

RECOGNITION OF DOMINANCE STATUS BY
CHEMORECEPTION IN THE RED SWAMP
CRAYFISH, *Procambarus clarkii*

REBECCA A. ZULANDT SCHNEIDER,
ROBB W. S. SCHNEIDER, and PAUL A. MOORE*

*Laboratory for Sensory Ecology
Department of Biological Sciences
Bowling Green State University
Bowling Green, Ohio 43403*

(Received July 10, 1998; accepted November 25, 1998)

Abstract—We tested the hypothesis that chemical signals play a role in the recognition of dominance status in the red swamp crayfish, *Procambarus clarkii*. Dominance was judged on the outcome of dyadic interactions in all male or female groups of three individuals. This resulted in a dominant, intermediate, and subordinate individual within each population. A choice paradigm in a flow-through Y maze was used to judge whether crayfish were able to recognize dominance through chemical cues alone. Both individuals that interacted with the animal producing the odor and naive individuals were tested. Irrespective of sex and previous experience, individuals increased their rates of locomotion in the presence of conspecific odor. Naive males investigated the dominant arm first, spent more time at the dominant nozzle, and responded more aggressively (as measured by meral spread) to dominant male odor and subordinate female odor. Intermediate males spent more time at the dominant male nozzle and responded more aggressively to dominant male odor. Naive females spent more time at the dominant nozzle. These results show that males recognize dominant animals. Since both naive and experienced males respond to water from dominant animals, we concluded that this is recognition of dominance and not just individual recognition. This signal may be important for the formation or reinforcement of dominance relationships. Based on the change in behavior between odors, we suggest that crayfish can use chemical cues to recognize the dominance status of conspecifics.

Key Words—crayfish, *Procambarus clarkii*, dominance status recognition, chemoreception.

*To whom correspondence should be addressed.

INTRODUCTION

In some crayfish populations dominance status is important in shelter and food acquisition, as well as for reproductive success (Bovbjerg, 1953, 1970; Hazlett, 1979; Rutherford et al., 1995). An organism's status within a population is determined over time by agonistic interactions with population members (Huber et al., 1997). Physical characteristics such as body size and chelae size and number can affect the results of these interactions and the overall probability that an individual will have a dominant or subordinate status (Berrill and Arsenault, 1984; Rubenstein and Hazlett, 1973).

Several species of crayfish, including *Procambarus clarkii*, have been shown to establish dominance relationships (Bovbjerg, 1953; Copp, 1986). Crayfish behavior towards an individual is influenced by the outcome of past conflicts with that individual and possibly the other individual's status, which leads to shorter interactions between organisms (Rubenstein and Hazlett, 1973). It was originally thought that these subsequent behaviors depended upon learned individual recognition of dominant members by subordinate members (Bovbjerg, 1953; Hazlett, 1969). Copp (1986), using results from Thorpe and Ammerman (1978), suggests that it is not recognition of individuals that is occurring, but recognition of aggressive state. Since Thorpe and Ammerman (1978) did not quantify aggression or agonistic interactions, the only conclusion that can be drawn is that animals can detect two conspecifics in the same tank. So the debate as to whether it is individual recognition or recognition of an aggressive state occurring continues. Some authors suggest that recognition occurs through visual cues such as initiation or rate of escalation (Thorpe and Ammerman, 1978; Winston and Jacobson, 1978). If crayfish use an aggressive state as a recognition signal, it may be due to some aspect of the physiological state of a crayfish and not individual recognition (Copp, 1986).

Chemical signals are important for many crayfish behaviors such as foraging, predation, and mating. Crayfish use chemoreception to find food sources, regardless of the substrate type, through chemical cues by orientating to odor plumes emanating from food (Moore and Grills, 1998). Some chemical signals have also been shown to be alarm signals. Crayfish avoid areas where a conspecific has been injured or killed based on the chemicals released from an injured or dead conspecific (Hazlett, 1985a, 1990). In social situations, chemical signals allow crayfish to distinguish between male and female conspecifics (Ameyaw-Akumfi and Hazlett, 1975; Dunham and Oh, 1996) and to identify the correct species in mate choice (Tierney and Dunham, 1982). Ameyaw-Akumfi and Hazlett (1975) discovered that male *P. clarkii* can distinguish females from males through a putative sex pheromone. Dunham and Oh (1996) found the same behavior occurs in female *P. clarkii*.

Olfaction may be important for all these chemically mediated behaviors.

