PREDATOR AVOIDANCE STRATEGIES OF THE CRAYFISH
ORCONECTES VIRILIS

BY

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ABSTRACT

Field experiments compared the chemically-mediated responses of the crayfish *Orconectes virilis* and *O. propinquus* to food stimuli, alarm substance, disturbance chemicals and a combination of food and alarm. The combination of alarm and food stimuli resulted in a very marked decrease in the number of *O. virilis* attending a site compared to the food stimulus alone. There were also differences between the disturbance and alarm responses of *O. virilis* with individuals spending less time near sources of alarm substance as compared to sources of disturbance chemicals.

Individuals of *O. propinquus* showed no differences in responses to the experimental treatments. Variations in the level of activity were consistent with lunar cycle of activity in *O. virilis*, with the greatest activity near new moon, and the least near full moon.

RÉSUMÉ

Des expériences sur le terrain ont comparé les réponses chimiquement provoquées des écrevisses *Orconectes virilis* et *O. propinquus* aux stimuli alimentaires, à une substance d'alarme, aux agents chimiques perturbants et à une combinaison de nourriture et d'alarme. La combinaison d'alarme et de stimuli alimentaires a provoqué une décroissance très marquée du nombre d'*O. virilis* assistant à un site en comparaison avec le stimulus alimentaire seul. Il y a eu aussi des différences entre les réponses à la perturbation et à l'alarme d'*O. virilis* avec les individus passant moins de temps près des sources de substance d'alarme en comparaison avec les sources d'agents chimiques de perturbation.

Les individus d'*O. propinquus* n'ont pas manifesté de différences dans les résponses aux traitements expérimentaux. Les variations dans le niveau d'activité étaient en rapport avec le cycle lunaire d'activité chez *O. virilis*, avec l'activité la plus grande vers la nouvelle lune, la plus faible vers la pleine lune.

INTRODUCTION

All animals face difficult behavioral decisions, requiring them to balance the benefits with the related costs of their activities. For example, movement generally increases the rate of acquiring food or finding mates, but it also increases an animal's exposure to predators (Werner & Anholt, 1993). We expect animals like crayfish to minimize the costs of moving by using various strategies to avoid contact with predators. Environmental cues that could indicate an increased risk of predation should be utilized whenever possible.

The predominantly nocturnal activity patterns of crayfish may be related to the avoidance of predators that rely on vision. In shallow waters this strategy would be less effective during periods of bright moonlight and lunar cycles have been linked to predator avoidance in some crustaceans (Gliwicz, 1986). Since crayfish tend to be nocturnal, we expect many species would use non-visual means (such as chemical cues) as indicators of increased predation risk. Stein & Magnuson (1976) showed that the presence of a predator induced changes in substrate use in some crayfish.

Two types of chemical cues that might be used by crayfish are disturbance chemicals and alarm chemicals. In contrast to disturbance chemicals (Hazlett, 1989, 1990), which are released when an organism is not physically damaged, alarm substances are released when an organism's skin or exoskeleton is broken during predation or other life-threatening events. An alarm response occurs if the alarm substances cause a reaction in conspecifics or in other ecologically similar organisms. Alarm responses have been documented in fish (Liley, 1982; Mathis & Smith, 1992), larval toads (Hews, 1988), sea urchins (Parker & Shulman, 1986), sea anemones (Howe & Skeikh, 1975), several crab species (Rittschof et al., 1992; McKillup & McKillup, 1992), marine snails (Atema & Stenzler, 1977) and crayfish (Hazlett, 1994).

All previous studies of alarm and disturbance responses in crayfish (Hazlett, 1989, 1990, 1994) have been conducted in the laboratory. Moreover, no previous study of the alarm or disturbance responses of a particular organism has attempted to distinguish between these two types of responses. The purpose of the present study is to examine the alarm and disturbance responses of *Orconectes virilis* (Hagen, 1870) in the field and compare its behavior to that of the sympatric crayfish *O. propinquus* (Girard, 1852). *O. virilis* was chosen as the primary species of interest because previous work (Hazlett, 1990) indicated that this species is more likely to show a disturbance response than are other crayfish species (*O. propinquus* and *O. rusticus* (Girard, 1852)) and in the laboratory *O. virilis* individuals show an alarm response while individuals of *O. propinquus* do not (Hazlett, 1994).

