ALARM RESPONSES IN THE CRAYFISH *Orconectes virilis* AND *Orconectes propinquus*

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Abstract—Individuals of two species of crayfish (*Orconectes virilis* and *O. propinquus*) were tested in the laboratory for responses to chemicals released from physically damaged conspecifics. Individuals of *O. propinquus* did not show an alarm response to crushed conspecifics. Individuals of *O. virilis* responded to a water-borne substance released from crushed conspecifics by assuming an intermediate posture and ceasing movement. Similar alarm responses were shown by individuals of *O. virilis* to crushed congeneric individuals (*O. propinquus*), and these responses were not eliminated by either freeze-thawing the crayfish used to prepare the signal or by treating freshly crushed crayfish with the enzyme trypsin. Individuals of *O. virilis* showed strong feeding responses to solutions prepared from frozen fish flesh but showed a mixture of alarm and feeding responses to freshly killed fish. These results indicate that the alarm substance used by *O. virilis* is widespread.

Key Words—Alarm, crayfish, *Orconectes virilis*, *Orconectes propinquus*, chemical signals.

INTRODUCTION

The use of chemical signals by aquatic organisms has been documented in a variety of contexts. Alarm responses shown to substances released from physically damaged conspecific individuals have been reported in a variety of fish (see review by Smith, 1992), amphibians (Pfeiffer, 1963), marine gastropods (Stenzler and Atema, 1976), and echinoderms (Snyder and Snyder, 1970). In addition, responses to substances released from physically undamaged but disturbed conspecific individuals have also been reported for such diverse groups as rats (Valenta and Rigby, 1968), earthworms (Ressler et al., 1968), and crayfish (Hazlett, 1985a,b, 1989). Alarm responses reduce the chances of predation

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(Hews, 1988; Mathis and Smith, 1993), the activity that would most commonly lead to the physical damage releasing the chemical, while disturbance responses increase the chances of a receiver avoiding any of a variety of potentially negative situations (Hazlett, 1985a,b).

Previous work on crayfish (Hazlett, 1985a,b, 1989, 1990a) focused on detection of sex pheromones and on the disturbance response shown by individuals of *Orconectes virilis*. Detection of substances released by disturbed-but-undamaged conspecifics or individuals of other crayfish species was followed by the assumption of a posture that is intermediate between the resting and the highly aroused postures, and by an increase in slow locomotory movements. Similar responses were demonstrated for a species of marine hermit crab (Hazlett, 1990b). However, alarm responses to damaged conspecifics have not been demonstrated for crayfish or indeed for very many crustaceans. Some hermit crabs respond to conspecific hemolymph by an increase in the frequency of gastropod shell manipulation or by fleeing, depending upon shell fit (Rittschof et al., 1992), and the pebble crab *Philyra laevis* is attracted to a food source much less if a crushed conspecific is nearby (McKillup and McKillup, 1992).

The experiments described in this report were designed to determine: (1) if crayfish show an alarm response to damaged conspecifics and, if so, (2) is that response specific to damaged conspecifics? A third set of questions involved initial characterization of the nature of the chemicals involved.

METHODS AND MATERIALS

Observations were done in the laboratory at the University of Michigan Biological Station near Pellston, Michigan, during the summers (June–August) of 1992 and 1993. Pilot studies were done in 1992, while data analyzed in this paper were gathered in 1993. The crayfish studied, adults of *Orconectes virilis* (Hagen 1870) and *Orconectes propinquus* (Girard 1852), were collected from the Maple River (Emmet County, Michigan), and the fish used for preparation of solutions to be tested were collected from Douglas Lake. The basic procedure followed in all tests were similar to that used in the study of other chemical-response systems in crayfish (Hazlett, 1985a,b, 1989, 1990a).