Although conclusive experiments have yet to be done, Ameya-Akumfi and Hazlett (1975) and later Dunham and Oh (1992) suggest that the sex pheromone is perceived primarily via chemoreceptors in the antennules of *P. clarkii*. The use of the antennules in agnostic interactions has been well documented (Smith and Dunham, 1996). In both light and dark environments, the rate of crayfish antennule flicking, an olfactory sampling behavior, during agnostic interactions is comparable (Bruski and Dunham, 1987). Dominant organisms exhibited an increased rate of antennule movement and duration of movement when compared to the rate and movements of a subordinate's antennule (Rutherford et al., 1996). The results of these studies suggest that crayfish are responding to chemical cues during conflicts and that these cues could play an important role in dominance status relationships.

Since both chemical communication and status relationships are integral parts of *P. clarkii*'s behavior, it is possible that there is a chemical signal associated with dominance status. We hypothesize that chemical signals play a role in dominance status recognition for the red swamp crayfish, *Procambarus clarkii*. This was tested by presenting both naive and "intermediate" crayfish with odors from dominant and subordinate individuals in a flow through Y maze that excluded all other sensory cues.

METHODS AND MATERIALS

Animals. Crayfish, *Procambarus clarkii*, were acquired from a commercial supplier (Carolina Biological Supply Company). They were separated by sex and housed in 10-gallon aquaria equipped with undergravel filters. Crayfish were maintained at a constant temperature of 23°C, a light-dark cycle of 14L:10D, and fed 0.125-cm³ pieces of frozen fish fillets (pollock, cod, herring, smelt) three times a week throughout the experimental period.

Population Structure. Populations of three same-sexed organisms were established. Dominance relationships among these organisms were examined using dyadic interactions that consisted of all possible pairwise combinations. Crayfish (carapace length ranging from 3.5 to 5.5 cm) were chosen randomly, marked with paint (Testors) on the carapace for individual identification, and introduced into a population tank at the same time. Male population tanks (78.7 × 78.7 × 31.8 cm) and female tanks (102.9 × 43.2 × 41.9 cm) contained five shelters (PVC pipe halves, 5 cm in diameter). Populations were allowed to interact for 72 hr, after which fight trials were conducted to determine dominance order. Tanks for males were larger than tanks for females because preliminary trials showed that aggression escalated to the point of death for males in smaller tanks.

Fight trials were performed in a glass test tank (50 × 25 × 30 cm) once a

day (09:00–12:00 hr) for each population. Animals participated in a single fight per day. Two crayfish were taken from the population tank and placed in separate opaque, plastic containers (28 × 18 × 13 cm). They were placed into the test tank at the same time and allowed to interact. The crayfish that tail flipped first was deemed the loser, and the other the winner. Previous work in our laboratory shows that tail flipping is the most obvious behavior exhibited by the loser at the end of the single encounters. More subtle behaviors, such as repeated retreats, are more reliable for repeated encounters between individuals. All fight trials resulted in a crayfish in each population with 2–0, 1–1, and 0–2 fight record. The crayfish in each population with a fight record of 2–0 was called dominant, 1–1 intermediate, and 0–2 subordinate. The tank, nets, and plastic holding bins were rinsed with distilled water for 2–3 min before each trial so that residual chemicals from the previous trial were eliminated. Naive males and females were isolated in separate opaque tanks (50 × 25 × 30 cm) for a week before being used in a trial. Populations were run through fight trials again after the Y maze study to ensure that the same hierarchy existed throughout the study period. Trials with population hierarchies that changed during the experiments or had crayfish molt during the experiments were removed from analysis (<4% of the populations).

Bioassay Arena. A flow-through Y maze (61 × 31 × 31 cm) was used for bioassays (Figure 1). This arena was large enough that animals could achieve full meral spread and turn around without striking the walls. A reservoir tank with two separate chambers (31 × 16 × 31 cm) supplied odor-laden water to the arms of the maze (Figure 1). All visual and mechanical stimuli between crayfish were eliminated using opaque paint on the outside of the tanks and opaque plastic wrap inside the tanks. Gravel was rinsed with distilled water and placed in each of the reservoir tanks and the Y maze before the start of a trial. Water flowed into the maze from the reservoir tanks through 1.0-cm-ID Nalgene tubing. The outflow pipes were 5 cm above the bottom of the maze. This height was chosen because it is the typical height of a crayfish nephropore, a potential source for chemical signals (Zulandt and Moore, 1998). Two in-line flowmeters (Manostat Riteflow #4) controlled flow. Dye trials, using commercial brand food coloring, were run at a rate of 168 ml/min to ensure that the flow from each holding tank was separate and equal when traveling through the arms of the Y maze.