The nature of the disturbance response in *O. virilis* in the laboratory is a longlasting "low level alert" (Hazlett, 1990) that could prepare the animal to react quickly to new stimuli. Individuals of *O. virilis* that have been exposed to disturbance chemicals are more reactive to stimuli in general and move about slowly. When individuals of *O. virilis* in the laboratory are exposed to chemicals released by crushed conspecifics they assume an intermediate posture and cease movement (Hazlett, 1994). They also often pull back into their burrows upon detection of the alarm substance(s).

In this study, field responses to different stimuli were compared to test the following hypothesis: (1) *O. virilis* avoid field sites where a recently crushed conspecific has been introduced. (2) *O. virilis* respond differently to disturbed conspecifics than to crushed conspecifics. (3) The sympatric but less chemically sensitive *O. propinquus* does not respond to disturbed or crushed *O. virilis*.

MATERIALS AND METHODS

Two study sites were chosen along the Maple River, one just south of Pellston, Michigan, and the other in the east branch of the Maple River near Bryant Road, both in Emmet County, Michigan, USA. The study sites were chosen for their high densities of crayfish and for the absence of *Orconectes rusticus*, which might have interfered with the experiment through agonistic interactions with *O. virilis* and *O. propinquus* (cf. Hazlett et al., 1992). The rate of water flow at both sites was relatively low, thus allowing for a slow dispersal of any chemicals, and the water depth was about 0.5 m.

Observations were done between 22:30 and 02:00 h from late June through mid-August, 1993. At each location, the four observation sites consisted of 0.5 m diameter circles, each demarcated by four stakes and each at least 1.5 m from the nearest circle. All *O. virilis* individuals used to prepare experimental treatments were between 23 and 28 mm carapace length (approximately 4 g in weight). Animals responding to the experimental treatments belonged to natural populations of *O. virilis* and *O. propinquus* at the study sites.

The two sets of observations followed the same protocol. Sources of possible chemical stimuli were prepared just before use and placed in plastic containers. These containers were partially filled with concrete (to hold them in place in the field) and the tops covered with plastic mesh to allow water circulation. Once the chemical source was in a container, it was placed in the center of one of the observation circles and observations started. The area of the circle was weakly illuminated with a red light source adjusted such that crayfish approaching the area showed no response to slight movements of the light source. During a

15 min observation period, the number and species identity of each crayfish that entered the circle was recorded as well as the number of approaches to within 1 cm of the plastic container. The number of seconds spent in the circle and number of seconds spent within 1 cm of the container were also recorded. Because the light level had to be quite low to avoid altering crayfish behaviour, particular postures could not be reliably observed, nor could the sex of the responding animals always be determined given the light conditions.

Alarm responses. — The first set of observations focused on alarm responses. The responses to four different sources were compared: control, alarm, food, and a food + alarm combination. The control container held only lake water. The alarm source was prepared by crushing a 4 g individual of *O. virilis* and placing it in the container. The food source was prepared by placing 4 g of recently thawed rock bass flesh (*Ambloplites rupestris* (Rafinesque, 1817)) in the container, while the combination source contained 2 g of rock bass flesh and 2 g of recently crushed *O. virilis* flesh. The combination container thus had the same weight of animal flesh as the food container. The fish flesh used was frozen and then thawed to promote decomposition and to eliminate possible fish alarm substances (Hazlett, 1994). The sequence of treatments tested and the sites used for particular sources was haphazardly varied during the 10 replicates. One or two replicates were done per night, depending upon weather conditions, and all four treatments were done the same night for any replicate.