Crayfish were placed in individual 10-gallon aquaria (bottom dimensions 25 × 50 cm) that were visually isolated from one another. The aquaria were continually aerated and contained 12.5 liters of lake water at a depth of 10 cm and a portion of a clay pot as a shelter. After two to three days of acclimation, crayfish were observed individually for 8-min periods during the morning and/ or afternoon. The posture of a crayfish (raised, lowered, intermediate) and whether the crayfish was locomoting or not was recorded on a portable computer equipped with an event program. When crayfish are in the lowered posture, the

chephalothorax is in contact with the substrate, the abdomen is curled, and the chelipeds are pulled into the body with the tips of the chelae touching the substrate. The lowered posture is the most common posture of undisturbed crayfish during the day. Locomotion rarely occurs when the crayfish is in the lowered posture. In the intermediate posture, the chephalothorax is elevated slightly above the substrate, the chelipeds are held below the horizontal but not in contact with the substrate, and the abdomen is almost parallel to the substrate but the telson is perpendicular to the substrate. In the raised posture, the chelipeds are held horizontal to the substrate or higher, the chephalothorax is clearly elevated above the substrate by several millimeters, and the telson is horizontal. Crayfish locomote in both the intermediate and raised postures, although rapid locomotion most commonly occurs with the raised posture.

The 8-min observation period was divided into a 2-min early period and a 6-min late period. This division was based on pilot observations that indicated differences in the responses shown under various conditions between these two periods. During the 2-min period, solutions were introduced into the aquarium via a peristaltic pump at the rate of 20 ml/min. The addition of 40 ml into 12,500 ml of lake water represents a dilution of greater than 1 : 300. The water introduced into the aquaria was either control ("self" water, circulated from the observation aquarium back into the same aquarium) or a test solution. An individual crayfish was tested with a maximum of four different test solutions over a two-day period, and then sex and chephalothorax length were determined.

Individuals of *O. propinquus* were tested with three solutions: the self-water control, a crushed-conspecific solution, and a food solution. For the crushed-conspecific solution, a medium-sized (approx. 3 g wet weight) individual of *O. propinquus* was crushed, placed in 400 ml of distilled water, and the mixture was stirred. All solutions used for both crayfish species were filtered to remove large particles (Fisher P8 Coarse grade filter paper) and introduced to the aquaria of individual crayfish. Introductions were initiated within 10 min after preparation of a solution. Five or fewer individuals were usually tested with one solution type during one observation session; thus, utilization of solutions was completed within an hour after preparation. The food solution was prepared by mixing 4 g of frozen then thawed rock bass flesh (*Amblopolites rupestris*, (Rafinesque 1817)) in 400 ml of distilled water and filtering. Given the results of the tests with these solutions (see Results), no additional solutions were tested with *O. propinquus*.

A total of nine solutions were tested with individuals of *O. virilis*, including the self-water control. The sequence of solutions tested was varied systematically. For tests with *O. virilis*, the crushed *O. propinquus* and food solutions were prepared as described above. The crushed conspecific tests used a 4-g individual of *O. virilis*. In order to initially characterize the nature of the alarm substance, two additional solutions were prepared. The freeze–thawed conspe-

cific solution used a 4-g *O. virilis* that was frozen, thawed shortly before use, and then crushed and mixed in 400 ml of distilled water. The trypsin + conspecific solution was prepared by crushing a live *O. virilis*, mixing it in 400 ml of distilled water, adding 25 mg of trypsin (Nasco), stirring for 5 min, and then filtering the mixture with coarse filter paper.

Observations during pilot studies indicated that individuals of *O. virilis* are much more likely to show a feeding response to freeze–thawed fish flesh than to freshly killed fish. Therefore, the last sets of solutions were prepared with 4 g of muscle tissue from freshly killed fish (rather than frozen), mixed in 400 ml of distilled water, filtered, and tested as soon as possible. Three species of freshly killed fish were tested with individuals of *O. virilis*: rock bass (*A. rupestris*), bluegill sunfish (*Lepomis macrochirus*, Rafinesque 1819) and yellow perch (*Perca flavecens*, (Mitchill 1814)).

The data analyzed were the number of seconds spent in particular postures (raised, intermediate, or lowered) and activities (moving/not moving) during the introduction of the different solutions. The number of transitions from one posture or activity to another (number of acts) was also examined as an overall measure of activity. All analyses were by ANOVA with post-hoc individual comparisons, using the Bonferroni procedure to adjust the critical values for the number of comparisons made (Wilkinson, 1988).

For both *Orconectes virilis* and *O. propinquus*, there were a number of variables that could be compared to examine the responses to the solutions introduced to individuals. In both species, the results of ANOVAs testing for differences among test solutions for particular variables followed the same pattern. There were highly significant differences (*P* values much less than 0.001) for time spent in different postures and the time spent moving in both the early (first 2 min) and late (last 6 min) portions of the observation period as well as in the sums for the full observation period. However, the statistical differences were almost always much more marked for the late, last-6-min portion. Therefore, all individual comparisons reported below focus on the later period. In addition, since the crayfish had to be in one of the three postures recognized (raised, intermediate, lowered), only two of the three can be statistically analyzed, although descriptions of differences in responses will include all three postures.