Behavioral Trials. Dominant and subordinate crayfish from populations were randomly assigned to reservoir chambers A and B using a random number table (Zar, 1984). Crayfish were acclimated in the separate chambers for 3 hr to allow treatment crayfish odor to accumulate in the experimental water and to allow test crayfish to explore the Y maze without the influence of flow or odor. Treatments consisted of dominant and subordinate odors from a population presented together, dominant and no odor (blank), subordinate and no odor (blank), and no odor (blank) in either of the reservoirs (control). Experimental subjects were intermediate same sex, naive same sex, and naive opposite sex.

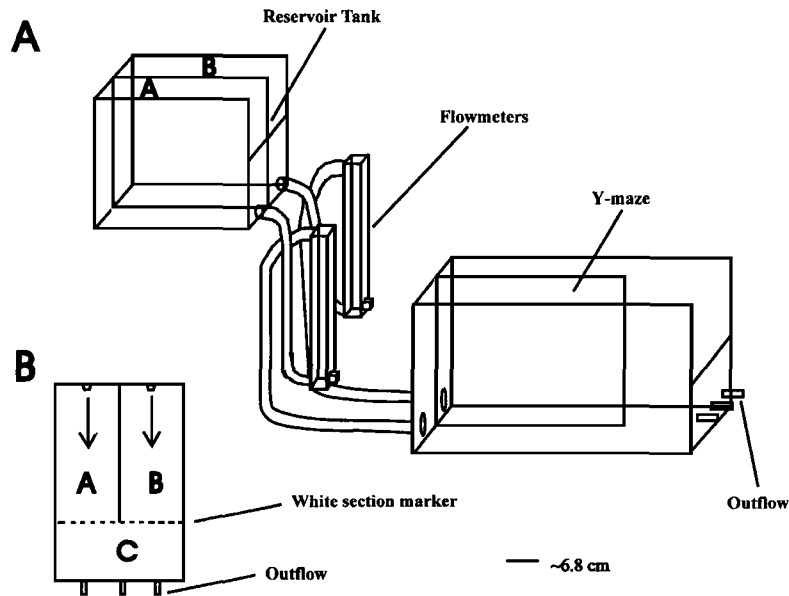


FIG. 1. Diagram of the flow-through Y maze showing the side view (A) and the overhead view (B). Water and odor in the reservoir tank flow to the same lettered sections in the Y maze.

At the start of each trial the flowmeters were set and maintained at a flow rate of 168 ml/min. A video camera (Panasonic wv-CL350) was set up 120 cm above the Y maze. The trials were recorded on a VCR (Panasonic AG-1980) and displayed on a monitor (Sony PVM-1351Q). All crayfish were returned to their respective population tanks after each trial. All experimental tanks and equipment were rinsed with distilled water before the start of each trial. Trials in which the test animal did not move more than one body length or in which the test animal was deemed visibly disturbed by the presence of the researchers were also removed from analysis (<12% of the total 88 trials were removed from analysis).

Data and Statistical Analysis. For each trial, initial arm choice, time spent in each arm, time spent at each nozzle, and meral spreads were measured by viewing videotapes. A crayfish was deemed in or out of an arm when its rostrum had crossed white lines painted on the top of the Y maze at the start of each arm (see Figure 1). The total amount of time spent in each arm was recorded, with time starting when the crayfish entered starting the arm and ending when it passed out of the arm. Time at the nozzle was defined as the total amount of time a crayfish spent directly in front of or touching the nozzle with at least one of its chelae.

Meral spread (distance between tips of chelae) has been used as a measure of aggression in many species by several investigators and was therefore used in this experiment (Thorpe and Ammerman, 1978; Bruski and Dunham, 1987). We measured meral spread at the beginning of the tank arm, 1/3 of the tank arm, 2/3 of the tank arm, and nozzle.

A binomial analysis was used to determine if there was an initial choice of Y maze arms different from random (Zar, 1984). A one-way ANOVA was used to determine if crayfish spent more time in any section of the Y maze in the absence of odor. These values were then used as expected values in a χ^2 analysis to determine if locomotory behavior changed with the addition of odor. Paired *t* tests were run to determine if one odor treatment was preferred over another in both total time in arm and time at nozzle comparisons (Zar, 1984). A repeated-measures nested ANOVA was used to analyze differences in meral spreads between odor treatments and arm choices. All statistics were run using a commercial statistics package (Statistica by StatSoft).