Disturbances vs alarm responses. — To determine whether *O. virilis* exhibit distinct alarm and disturbance responses in the field, we prepared four experimental containers: one each for control, alarm, disturbance, and food stimulus sources. Each container held a small mesh bag tied to a monofilament lead. The bag in the control container was empty; the alarm container bag contained a crushed, freshly killed *O. virilis*; the disturbance container bag held a live *O. virilis*; and the food container bag contained 4 g of freeze-thawed rock bass.

Weather permitting, a replicate was run at both locations on each night of the season, with the first location visited changed every night. Treatments were haphazardly assigned to circles at each site, and the sequence of circles used was varied haphazardly. To maintain the disturbance level of the live *O. virilis* in the disturbance treatment, the monofilament lead attached to the mesh bag was tugged a few times each minute. The leads on the bags in the three other containers were tugged at the same rate as a control for procedural effects.

Data that were normally distributed were analyzed with ANOVA, and data than were non-normally distributed were analyzed with Kruskal-Wallis tests for

all comparisons between more than two means, and Mann-Whitney U tests for paired comparisons. To adjust for making multiple comparisons, we multiplied all P values by the number of comparisons made.

RESULTS

Alarm responses. — In the case of *O. virilis*, there were very significant differences among treatments in the number of approaches to the observation circle (ANOVA $F = 19.5, P < 0.0001$) and the number of approaches to within 1 cm of the container ($F = 5.2, P = 0.004$). The much higher number of approaches to the food stimulus would appear to be the main contributor to these overall (table I). Three of the possible pairwise comparisons were of primary interest: control vs alarm, control vs alarm + food, and food vs food + alarm. There were no significant differences in approaches to the control compared to alarm containers or the combination of food + alarm (all $P > 0.50$). However, the food + alarm container was approached very significantly less often than the food-alone container ($F = 36.0$, $P < 0.0001$ for observation circle approaches, $F = 9.17$, $P = 0.005$ for the 1 cm approaches). Thus there clearly was a behavioral effect of the presence of substances released from a crushed conspecific, eliminating any food-related responses.

In the case of *O. propinquus*, none of the overall comparison values were significant ($P > 0.10$ for all three variables tested) and none of the individual comparisons were significant for the control vs alarm comparison. The number of approaches did not vary significantly ($F = 3.21$, $P = 0.08$ for approaches to the observation circle, $F = 0.95$, $P = 0.335$ for 1 cm approaches) but there was a significant increase in the number of seconds spent within 1 cm of the container for the combination of signals compared to the food-alone signal ($F = 5.38$, $P = 0.026$). This may have been a secondary effect of the lack

TABLE I

The mean number of approaches per observation period (standard error in parentheses) by crayfish *Orconectes virilis* (Hagen) and *Orconectes propinquus* (Girard) depending upon the treatment category

	Control	Alarm	Alarm + food	Food stimulus
No. *O. virilis* to large circle	1.4 (0.3)	1.0 (0.3)	1.4 (0.2)	5.0 (0.6)
No. *O. virilis* within 1 cm	0.3 (0.1)	0.4 (0.1)	2.0 (0.2)	3.3 (1.2)
No. *O. propinquus* to large circle	1.5 (0.5)	0.9 (0.4)	2.4 (0.8)	1.0 (0.3)
No. *O. propinquus* within 1 cm	0.4 (0.1)	0.5 (0.3)	0.5 (0.2)	0.2 (0.1)

of (larger) individuals of *O. virilis* in the vicinity of the container with alarm substance, although correlations between response levels of *O. virilis* and *O. propin-quus* were not significant.

Disturbance and alarm response of *O. virilis*. — Kruskal-Wallis one-way ANOVA testing for treatment effects on the number of approaches by *O. virilis* into the observation circles and to within 1 cm of the experimental containers were highly significant (P values < 0.0005, K-W statistics > 35). Differences among treatments in the length of time spent by *O. virilis* within study circles and within 1 cm of the experimental containers were also significant (P values < 0.0005, K-W statistics > 30) (fig. 1). In all of these cases, animals spent much more times or made many more approaches to the food container.

