have shown that one week of isolation is enough to remove any prior social effects (Karavanich & Atema, 1998b; Guiasu & Dunham, 1999b). Crayfish were sized matched into pairs that did not differ by more than 3 mm in carapace length. Crayfish were used only once in the course of the experiments.

Each crayfish participated in two rounds of fighting. The first round of fights established a dominance and subordination relationship with a specific opponent. Second fights were designated as either familiar or unfamiliar. Crayfish in the familiar fights fought the same opponent that they fought in the first fight. In this case both the identity of the opponent and the status of the opponent have been encountered previously by the combatants. In the unfamiliar treatment, crayfish fought an opponent who had the same fight history as in the familiar treatment, but was unknown to that particular crayfish. In this case the individual identity of the opponent is unfamiliar, but the opponent's status was not (See Fig. 1). Ten sets of fights were run in each treatment.

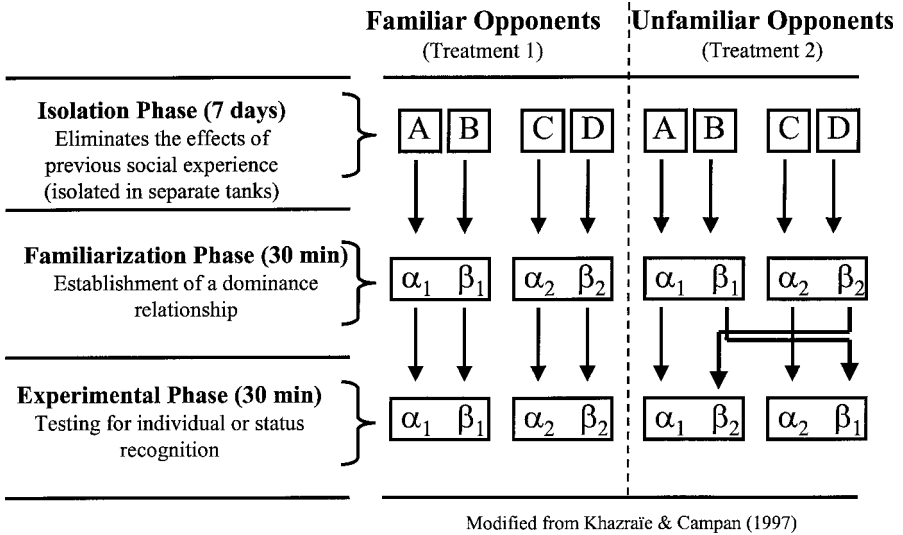


Fig. 1. A schematic diagram showing the experimental fight set up.  $\alpha$  indicates a dominant individual while  $\beta$  signifies a subordinate individual. In the isolation phase organisms were isolated for one week to eliminate any prior experience. A, B, C, and D represent organisms isolated in separate tanks during the isolation phase. In the familiar experimental phase organisms fought their opponents from the first fight. In the unfamiliar experimental phase opponent's status had been encountered before but not the actual individual. Arrows show the movement of crayfish from treatment to treatment.

*Experiment 2: Urine release*

Experimental design

To examine the role that urine plays in individual and status recognition, crayfish nephropores were blocked 24 hours prior to experimentation. Urine is the source of other context specific social signals in crayfish (Zulandt Schneider & Moore, 2000) and has been shown to be important sources of information in other crustacean species (Bushmann & Atema, 1997; Karavanich & Atema, 1998a). Previous studies have shown that catheterized *Procambarus clarkii* do not release urine indiscriminately (Zulandt Schneider & Moore, 2000). Simple movements, walking and feeding do not illicit urine release and no appreciable amount of urine could be collected over a 24-hour period. Urine is only released within certain behavioral context such as a distress situation. Under these conditions, significant volumes (up to 1.04 ml) can be released (Zulandt Schneider & Moore, 2000). Given these findings, we concluded that blocking the nephropores had no significant effect on the mechanics of movement or fighting.

Urine blocking

Crayfish were randomly placed into two experimental groups, urine present and urine absent. Crayfish in both groups were removed from their containers and restrained from movement on their backs using a customized restraint board. Three coats of 5-minute epoxy (Devcon®)

were applied over the nephropores to block urine output (approximately 0.3 mm thick). Each coat dried for approximately six minutes before the next coat was applied. Animals were placed back into their containers and the epoxy was allowed to cure for one hour before crayfish were returned to the holding tank. Animals were acclimated to the blocked nephropores for 24 hours before they were used in the experiment.