RESULTS

Effect of Odor on Time Spent in Y Maze Sections. In the absence of odor, both male and female crayfish spent significantly more time in section C of the Y maze (ANOVA: $F_{2,10} = 52.7$, $P < 0.001$; $N = 7$ for males and $N = 6$ females) (Figure 2). With the addition of odor, the preference of crayfish for a section changed, with a significant increase in time spent in the dominant and subordinate odor arms. Time spent in section C in the odor treatment significantly decreased. This was true for both male and female crayfish in all treatments.

Effect of Odor on Initial Arm Choice. Males show significant initial arm choice to only one of the conspecific odor treatments. Naive males chose dominant odor when paired with subordinate odor (binomial analysis, $P < 0.05$, $N = 9$) (Table 1). Females chose subordinate odor significantly more often when paired with no odor (binomial analysis, $P < 0.05$, $N = 6$) (Table 1). All other choices by females were not significantly different from random.

Effect of Odor on Time Spent at Nozzle. Naive males spent significantly more time at the nozzle of dominant animals of the same sex (Paired *t* test: $t_8 = 2.306$, $P < 0.05$, $N = 9$) (Table 2). Crayfish exhibited no differences in time spent at the nozzle in any other treatments.

Effect of Conspecific Odor on Meral Spread. Female crayfish did not exhibit a difference in meral spread size when exposed to any odor treatment (Figure 3B and C and Figure 4C). Naive male crayfish have larger meral spreads in the presence of subordinate female conspecific odor than dominant female odor (repeated-measures nested ANOVA: $F_{1,40} = 12.25$, $P < 0.01$, $N = 6$) (Figure 3A).

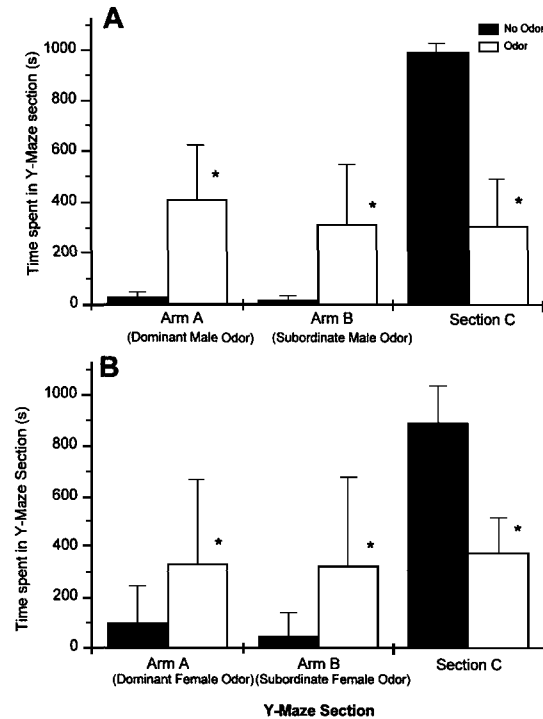


FIG. 2. The effect of male (A, $N = 7$) and female (B, $N = 6$) odor sources on crayfish time in Y maze sections. Black bars represent the no-odor treatment, and white bars represent the odor treatment. Bars are mean (+ SEM values) for the intermediate vs. dominant and subordinate odor trials. Asterisks mark significant differences between treatments at $P < 0.01$ using a χ^2 analysis. Both treatments were significantly different from the no odor treatment.

Intermediate males had a larger meral spread in the presence of dominant conspecific odor than subordinate conspecific odor (repeated-measures nested ANOVA: $F_{1,40} = 12.1$, $P < 0.001$, $N = 7$) (Figure 4B). Naive males had a larger meral spread in the presence of dominant conspecific odor than subordinate odor (repeated-measures nested ANOVA: $F_{1,52} = 24.31$, $P < 0.001$, $N = 9$) (Figure 4A). Intermediate males also exhibited a larger meral spread when presented with subordinate conspecific odor versus no odor (not shown) (repeated-measures nested ANOVA: $F_{1,32} = 5.547$, $P < 0.05$, $N = 7$). The subordinate odor induced meral spreads (mean \pm SEM) of 3.71 ± 0.88 cm and 4.60 ± 1.12 cm at 2/3 the arm length and at the nozzle. The blank arm meral spreads were 2.31 ± 0.91 cm at 2/3 the arm length and 1.76 ± 1.00 cm at the nozzle.