Pair-wise comparisons between control and alarm treatments, and between control and disturbance treatments were not significantly different for any experimental variables (all P values > 0.25). However, the responses of *O. virilis* to the alarm and disturbance treatments were nearly significantly different ($P = 0.051$, $\chi^2 = 5.7$) in the lengths of time individuals spent in the experimental circles. Combined with a nearly significant ($P = 0.051$, $\chi^2 = 5.7$) difference in the time per approach into the experimental circle, these results indicate that although individuals of *O. virilis* approached the disturbance and alarm treatments at the same rate ($P > 0.10$), they tended to spend less time near a crushed conspecific than a disturbed one. There was no significant difference
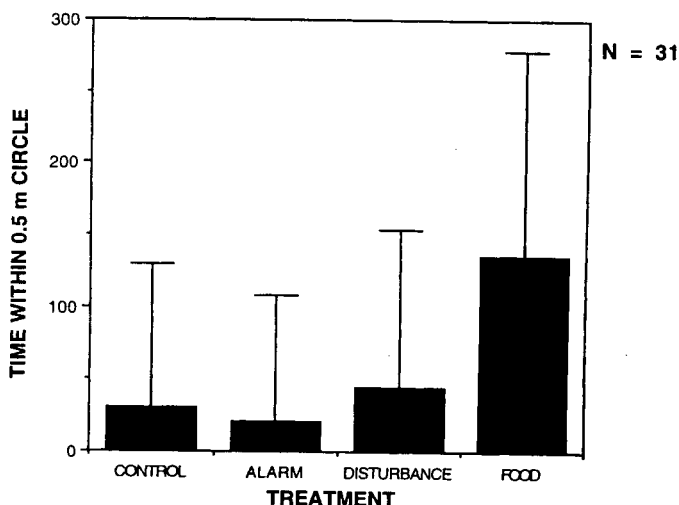

Fig. 1. Average (standard deviation) time spent within the 0.5 m experimental circles by individuals of *Orconectes virilis* (Hagen, 1870) in the different treatments.
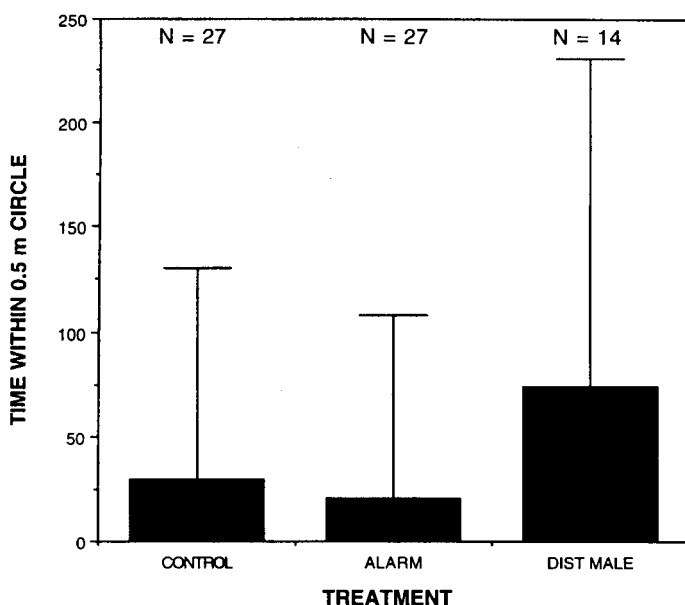
Fig. 2. Average time spent within the 0.5 m circles by *Orconectes virilis* (Hagen, 1870) when the disturbed animals were males.

in the length of time individuals spent within 1 cm of the experimental container, nor was there a difference in the number of close approaches to the containers (all P values > 0.10).