The crayfish in the urine present experimental group had the epoxy blocking their nephropores removed before the crayfish were placed into their respective sections of the experimental tank. In the urine absent experimental group the epoxy was not removed. To control for handling effects, the crayfish were handled in the same manner regardless of treatment. Crayfish were then subjected to either the familiar or unfamiliar fight protocol as explained in experiment 1.

#### Experimental protocol

A Plexiglas tank ( $40 \times 40 \times 14$  cm) was constructed with four removable dividers that separated the tank into four equal sections ( $20 \times 20 \times 14$  cm). A crayfish was placed in each section and allowed to acclimate for 15 minutes. After 15 minutes, dividers were lifted and the first encounter commenced. The crayfish had the opportunity to interact for 30 minutes during the first encounter. At the end of the first encounter the crayfish were removed from the fight arena and returned to their individual containers. The experimental tank was drained, and all dividers removed. Both the tank and dividers were rinsed for one minute with distilled water. The tank was refilled, the dividers replaced, and the crayfish returned to their original sections. Crayfish were then acclimated for one hour. Dividers were again lifted and crayfish were exposed to a second thirty-minute encounter. Previous work has shown that crayfish under these time and fight conditions have the energy reserves to produce similar fight durations and intensities (Grills, Konzen and Moore unpubl. results). A video camera (Panasonic WV-CL350) was set one meter above the tank. All trials were recorded on a VCR (Panasonic AG-1980) and displayed on a monitor (Sony PVM-1351G). Each encounter was given a number code for subsequent blind analysis of the videotapes.

#### Data analysis

Analysis of behavior was performed using the number codes assigned after each encounter. The observer analyzing the video had no knowledge of fight treatment, urine treatment, or encounter round. Crayfish interactions can be described as a series of smaller scale (in time) interactions that occur periodically within a larger scale (in time) encounter. The thirty-minute period in which crayfish have the potential to interact is termed the observation period and each aggressive interaction within that thirty-minute period is termed an encounter. Observation periods that contained only one encounter were removed from further analysis (1% of the total 120 encounters analyzed). Crayfish encounters were analyzed using criteria described elsewhere (Huber & Delago, 1998). A crayfish's behavior was analyzed for each second for the entire thirty-minute encounter. Based on the qualitative description of observation periods and preliminary data analysis, it was clear that dominance relationships were established within the first 5 minutes of an observation period. Thus, we used the first 5 minutes of data from each observation period in our analysis. This data was then used to examine bout duration, maximum intensity, and time to intensities 2 and 3.

### Statistics

A 2-way ANOVA was used to compare the duration of first fights in experiment one with the duration of first fights in the odor treatment of experiment 2. An ordinal regression was used to compare the maximum intensity of first fights in experiment one with the maximum intensity of first fights in the odor treatment of experiment 2. This was done to test for any behavioral changes due to handling and treatment with epoxy. No significant differences were found between crayfish that were handled and treated with epoxy and those that were not handled or treated with epoxy (Two-way ANOVA,  $F = 2.43$ ,  $p < 0.13$ ). Therefore the data from experiment 1 was combined with the appropriate groups in experiment 2. A 3-way ANOVA was used to examine the effects of odor treatment, fight treatment, and encounter round on encounter duration, and a 3-way MANOVA was used to examine time to intensities 2 and 3. The effects of odor treatment, fight treatment, and fight round on maximum intensity was examined using an ordinal regression. All statistics were performed using a commercial statistical program (Statistica by StatSoft).

### Results

Overall effects were seen in all three treatments: fight round, fight treatment, and urine treatment. First fight rounds had significantly different fight dynamics when compared to second fight rounds (Three-way ANOVA; Table 1). The encounter duration of first fights was higher than those of second fights (Three-way ANOVA,  $F = 16.45$ ,  $p < 0.0001$ ,  $N = 60$  pair) (Fig. 2).

Encounters in the familiar treatment had significantly different fight dynamics when compared to the unfamiliar treatment (Three-way ANOVA/Ordinal regression; Table 1). Familiar encounters were longer in duration than unfamiliar bouts (Three-way ANOVA,  $F = 3.92$ ,  $p < 0.0483$ ,  $N = 60$  pair) (Fig. 2).

Urine absent encounters had significantly different fight dynamics from encounters in which urine was present (Three-way ANOVA/Ordinal regression; Table 1). Encounters without urine were longer and more intense than bouts with urine (Three-way ANOVA,  $F = 12.09$ ,  $p < 0.0006$ ,  $N = 60$  pair) (Ordinal regression,  $\chi^2 = 11.55$ ,  $p < 0.0007$ ,  $N = 60$  pair) (Figs 2 & 3).