TABLE 1. MALE AND FEMALE INITIAL ARM CHOICES IN RESPONSE TO CONSPECIFIC ODOR TREATMENTS

Sex and treatment	N	Percentage		
		Dominant arm	Subordinate arm	Blank arm
Male				
Intermediate male	7	33.3	66.7	
Intermediate male	7	50		30
Intermediate male	7		50	50
Naive female	7	50	50	
Naive male ^a	9	90	10	
Female				
Intermediate female	6	50	50	
Intermediate female	6	33.3		66.7
Intermediate female ^a	6		83.3	16.7
Naive female	6	50	50	
Naive male	6	66.7	33.3	

^aIndicates a significant difference between arm choice in a treatment ($P < 0.05$, binomial analysis on raw data).

TABLE 2. AVERAGE TIME THAT MALE AND FEMALE CRAYFISH SPENT AT NOZZLE OF Y-MAZE ARM IN RESPONSE TO CONSPECIFIC ODOR TREATMENTS

Sex and treatment	N	Time (sec \pm SEM)		
		Dominant nozzle	Subordinate nozzle	Blank nozzle
Male				
Intermediate male	7	15.83 \pm 6.72	68.17 \pm 59.07	
Intermediate male	7	7.83 \pm 5.4		34.5 \pm 32.54
Intermediate male	7		32.21 \pm 15.9	3.2 \pm 1.98
Naive female	7	33.33 \pm 19.42	29.67 \pm 13.61	
Naive male ^a	9	34.55 \pm 16.3	1.11 \pm 1.0	
Female				
Intermediate female	6	47.33 \pm 26.44	54.5 \pm 35.62	
Intermediate female	6	7.71 \pm 3.86		6.83 \pm 4.45
Intermediate female	6		8 \pm 6.7	5 \pm 3.64
Naive female	6	39.83 \pm 21.2	11.5 \pm 8.6	
Naive male	6	40.33 \pm 22.6	36 \pm 21.57	

^aIndicates a significant difference between nozzle times within a treatment ($P < 0.05$, paired t test).

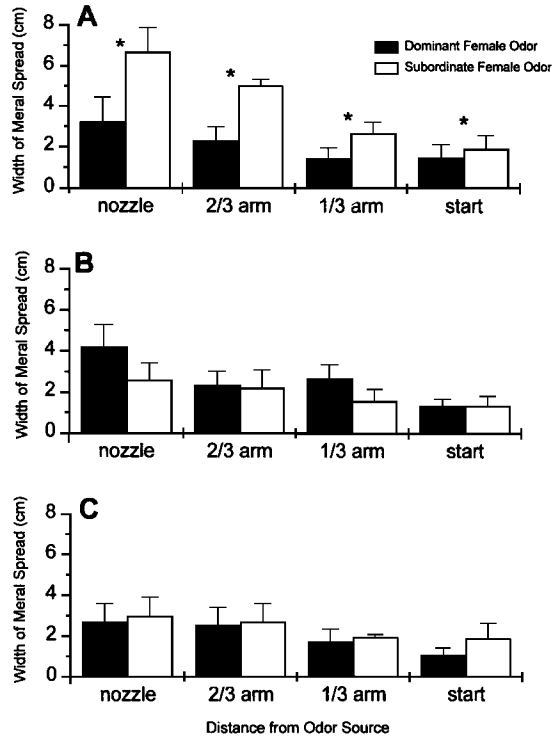


FIG. 3. The effect of female conspecific odor on naive male (A), intermediate female (B), and naive female (C) meral spreads to dominant (black) and subordinate (white) odors. Measurements were made at the nozzle, 2/3 the way up the arm, 1/3 the way up the arm, and at the start of each arm. Bars are mean meral spread widths (+ SEM); $N = 6$ for all trials. Asterisks mark significant differences between odor treatments at $P < 0.05$ using a nested ANOVA design.

DISCUSSION

Both male and female crayfish can detect conspecific odors. These odors cause a change in behavior that is reflected in the change in time spent in Y maze sections (Figure 2). The addition of odor caused the crayfish to become more active and to explore the arms of the Y maze.