If trials in which the disturbed (source) *O. virilis* was female are excluded from the analysis, the number of approaches into the 0.5 m circles by *O. virilis* were almost significantly different ($P = 0.063$, $\chi^2 = 5.3$) and both the number of approaches to within 1 cm of the experimental container ($P = 0.048$, $\chi^2 = 5.8$) and the length of time spent within 1 cm of experimental containers ($P = 0.045$, $\chi^2 = 5.9$) (fig. 2) differed between the alarm and disturbance treatments. The length of time individuals spent within 0.5 m circles were also different ($P = 0.015$, $\chi^2 = 7.9$) for the alarm versus disturbance comparison, as were the number of seconds per approach within the experimental circles ($P = 0.015$, $\chi^2 = 7.9$). In all cases, individual *O. virilis* responded differently to the alarm than to the disturbance treatment, making fewer approaches and spending less time within observation circles when they contained a source of alarm substance.

Responses of *O. propinquus*. — Kruskal-Wallis tests for differences in the response of *O. propinquus* among the experimental treatments were all nonsignif-

icant (all P values > 0.10), indicating that individuals made similar numbers of approaches within circles and near containers, and spent similar amounts of time within circles and near containers, regardless of the experimental treatment or the location of the tests.

Variability among replicates over time. — While collecting data for comparison of the disturbance and alarm responses, we noted that the number of individuals of *O. virilis* and *O. propinquus* recorded was highly variable between nights, and that numbers at the two study sites tended to covary. There are several potential causes for this variability in crayfish numbers across days. We first looked for a relationship between the number of days since the last test replicate at a study site and the numbers recorded. Individuals of *O. virilis* spent different amounts of time within experimental circles depending upon the number of days since the last trial ($P = 0.038$, $K\text{-}W$ statistic $= 8.4$). This difference was not linear, though: animals spent more time within the circles after one or three days, and less time after two or more than three days. In addition, there was no significant difference ($P > 0.10$) in the number of approaches by *O. virilis* into experimental areas nor any of the responses of *O. propinquus* based on days since the last replicate (all P values > 0.10 at each study site). Thus most of the variability in response parameter over days remained unexplained.

Another possible cause of the variation over days in response levels could be a lunar cycle. A second order polynomial regression comparing the number of approaches into the observation circles by *O. virilis* over days of observation was highly significant ($R^2 = 0.726$, $F > 15.6$, $P < 0.0005$; fig. 3). A similar polynomial regression comparing the total time per replicate spent within experimental circles by *O. virilis* over days was also significant ($R^2 = 0.497$, $F = 3.9$, $P = 0.033$; fig. 4). These results indicate that *O. virilis* activity varied in a manner predicted by a second order polynomial equation, with the least activity at the time of the full moon.