RESULTS

In *O. propinquus*, the only significant differences in responses to the three solutions tested were for the raised posture (ANOVA, $F = 4.73$, $P = 0.03$) and time spent moving (ANOVA, $F = 4.77$, $P = 0.012$) during the last 6 min of the observation period. Individual post-hoc comparisons showed that the

differences between responses to crushed conspecific and the food stimulus were significant (raised posture, $F = 9.4$, $P = 0.003$; moving, $F = 9.2$, $P = 0.004$), but there were no significant differences between the crushed conspecific and control solutions (raised $F = 2.4$, $P = 0.121$; move, $F = 1.0$, $P = 0.309$). Thus, although individuals of *O. propinquus* spent less time in the raised position and moved less when a solution of crushed conspecific was introduced compared to a food stimulus (Table 1), their behavior was not different from that shown during a control period of self-water introduction. None of the other variables measured showed a significant overall ANOVA for these crayfish.

In *O. virilis*, there were very significant differences in responses to all nine tests in the time spent in the low posture ($F = 6.1$, $P = 0.0001$), raised posture ($F = 19.4$, $P = 0.0001$), time spent moving ($F = 18.8$, $P = 0.0001$), and in the number of acts executed during the total observation period ($F = 7.0$, $P = 0.0001$). Crayfish spent more time in the intermediate position when a crushed conspecific solution was introduced, more time in the raised position and moving when a frozen fish solution was introduced, and more time in the lowered posture during the control water introduction (Table 2). When crushed conspecific stimulus was introduced, the crayfish spent less time moving than when frozen fish stimuli were presented, but there was no difference in time spent moving between the crushed conspecific stimuli and control (Table 3). Thus, when a signal associated with a physically damaged conspecific was detected, individuals of *O. virilis* assumed an intermediate, "watchful" posture but did not move. While not quantified regularly, it was frequently observed that if a crayfish was outside its clay burrow when the crushed conspecific stimulus was introduced, the crayfish would rapidly back into its burrow and then assume the intermediate posture. In some cases, especially during pilot tests in 1992, individuals that had been moving slowly about the aquarium prior to the introduction of alarm substance seemed to freeze and cease all motion for some minutes.

TABLE 1. TIME SPENT BY INDIVIDUALS OF *Orconectes propinquus* EXPOSED TO VARIOUS SOURCES OF POTENTIAL CHEMICAL SIGNALS[a]

	Seconds, mean (SE)				Acts, N (SE)
	Low posture	Intermediate posture	High posture	Moving	
Control	163 (37)	125 (25)	72 (29)	46 (21)	13 (4)
Crushed *O. propinquus*	104 (30)	242 (31)	14 (11)	14 (9)	10 (3)
Freeze–thawed rock bass	72 (26)	163 (37)	125 (30)	107 (28)	15 (3)

[a]The values for postures and time spent moving are for the last 6 min of the observation periods while the number of acts executed is for the full 8-min periods.

TABLE 2. TIME SPENT BY INDIVIDUALS OF *Orconectes virilis* EXPOSED TO VARIOUS
SOURCES OF POTENTIAL CHEMICAL SIGNALS.[a]

	Seconds, Mean (SE)				
	Low posture	Intermediate posture	Raised posture	Moving	Acts, N (SE)
Control	233 (34)	108 (30)	17 (10)	14 (8)	7 (2)
Crushed *O. virilis*	137 (34)	205 (32)	17 (10)	15 (8)	7 (2)
Freeze–thaw rock bass	36 (18)	111 (23)	211 (29)	192 (27)	21 (3)
Crushed *O. propinquus*	165 (30)	190 (29)	3 (2)	1 (2)	4 (1)
Crushed *O. virilis* + trypsin	211 (32)	142 (31)	5 (5)	5 (5)	4 (1)
Freeze–thaw *O. virilis*	128 (24)	217 (25)	13 (9)	11 (8)	5 (2)
Fresh rock bass	79 (19)	197 (26)	83 (21)	75 (20)	12 (2)
Fresh bluegill	139 (27)	67 (15)	153 (31)	125 (27)	14 (2)
Fresh perch	45 (25)	143 (27)	171 (30)	153 (29)	21 (4)

[a] The values for postures and time spent moving are for the last 6 min of the observation periods
while the number of acts executed is for the full 8-min periods.