Naive males recognized both male and female dominance status. This is evident in the naive male's change in behavior when conspecific dominant and subordinate odors were present. The initial choice of naive males was the dominant arm significantly more times than the subordinate arm (Table 1), and they spent significantly more time at the nozzle with same-sex dominant odor (Table

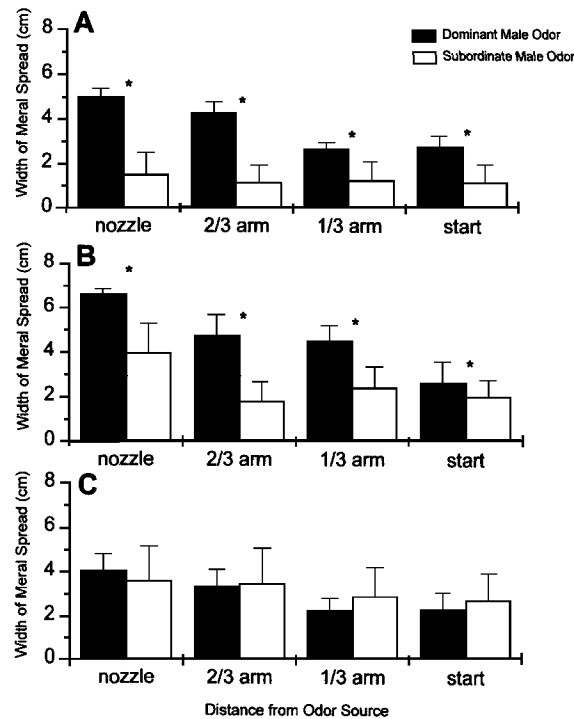


FIG. 4. The effect of male conspecific odor on naive male (A, $N = 9$), intermediate male (B, $N = 7$), and naive female (C, $N = 7$) meral spreads to dominant (black) and subordinate (white) odors. Measurements were made at the nozzle, 2/3 the way up the arm, 1/3 the way up the arm, and at the start of each arm. Bars are mean meral spread widths (+ SEM). Asterisks mark significant differences between odor treatments at $P < 0.05$ using a nested ANOVA design.

2). The naive males also had larger meral spreads in the presence of dominant male conspecific odor (Figure 4) and subordinate female odor (Figure 3).

Males that had previous exposure to test populations responded differently to water from a dominant male than from a subordinate male. Intermediate males had a larger meral spread in the presence of dominant male odor than in the presence of subordinate male odor (Figure 4B). Females that had previous exposure to test populations responded differently only to subordinate female odor (Table 1).

A possible explanation for differences in naive and intermediate results may be individual recognition. Previous exposure to a population results in different responses to odors from dominant and subordinate animals, but it is not clear whether this is due to individual recognition of the crayfish or recognition of a

status chemical by the experienced individual. The results from trials with naive animals support the idea that dominance status is recognized through chemical signals at least with naive individuals. Since all other cues have been eliminated, we conclude that naive females and males can recognize the hierarchical status of same-sex conspecifics through chemoreception (Tables 1 and 2, Figure 4). Naive males can also recognize the status of females (Figure 3). These signals could play an important role in the structure and maintenance of crayfish social communities.

There are several mechanisms by which dominance status could be recognized: a specific signal chemical, a unique mixture of chemicals, by volume of signal released, or the concentration of chemicals released. One mechanism could be through the detection of status-specific chemicals. Goldfish have a single chemical as an indicator of female sexual status (DeFraipont and Sorenson, 1993). The presence of this preovulatory pheromone causes males to increase sperm production in time for spawning (DeFraipont and Sorenson, 1993). Many organisms, however, use a blend of several chemicals for a single signal. Males of many moth species require a specific ratio of female mating pheromone chemicals to initiate mating behavior and to orient and find the female moth (Baker and Cardé, 1979; Akers and O'Connell, 1988; Liu and Haynes, 1993).

Another possible mechanism of recognition is through intensity differences between dominant and subordinate animals. A dominant crayfish could concentrate more chemicals or release more of the signal than a subordinate animal. If the signal is released in the urine, dominant animals may have the capacity to produce more urine, and therefore release a larger volume of urine than a subordinate animal would. This increased volume of urine produced by the dominant individual could play a role in the recognition of dominance status.

Status recognition through chemical cues has been documented in the cockroach. In these organisms, males produce a blend of three chemicals. The proportion of these chemicals emitted by a cockroach determines its hierarchical status to other cockroaches (Moore et al., 1997). Although hierarchical status recognition through chemical cues has not been studied in other systems, individual recognition has. Many rodents and insects have the ability to recognize individuals and conspecifics in their populations through a chemical cue (Johnston and Robinson, 1993; Hefetz, 1992).

Dominance status in the crayfish *P. clarkii* may also be under neural and hormonal modulation. Yeh et al. (1996, 1997) found hormone levels in crayfish changed depending upon the dominance status of the individual. Serotonin can modify the threshold of the tail flip (a sign of submission in agnostic interactions), suggesting the past fight history via changes in serotonin levels could play a role in dominance status recognition (Huber et al., 1997). This change in serotonin level may possibly be linked to the status pheromone in that it could be the entire chemical signal or one of its components.