Additionally, although the response of *O. virilis* did not vary based on the starting time of trials ($P > 0.25$ when the data were divided into 15-min blocks of time), there was a significant relationship between starting time and numbers of individuals approaching experimental treatments during the third quarter of the lunar cycle ($R^2 = 0.358$, $F = 7.4$, $P = 0.009$), with less activity occurring later in the night. There were no significant differences based on cloudy versus clear weather conditions in the activity of crayfish (total time within, and the number of approaches into experimental circles) during times when the moon was above the horizon (P values > 0.50).
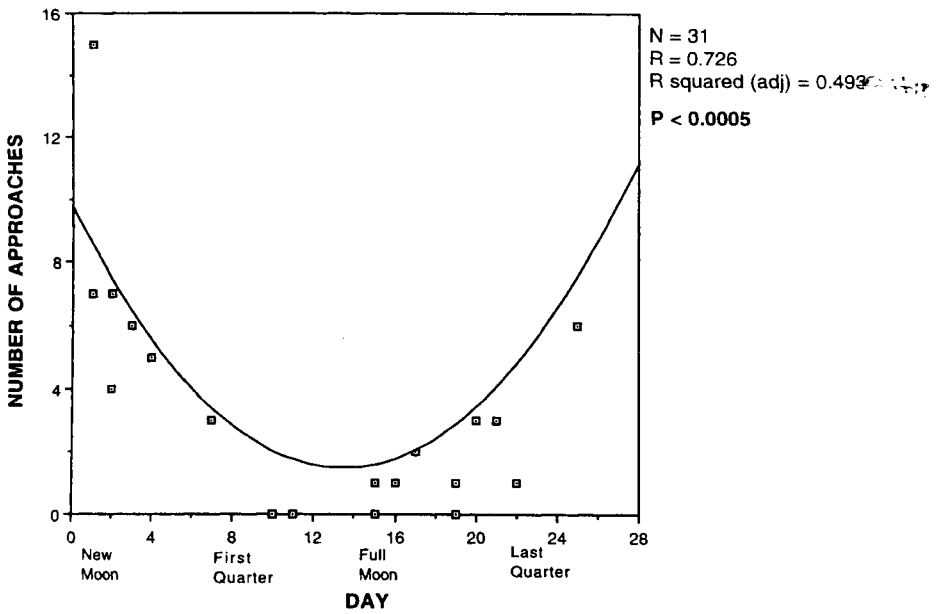
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Fig. 3. Possible lunar cycle in the number of approaches into the 0.5 m circles by individuals of *Orconectes virilis* (Hagen, 1870). Day 1 corresponds to July 19, 1993 and Day 28 to August 15, 1993.
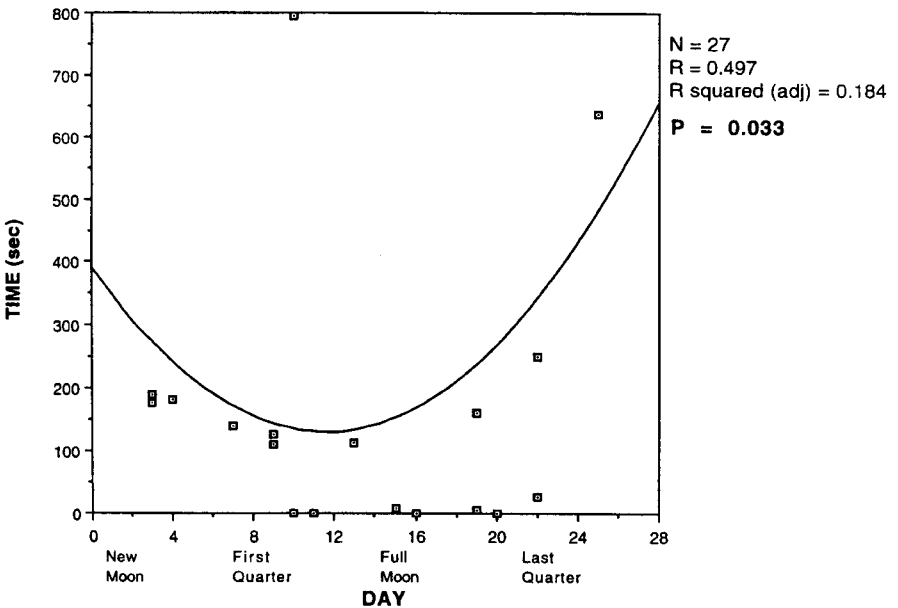

Fig. 4. Possible lunar cycle in the number of seconds spent within the 0.5 m experimental circles by *Orconectes virilis* (Hagen, 1870).

The data for the total number of approaches of *O. propinquus* at the Maple River site are suggestive of a possible cycle, but the trend is nonsignificant ($R^2 = 0.327$, $P > 0.10$ for a second order polynomial regression).

DISCUSSION

The highly significant overall treatment effects on *O. virilis* responses indicate that freeze-thawed rock bass is a potent attractor of *O. virilis* individuals as has been demonstrated in the laboratory (Hazlett, 1994). In the first series of experiments, the clear effect of the alarm substance in reducing the rate of approaches to and time spent in the vicinity of a food stimulus illustrate the marked alteration of behavior in the field when such a danger signal is detected. In the second series of experiments, the highly variable results and a generally low number of individuals responding makes a comparison among the experimental conditions more difficult. However, there was a strong tendency for *O. virilis* to avoid crushed conspecifics, and to approach disturbed ones, as indicated by the time spent by animals within experimental circles. The nearly significant trends of individuals spending less total time within experimental circles, and of making shorter visits per approach for alarm trials than for disturbance ones (both P values = 0.051) show that *O. virilis* spend less time near a crushed animal than a disturbed one, despite similar approach rates.