Urine treatment and fight round showed a significant interaction effect (Three-way ANOVA; Table 1). First fight encounters with urine had shorter durations than first fight encounters without urine (Three-way ANOVA,  $F = 7.55$ ,  $p < 0.0063$ ,  $N = 60$  pair) (Fig. 2). Second fight encounters with urine had significantly shorter bout duration than second fight encounters

TABLE 1. *Three-way ANOVA (A) and Ordinal regression (B) results for duration and maximum intensity*

A				
ANOVA (Duration) Effect	df Effect	df Error	<i>F</i>	<i>p</i> value
Encounter number	1	330	16.45	<b>0.0001*</b>
Fight treatment	1	330	3.92	<b>0.0483*</b>
Urine	1	330	12.09	<b>0.0006*</b>
Fight treatment vs Encounter number	1	330	1.55	0.2136
Urine vs Fight treatment	1	330	2.64	0.1045
Urine vs Encounter number	1	330	7.55	<b>0.0063*</b>
Urine vs Encounter number vs Fight Treatment	1	330	0.98	0.3232
B				
Ordinal regression (max intensity) Effect	df Effect		$\chi^2$	<i>p</i> value
Encounter number	1		1.31	0.2516
Fight treatment	1		0.87	0.3484
Urine	1		11.55	<b>0.0007*</b>
Fight treatment vs Encounter number	1		1.13	0.2887
Urine vs Fight treatment	1		2.56	0.1098
Urine vs Encounter number	1		0.05	0.8155
Urine vs Encounter number vs Fight Treatment	1		0.83	0.3618

\* Indicates a significant difference at  $p < 0.05$ .

without urine (Three-way ANOVA,  $F = 7.55$ ,  $p < 0.0063$ ,  $N = 60$  pair) (Fig. 2).

No significant differences were found between treatments in time to intensities 2 and 3 (Three-way MANOVA,  $R > 1.88$ ,  $p > 0.18$ ,  $N = 60$  pair).

## Discussion

Our results clearly show a number of important factors regulating fight dynamics in crayfish. The largest statistical effect was evident between first and second fights. First fights were significantly longer in duration but equal in intensity when compared to second fights (Table 1 and Fig. 2). This

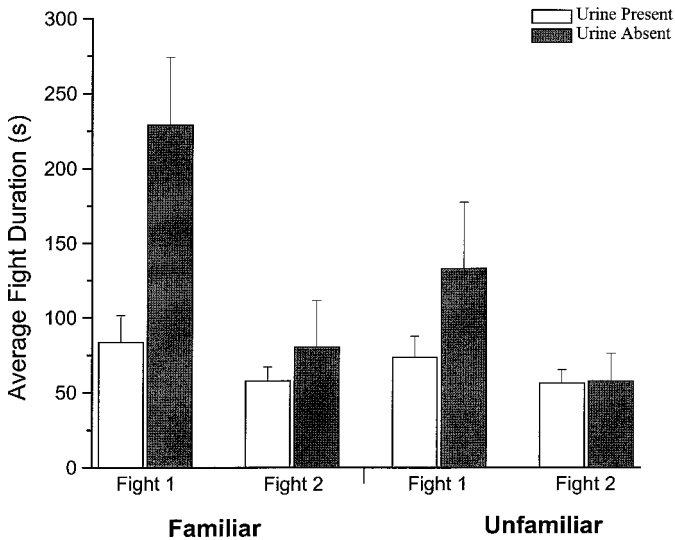


Fig. 2. The average fight duration of crayfish in familiar and unfamiliar fights in urine present and urine absent treatments. The white bars indicate urine present treatments ( $x \pm$  SEM) while gray bars indicate urine absent treatments ( $x \pm$  SEM). There was a significant affect of urine treatment (Three-way ANOVA,  $F = 12.09$ ,  $p < 0.0001$ ,  $N = 60$  pair) fight treatment (Three-way ANOVA,  $F = 3.92$ ,  $p < 0.048$ ,  $N = 60$  pair) and fight number (Three-way ANOVA,  $F = 12.09$ ,  $p < 0.0001$ ,  $N = 60$  pair). There was also a significant interaction between encounter round and urine treatment (Three-way ANOVA,  $F = 7.55$ ,  $p < 0.0063$ ,  $N = 60$  pair).

result could be due to a number of different phenomena. First, there are known winner and loser effects in organisms, in general, and crayfish more specifically (Franck & Ribowski, 1987; Whitehouse, 1997; Hsu & Wolf, 1999; Goessmann *et al.*, in press). With this phenomenon, a crayfish that has won in a previous encounter has a higher tendency to dominate in a second encounter. In addition, a crayfish that has lost in a previous encounter has a higher tendency to lose in the next encounter. If winner and loser effects were occurring in our experiments, we would expect to see a decrease in both encounter durations and intensities independent of the familiar/unfamiliar treatment.