Since recognition of dominance status does occur in our organism, the question arises as to whether the signal conveyed determines or reflects the status. In the cockroach, *Nauphoeta cinera*, the presence of the male sex pheromone determines rather than reflects the status (Moore, 1997). Thus, if the pheromone is produced, the organism is dominant; if not, it is subordinate. We would argue that in our system, the dominance signal most likely reflects rather than determines the status of the individual emitting it. It has been shown that the aggressive state of crayfish is closely linked to serotonin levels in the body and that these levels change depending upon the past fight history of an organism (Yeh et al., 1996, 1997; Huber et al., 1997). These levels can be reflected in released signals and therefore conceivably communicated to opponents. The signal therefore would not determine the status of the individual; rather it would reflect the success of encounters that dictates the dominance status.

Several authors have suggested that dominance recognition occurs through visual cues. Rubenstein and Hazlett (1973) showed that crayfish were able to recognize the aggressive state through visual displays of their chelae. They found a correlation between the area of the white meri displayed, aggression, and dominance. Copp (1986) also showed that visual cues were important in dominance status recognition. Both of these studies suggest a role for chemical signals, but none was able to determine conclusively if chemical recognition occurred.

In addition to visual cues, it seems plausible that benthic organisms such as *P. clarkii* would most likely have a status chemical signal as a consequence of the environment in which they live. Vision is not the only means of gathering information about the surrounding environment that is available to these animals. Crayfish use chemicals to recognize the sex of conspecifics and to avoid predation through the recognition of chemicals released from crushed conspecifics (Hazlett, 1985a,b). Because crayfish actively use chemical signals to acquire information about their environment, the use of chemicals in status recognition could be an invaluable form of communication for crayfish and play a large role in mate and resource acquisition.

Acknowledgments—We would like to thank Drs. C. Derby, R. Huber, S. Vessey, and D. Wiegmann for helpful reviews of the manuscript. This project was funded through a grant from the National Science Foundation awarded to P.A.M. (IBN-9614492).

REFERENCES

- AKERS, P. R., and O'CONNELL, R. J. 1988. The contribution of olfactory receptor neurons to the perception of pheromone component ratios in male redbanded leafroller moths. *J. Comp. Physiol. A.* 163:641–650.
- AMEYAW-AKUMFI, C. E., and HAZLETT, B. A. 1975. Sex recognition in the crayfish *Procambarus clarkii*. *Science* 190:1225–1226.
- BAKER, T. C., and CARDÉ, R. T. 1979. Analysis of pheromone-mediated behaviors in male