The exclusion of the results from the disturbance trials in which female *O. virilis* had been used was based upon the laboratory observations that individuals of *O. virilis* respond more to male disturbed animals than to females (Hazlett, 1985, 1989). The length of time that animals remained within experimental circles, the number of seconds par approach, the number of approaches to within 1 cm of treatment containers, and the length of time spent within 1 cm were all significantly lower for the alarm than for the disturbed male treatment. The number of individuals entering the experimental circles showed a nearly significant difference between alarm and disturbed male treatments, with *O. virilis* tending to enter alarm circles less often than disturbance ones.

The data suggest that disturbed male *O. virilis* tend to attract conspecifics, and that crushed animals tend to repel *O. virilis*. Although we did not predict that disturbed animals would attract conspecific individuals, this is understandable when the increased rate of slow locomotion observed in the laboratory is considered and would be plausible if disturbance is a weak indicator of predation or other forms of risk. The chemical that signals disturbance in crayfish could potentially be released in a number of different situations, including feeding, mating, and predator avoidance. The possible benefits of approaching a disturbed animal and

thereby increasing information about the source of the disturbance may outweigh the risk of predation.

The lower approach rate by *O. virilis* to a source of signals indicating the presence of crushed conspecifics than to disturbed males is consistent with the idea that crushed conspecifics are a clear indicator of predation risk. Since most causes of physical damage (such as intraspecific aggression, predation, and accidents) are potentially life-treatening to nearby conspecifics, the benefits of approaching a crushed conspecific should be considerably lower than the benefits of remaining still, or avoiding the area.

The lack of a difference in the responses of *O. propinquus* to different treatments in both series of experiments is puzzling but consistent with earlier findings in the laboratory. Individuals of *O. propinquus* showed neither a response to disturbed conspecifics (Hazlett, 1989, 1990) nor a response to crushed conspecifics (Hazlett, 1994). The fact that *O. propinquus* responded similarly to all the treatments indicates that this species is relatively insensitive to most odors, including food. An alternative explanation for some of these field data is that individuals of *O. virilis* and *O. propinquus* are negatively interacting. The strong response of individuals of *O. virilis* to food stimuli could inhibit the approach or retention of individuals of *O. propinquus*, decreasing the recorded magnitude of its feeding response. However, our data did not support the hypothesized interaction between species (regressions comparing variables for *O. virilis* and *O. propinquus* all had P values > 0.25).

This paper presents the first field evidence of a lunar cycle in crayfish. Second order polynomial regressions of the number of approaches into and the length of time spent within experimental circles by *O. virilis* (figs. 3, 4) were both significant and the regressions followed the lunar cycle, with minimums at the time of the full moon, and maximums near the new moon. Cloud cover had no effect on the lunar cycle; when the moon was near full, individual *O. virilis* were less active, even during the low-light conditions of a heavy overcast.

Reduction of predation risk is one of the most common explanations for lunar cycles in organisms (Gliwicz, 1986; Daly et al., 1992; although see Lohmann & Willows, 1987 and Farbridge & Leatherland, 1987, for alternative explanations), and we propose that predation reduction is the most reasonable functional explanation in this case. Crayfish predators include a large number of birds (including ducks and herons), numerous fishes, snapping turtles, and mammals (including raccoons, muskrats, and humans) (Hobbs, 1993). Most of the predators of crayfish are primarily visual hunters. These predators would have a much easier time detecting crayfish on bright, moonlit nights. The lack of a difference in *O. virilis*

activity levels between cloudy and clear nights near the full moon indicates that the observed lunar cycle is not based solely on differences in light levels.