A second possible phenomenon is that individual recognition is occurring. If individual crayfish can recognize a previous opponent and remember the outcome of the previous interaction, we would expect that second fight encounters would be shorter in duration and less intense. We can make this prediction based on the results of previous studies (Johnsson, 1997; Höjesjö

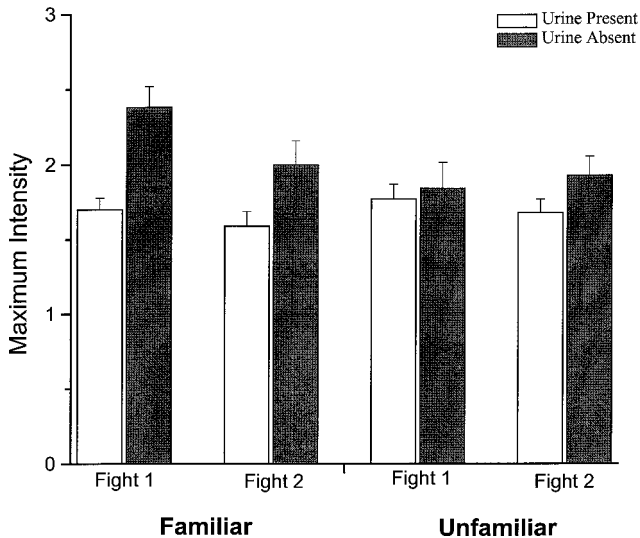


Fig. 3. The maximum fight intensity of crayfish in Familiar and Unfamiliar fights in urine present and urine absent treatments. The white bars indicate urine present treatments ( $x \pm \text{SEM}$ ) while gray bars indicate urine absent treatments ( $x \pm \text{SEM}$ ). There was a significant affect of urine treatment (Ordinal regression,  $\chi^2 = 11.55$ ,  $p < 0.0007$ ,  $N = 60$  pair).

*et al.*, 1998; Karavanich & Atema, 1998b). Individual recognition has been examined in lobsters (*H. americanus*) and it appears that lobsters remember prior opponents and their encounters with them. Similar to our studies, subordinates immediately backed away from known dominants avoiding a second fight, thus the second fights were less intense and of shorter duration than the first fights (Karavanich & Atema, 1998b).

Individual recognition has also been suggested in lizards (*Eumeces laticeps* & *Iguana iguana*) and two species of trout (*Salmo trutta* & *Onchorhynchus mykiss*). Lizards exhibit differential rates of tongue flicking to conspecific odors from familiar and unfamiliar opponents, suggesting that they are able to recognize the odors released from familiar individuals (Alberts & Werner, 1993; Cooper, 1996). Trout reduce their aggressiveness in second contests with familiar individuals, while in contests with unfamiliar individuals aggression is consistent between the first and second contests (Johnsson, 1997; Höjesjö *et al.*, 1998). Again the results of these studies are consistent with the results found with our encounter effect in that second encounters were shorter in duration.

In our studies, individual recognition can only occur in the familiar fights. Thus, if the crayfish in our studies are performing individual recognition and this recognition is the only phenomenon accounting for the changes between first and second fights, we would expect to see a statistical interaction between fight number and the familiar/unfamiliar treatment. This interaction was not significantly different, so we feel confident in ruling out the possibility of individual recognition in our experimental set-up.

A third possible phenomenon is that status recognition is occurring. If crayfish have the ability to recognize the status of an opponent then we would expect that second encounters be shorter in duration and less intense. Since status recognition would be occurring in both familiar and unfamiliar treatments, we would expect that the statistical interaction between fight number and familiar/unfamiliar treatment to be similar. Our results are in agreement with this conclusion (Table 1).

Status recognition is also supported through the comparison of familiar and unfamiliar fight duration. Unfamiliar fights are shorter in duration than familiar fights, suggesting that status recognition is utilized. Further fine scale analysis of crayfish fighting behavior is needed to determine why fights between familiar crayfish have longer fight durations than fights between unfamiliar crayfish. However shorter fights between unfamiliar crayfish support the hypothesis that crayfish utilize status recognition.