- Grapholitha molesta*, the oriental fruit moth (Lepidoptera: Tortricidae). *Environ. Entomol.* 8:956–968.
- BERRILL, M., and ARSENAULT, M. 1984. The breeding behavior of a northern temperate orconectid crayfish, *Orconectes rusticus*. *Anim. Behav.* 32:333–339.
- BOVBERG, R. V. 1953. Dominance order in the crayfish *Orconectes virilis* (Hagan). *Physiol. Zool.* 26:173–178.
- BOVBERG, R. V. 1970. Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). *Ecology* 51:225–236.
- BRUSKI, C., and DUNHAM, D. W. 1987. The importance of vision in agonistic communication of the crayfish *Orconectes rusticus* I: An analysis of bout dynamics. *Behaviour* 103:83–107.
- COPP, N. H. 1986. Dominance hierarchies in the crayfish *Procambarus clarkii* (Girard, 1852) and the question of learned individual recognition (Decapoda, Astacidea). *Crustaceana* 51:9–24.
- DEFRAIPONT, M., and SORENSEN, P. W. 1993. Exposure to the pheromone 17 α ,20 β -dihydroxy-4-pregnen-3-one enhances the behavioural spawning success, sperm production and sperm motility of male goldfish. *Anim. Behav.* 46:245–256.
- DUNHAM, D. W., and OH, J. W. 1992. Chemical sex discrimination in the crayfish *Procambarus clarkii*: Role of antennules. *J. Chem. Ecol.* 18:2363–2372.
- DUNHAM, D. W., and OH, J. W. 1996. Sex discrimination by female *Procambarus clarkii* (Girard, 1852) (Decapoda, Cambaridae): Use of chemical and visual stimuli. *Crustaceana* 69:534–542.
- HAZLETT, B. A. 1969. Individual recognition and agonistic behaviour in *Pagurus bernhardus*. *Nature* 222:268–269.
- HAZLETT, B. A. 1979. Individual distance in Crustacea: IV. Distance and dominance hierarchies in *Pagurus pollicaris*. *Mar. Behav. Physiol.* 6:225–242.
- HAZLETT, B. A. 1985a. Chemical detection of sex and condition in the crayfish *Orconectes virilis*. *J. Chem. Ecol.* 11:181–189.
- HAZLETT, B. A. 1985b. Disturbance pheromones in the crayfish *Orconectes virilis*. *J. Chem. Ecol.* 11:1695–1711.
- HAZLETT, B. A. 1990. Source and nature of disturbance-chemical system in crayfish. *J. Chem. Ecol.* 16:2263–2275.
- HEFETZ, A. 1992. Individual scent marking of the nest as a mechanism of recognition in *Xylocopa pubescens* (Hymenoptera, Anthophoridae). *J. Insect Behav.* 5:763–772.
- HUBER, R., SMITH, K., DELAGO, A., ISAKSSON, K., and KRAVITZ, E. A. 1997. Serotonin and aggressive motivation in crustaceans: Altering the decision to retreat. *Proc. Natl. Acad. Sci. U.S.A.* 94:5939–5942.
- JOHNSTON, R. E., and ROBINSON, T. A. 1993. Cross-species discrimination of individual odors by hamsters (Muridae: *Mesocricetus auratus*, *Phodopus campbelli*). *Ethology* 94:317–325.
- LIU, Y., and HAYNES, K. F. 1993. Pheromone-mediated responses of male cabbage looper moths, *Trichoplusia ni*, following various exposures to sex pheromone or (Z)-7-dodecenol. *J. Chem. Ecol.* 19:503–515.
- MOORE, P. A., and GRILLS, J. 1999. Chemical orientation to food by the crayfish, *Orconectes rusticus*: Influence by hydrodynamics. *Anim. Behav.* In press.
- MOORE, P. J., REAGAN-WALLIN, N. L., HAYNES, K. F., and MOORE, A. J. 1997. Odour conveys status on cockroaches. *Nature* 389:25.
- RUBENSTEIN, D. I., and HAZLETT, B. A. 1973. Examination of agonistic behavior of the crayfish *Orconectes virilis* by character analysis. *Behaviour* 50:193–216.
- RUTHERFORD, P. L., DUNHAM, D. W., and ALLISON, V. 1995. Winning agonistic encountering by male crayfish *Orconectes rusticus* (Girard) (Decapoda, Cambaridae): chela size matters but chela symmetry does not. *Crustaceana* 68:526–529.
- RUTHERFORD, P. L., DUNHAM, D. W., and ALLISON, V. 1996. Antennule use and agonistic suc-

- cess in the crayfish *Orconectes rusticus* (Girard, 1852) (Decapoda, Cambaridae). *Crustaceana* 69:117–122.
- SMITH, M. A., and DUNHAM, D. W. 1996. Antennae mediate agonistic physical contact in the crayfish *Orconectes rusticus* (Girard, 1852) (Decapoda, Cambaridae). *Crustaceana* 69:668–674.
- THORPE, J. H., and AMMERMAN, K. S. 1978. Chemical communication and agonism in the crayfish, *Procambarus acutus acutus*. *Am. Mid. Nat.* 100:471–474.
- TIERNEY, A. J., and DUNHAM, D. W. 1982. Chemical communication in the reproductive isolation of the crayfishes *Orconectes propinquus* and *Orconectes virilis* (Decapoda, Cambaridae). *J. Crust. Biol.* 2:544–548.
- WINSTON, M. L., and JACOBSON, S. 1978. Dominance and effects of strange conspecifics on aggressive interactions in the hermit crab *Pagurus longicarpus* (Say). *Anim. Behav.* 26:184–191.
- YEH, S., FRICKE, R. A., and EDWARDS, D. H. 1996. The effect of social experience on serotonergic modulation of the escape circuit of crayfish. *Science* 271:366–369.
- YEH, S., MUSOLF, B. E., and EDWARDS, D. H. 1997. Neuronal adaptations to changes in the social dominance status of crayfish. *J. Neurosci* 17:697–708.
- ZAR, J. H. 1984. *Biostatistical Analysis*, 2nd ed. Prentice Hall, Englewood Cliffs, NJ.
- ZULANDT, R. A., and MOORE, P. A. 1998. Characterization of the nature of information between chemical signal sources in the crayfish *Procambarus clarkii*. *Chem. Senses* 23:637.