LITERATURE CITED

ATEMA, J. & D. STENZLER, 1977. Alarm substance of the marine mud snail, *Nassarius obsoletus*: biological characterization and possible evolution. Journ. chem. Ecol., **3**: 173-187.

DALY, M., P. R. BEHRENDS, M. I. WILSON & L. F. JACOBS, 1992. Behavioral modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. Anim. Behav., **44**: 1-9.

FARBRIDGE, K. J. & J. F. LEATHERLAND, 1987. Lunar cycles of Coho salmon, *Oncorhynchus kisutch*. Journ. exp. Biol. **129**: 165-178.

GLIWICZ, J. M., 1986. A lunar cycle in zooplankton. Ecol., **67**: 883-897.

HAZLETT, B. A., 1985. Disturbance pheromones in the crayfish *Orconectes virilis*. Journ. chem. Ecol., **11**: 1695-1711.

— —, 1989. Additional sources of disturbance pheromone affecting the crayfish *Orconectes virilis*. Journ. chem. Ecol., **15**: 381-385.

— —, 1990. Source and nature of disturbance-chemical system in crayfish. Journ. chem. Ecol., **16**: 2263-2275.

— —, 1994. Alarm responses in the crayfish *Orconectes virilis* and *Orconectes propinquus*. Journ. chem. Ecol., **20**: 1525-1535.

HAZLETT, B. A., D. RITTSCHOF & D. RUBENSTEIN, 1974. Behavioral biology of the crayfish *Orconectes virilis*. I. Home range. American Midl. Natural., **92**: 301-319.

HAZLETT, B. A., F. E. ANDERSON, L. A. ESMAN, C. STAFFORD & E. MUNRO, 1992. Interspecific behavioral ecology of the crayfish *Orconectes rusticus*. Journ. Freshwat. Ecol., **7**: 69-76.

HEWS, D. K., 1988. Alarm response in larval Western Toads, *Bufo borealis*: release of larva chemicals by a natural predator and its effect on predator capture efficiency. Anim. Behav., **36**: 125-133.

HOBBS, H. H., III, 1993. Trophic relationships of North American freshwater crayfishes and shrimps. Milwaukee Museum Contributions, **85**: 1-110.

HOWE, N. R. & Y. M. SHEIKH, 1975. Anthopleurine: a sea anemone alarm pheromone. Science, New York, **189**: 386-388.

LILEY, N. R., 1982. Chemical communication in fish. Canadian Journ. Fish. aquatic Sci., **39**: 22-35.

LOHMANN, K. J. & A. O. D. WILLOWS, 1987. Lunar-modulated geomagnetic orientation by a marine mollusk. Science, New York, **235**: 331-334.

MATHIS, A. & R. F. J. SMITH, 1992. Avoidance of areas marked with a chemical alarm substance by Fathead Minnows (*Pimephales promelas*) in a natural habitat. Canadian Journ. Zool., **70**: 1473-1476.

McKILLUP, S. C. & R. V. McKILLUP, 1992. Inhibition of feeding in response to crushed con-
     specifics by the pebble crab *Philyra laevis* (Bell). Journ. exp. mar. Biol. Ecol., **161**: 33-43.

PARKER, D. A. & M. J. SHULMAN, 1986. Avoiding predation: alarm responses of Caribbean sea
     urchins to simulated predation on conspecific and heterospecific sea urchins. Mar. Biol., **93**:
     201-208.

RITTSCHOF, D., D. W. TSAI, P. G. MASSEY, L. BLANCO, G. L. KEUBER, JR. & R. J. HAAS, JR.,
     1992. Chemical mediation of behavior in hermit crabs: alarm and aggregation cues. Journ.
     chem. Ecol., **18**: 959-983.

STEIN, R. A. & J. J. MAGNUSON, 1976. Behavioral response of crayfish to a fish predator. Ecology,
     57: 751-761.

WERNER, E. E. & B. R. ANHOLT, 1993. Ecological consequence of the trade-off between growth
     and mortality rates mediated by foraging activity. American Nat., **142**: 242-272.