TABLE 3. INDIVIDUAL COMPARISON VALUES (F Value and Associated P Values) FROM
POST-HOC COMPARISONS OF TIME SPENT BY INDIVIDUALS OF *O. virilis* DURING
DIFFERENT STIMULUS PRESENTATIONS

Crushed conspecific vs	Low posture	Raised posture	Moving
Control			
F	7.2	0.001	0.001
P	0.008	0.97	0.99
Frozen rock bass			
F	6.0	62.8	62.6
P	0.015	0.000	0.000
Crushed Congeneric			
F	0.44	0.28	0.35
P	0.51	0.60	0.56
Freeze-Thawed Conspecific			
F	0.42	0.02	0.02
P	0.83	0.88	0.89
Conspecific + trypsin			
F	3.3	0.22	0.20
P	0.07	0.64	0.66

In order to further understand the nature of the alarm signal and test if it was specific to individuals of *O. virilis*, the responses to solutions made from freshly crushed conspecifics were compared to the responses to freshly crushed individuals of congeneric individuals (*O. propinquus*), freshly crushed conspecifics treated with trypsin, and freeze–thawed conspecifics. There were clearly no differences between the responses to solutions made from freshly crushed conspecifics, freshly crushed congenerics, or freeze–thawed conspecifics (Tables 2 and 3). Although there was a slight tendency for the responses to the trypsin-treated conspecific solution to include less time in the intermediate posture and more in the low posture, i.e., closer to the control responses, the differences were not significant. Thus, it appears that the chemical(s) involved in the alarm response shown by individuals of *O. virilis* are (1) present in individuals of a related species and (2) not destroyed by either treatment with the enzyme trypsin or freezing and then thawing.

The use of frozen fish as the basis for a food stimulus was initially motivated by convenience. However, based upon pilot tests, it appeared that frozen fish may be a stronger food stimulus than freshly killed fish. The responses of crayfish to freshly killed rock bass were different from the responses to either frozen rock bass or to crushed conspecifics (Table 4). Because the amount of time spent in raised and intermediate postures and the time spent moving appear to be about halfway between the extremes of alarm response and food stimuli response (Table 2), it appears that a freshly killed rock bass presents both alarm and food stimuli to individuals of *Orconectes virilis*. The responses to solutions

TABLE 4. INDIVIDUAL COMPARISON VALUES (*F* Value and Associated *P*) FROM POST-HOC COMPARISONS OF TIME SPENT BY INDIVIDUALS OF *O. virilis* IN DIFFERENT POSTURES AND ACTIVITIES DURING DIFFERENT STIMULUS PRESENTATIONS

Fresh rock bass vs	Low posture	Raised posture	Moving
Frozen rock bass			
F	1.08	26.7	26.4
P	0.300	0.000	0.000
Crushed conspecific			
F	1.9	7.0	7.2
P	0.17	0.009	0.008
Fresh bluegill			
F	1.3	4.9	2.9
P	0.26	0.027	0.89
Fresh Perch			
F	0.47	8.5	7.7
P	0.49	0.004	0.006

prepared from freshly killed bluegill sunfish were similar to those shown to the freshly killed rock bass. However, the responses shown to fresh perch were different than those shown to fresh rock bass (Table 4) and more closely resembled the feeding responses shown to frozen rock bass.

DISCUSSION

Results from this study demonstrate the presence of an alarm response in the crayfish *Orconectes virilis*. The alarm response (intermediate posture without movement) is similar to the alarm responses shown by some other taxa and presumably functions to reduce the probability of predation. Assumption of the intermediate posture may simply be a correlate of the receiver of the signal no longer being in a relaxed, resting state but rather on alert for potential danger. By not moving, the crayfish reduces the chance of detection by possible predators. This response has been reported for other aquatic animals and demonstrated to reduce the chances of predation (Werner and Anholt, 1993).