Previous studies support the idea that crayfish have the capability for status recognition. Copp (1986) suggests that status recognition through the recognition of aggressive state occurs in crayfish due to a reduced number of aggressive encounters and a decrease in initiation by subordinate organisms in an established dominance hierarchy. Results from studies with *Procambarus clarkii* showed that animals respond differently in the presence chemical cues from dominant and subordinate crayfish (Zulandt Schneider *et al.*, 1999). In particular, male crayfish with no social history and males with a known social history both showed increased aggression when presented with chemical cues from a dominant male crayfish. Conversely, only naïve male crayfish responded more aggressively to chemical cues from a subordinate female (Zulandt Schneider *et al.*, 1999). If taken together, the studies discussed above and the current study support the conclusion that the changes seen in fight dynamics between first and second encounters may be due to status recognition.

Other studies have demonstrated status recognition in different species. The results of studies in hermit crabs (*P. longicarpus*) that examine status recognition found similar reductions in duration when unfamiliar individuals of a known status encountered one another (Winston & Jacobson, 1978). However, they found that these changes in encounter dynamics were identical to the trends seen in intensity and duration of familiar animals. Male cockroaches (*N. cinerea*) also use status recognition to recognize the dominance or subordination of conspecifics. Moore *et al.* (1997) found by manipulating the chemical compound associated with males paired with unfamiliar and unfamiliar organisms, they affect the status of the organism. Because results were the same in both familiar and unfamiliar groupings and because odor plays such a large role in determining status, cockroaches use chemical cues to convey status (Moore *et al.*, 1997).

Urine was found to play an important role in the dynamics of encounters. Encounters without urine had significantly longer durations and higher intensity (Table 1 and Figs 2 and 3). This change in fight dynamics is seen in both the familiar and unfamiliar fight treatments. Analysis of interactions between treatments shows a significant effect between the presence of urine and encounter number. In particular, first encounters without urine were significantly longer than any other type of encounter. These results support the idea that urine may be providing a critical cue for determining when to end an encounter with an opponent. Which may mean that crayfish urine plays an important communicative role during agonistic encounters. These ideas are consistent with the results of other studies in which animals are deprived of sensory cues.

Bruski & Dunham (1987) removed visual cues from crayfish by depriving them of light and examined the fight dynamics under light deprived and ambient conditions. They found that crayfish devoted more time and energy to fighting as light levels decreased. They suggest that this effect is due to sensory information being inaccurately perceived by combatants which lead to longer interactions with more behavioral acts per bout of fighting. Similar to our studies a critical cue that signals the end of fighting appears to be absent.

Visual cues have also been manipulated in social recognition studies involving crabs (*P. fluviatile*) and dark-eyed juncos (*Junco hyemalis*). In both of these studies a physical feature associated with recognition was manipulated and affected the perception of the individuals by other organisms. Vanini & Gherardi (1981) examined the ability of organisms to recognize one

another by changing the visual cues associated with them. If an organism's tag was changed from its original, conspecifics grouped with it increased their aggression towards that individual (Vannini & Gherardi, 1981). Control organisms did not exhibit an increase in aggression. By depriving crabs of visual information, the investigators have caused a change in their fight behaviour, mainly increasing aggression. Visual cues are therefore important in determining fight dynamics between familiar and unfamiliar organisms.

Grasso *et al.* (1996) examined the role of visual cues in status recognition in dark-eyed juncos. By changing the color of the plumage associated with individual juncos, they were able to change the status associated with these individuals. By darkening subordinate birds' plumage, subordinates were perceived by conspecifics as dominant (Grasso *et al.*, 1996). Conversely by lightening dominant birds plumage, dominants were perceived by conspecifics as subordinate (Grasso *et al.*, 1996). Visual cues are therefore hypothesized to play a role in the initial recognition of a conspecific's status and by changing the visual cues associated with an organism it is possible to change the perception of the organism's status and therefore the subsequent encounter between two organisms.

Chemical cues have been shown to play a role in other crustacean social interactions. Karavanich & Atema (1998a) examined how lesioning the primary chemoreceptive organs of lobsters (*H. americanus*) affects the ability of lobsters to recognize familiar opponents. They found that organisms void of the ability to sense chemicals are unable to recognize familiar opponents in that the duration and intensity of second fights is similar to that of first fights in these organisms (Karavanich & Atema, 1998a).

In conclusion, crayfish appear to be recognizing the status of opponents in agonistic interactions. Urine plays an important role in decreasing the aggressiveness and duration of fights between organisms. It is possible that a cue that signifies the end of a contest is missing when odor is absent and therefore organisms continue to fight for longer periods and at higher intensities. Thus urine may play an important communication role during agonistic contests between crayfish. Because status recognition reduces the duration of fights it plays an important role in the maintenance of dominance relationships in this species. Therefore future studies should address the longevity of social recognition in this species by determining how long an opponent is remembered.

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