The behavior of *O. virilis* is influenced in a wide variety of ways by chemical signals. Pheromones and other chemicals are used to identify sex (Hazlett, 1985a), species (Tierney and Dunham, 1982), maternal condition (Ameyaw-Akumfi, 1976), the presence of food (Tierney and Atema, 1988), the presence of animals that are stressed or disturbed (Hazlett, 1990a,b), and the presence of physically damaged individuals. The detection of the chemical signals associated with each of these situations or conditions contributes to distinct responses by crayfish.

The observation that individuals of the related species *Orconectes propinquus* did not show a statistically significant alteration of behavior when solutions made from crushed conspecifics were introduced, compared to the control solutions, was a bit surprising. However, individuals of this species also did not show a response to disturbance pheromone (Hazlett, 1990a,b) and the responses to sex pheromone appear less well developed in this species (Tierney and Dunham, 1982). The reduced sophistication of chemical communication in *O. propinquus* compared to that of *O. virilis* is puzzling given how close these species are phyletically, although they are in different subgenera (Fitzpatrick, 1987), and how similar they are ecologically. While there are some slight differences in habitat use, individuals can occur almost side by side in many habitats and are faced with a similar array of predators (Hobbs, 1993) and other dangers. Because *O. propinquus* is slightly more active during the day than *O. virilis* (although both are basically nocturnal), *O. propinquus* may rely less upon chemical communication.

The existence of both a disturbance response and a distinct alarm response in the same species leads to a variety of questions. Individuals of *O. virilis*

behave in a low-level alert fashion upon detection of disturbed individuals in the area and move out of their burrow and around their environment as if looking for the source of disturbance. In contrast, the alarm response involves a reduction of locomotion and pulling back into their burrow if the crayfish is out in the open. These responses would appear to be a defense against a particular type of danger, predation. While the exoskeleton of a crayfish could be broken and the alarm substances released by a variety of situations (e.g., a rock falling on the animal, extremes of aggressive interactions, predation), the response shown appears appropriate for this one source of damage.

It is very interesting that for both the disturbance response and the alarm response of *O. virilis*, animals other than conspecifics can be sources of the chemicals involved. In addition to other species and genera of crayfish, other taxa of amenotilic animals can be sources of disturbance chemicals (Hazlett, 1989, 1990a). Similarly, other crayfish as well as fish can be a source of the signal that predatory danger is present. While some predators in aquatic habitats may well specialize on one taxa or another, it is not unusual for predators such as wading birds, snapping turtles, or larger fish to eat a variety of prey that would include both crayfish and small fish. Working with the marine snail *Ilyanassa*, Stenzler and Atema (1976) found some response to damaged congenerics, but this was reduced compared to the response shown to damaged conspecifics—unlike the situation with *O. virilis* where there was no difference in responses to conspecific and congeneric damage.

The alarm responses of *O. virilis* and lack of them in *O. propinquus* may help explain some differences in the feeding behavior of the two species. Individuals of *O. virilis* that are reasonably well fed in the laboratory will not feed upon recently killed conspecifics or upon recently killed fish such as bluegill or rock bass. They will do so if the flesh of these animals has decayed for several days or if the crayfish have not fed recently. In contrast, individuals of *O. propinquus* will readily feed upon conspecifics and freshly killed fish even when well supplied with other sources of food. Traps placed in the field and baited with freshly killed fish often catch more *O. propinquus* initially and catch individuals of *O. virilis* only after a few days of decay (unpublished observations). Differences between the species in the results of field tests of alarm and food signals (Mitchell and Hazlett, in preparation) are consistent with suggestions from the laboratory.

The experiments with crushed congeneric individuals indicate that the chemicals involved are not specific to *O. virilis*. Indeed, the experiments with fresh fish suggest that at least a partial representation of those chemicals that trigger the alarm response may be found in a variety of freshwater animals. The fact that the freeze–thawed preparation of conspecifics resulted in no detectable reduction of alarm substance potency points to the possibility that the chemical(s) involved survived the array of autochthanous enzymes released from the cells

of organisms following this physically damaging technique (Rittschof, 1980).
The fact that the enzyme trypsin did not significantly alter the responses shown
suggests that if the chemicals involved include proteins or shorter peptides, those
molecules are not destroyed (as signals of danger) by cleavage of lysine or
arginine peptide bonds. Clearly, much work remains to be done concerning the
characterization of the moieties involved in these chemical communication sys-
tems and the differences between them, as well as the ways the integration of
these multiple inputs affects individuals in nature.

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