

Foraging in complex odor landscapes: chemical orientation strategies during stimulation by conflicting chemical cues

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Abstract. The concept of trade-offs and the decisions organisms make regarding them have become a driving force in ecological research. One well-studied trade-off, maximizing growth while minimizing mortality, affects decisions an organism makes regarding activity levels, habitat selection, and refuge use. Our study addressed how complex odor cues (e.g., a predation event and food combined) and their physical properties (e.g., concentration and spatial distribution) can affect foraging. Experiments were carried out using the crayfish *Orconectes virilis* in an artificial stream. A 2 × 2 factorial design was used with 2 odor treatments (food and food + alarm) and 2 shelter treatments (shelter and no shelter). Crayfish in the alarm treatment found the food source less often. They also took significantly longer to find the food source and spent more time in shelters. Crayfish in the presence of alarm stimuli used side shelters significantly more than shelters in the center of the flume, whereas crayfish in the control did not show a preference. Also, concentration of the alarm odor significantly affected the alarm response of the crayfish. Electrochemical recordings showed that the dopamine tracer was present in high concentrations down the center of the flume but in very low concentrations or absent along the sides of the flume for both the food and alarm trials. Our study illustrated the importance of chemical signals in aquatic systems for both locating food and avoiding predators. Complex odors influenced habitat use as well as foraging efficiency and success. The content, concentration, and distribution of complex chemical signals appear to be an important part of risk assessment during foraging, and may provide the necessary information to facilitate ecological interactions.

Key words: *Orconectes virilis*, olfaction, search strategies, foraging, predator avoidance, alarm chemicals, chemoreception.

Recognition of the importance of trade-offs in shaping the decisions organisms make has provided a model for understanding individual behavior and the structure of ecological communities. One well-characterized trade-off an organism faces is maximizing growth while minimizing mortality, or the trade-off between foraging and avoiding predation (Werner and Gilliam 1984, Dill 1987, Lima and Dill 1990, Werner and Anholt 1993). In many cases, optimal foraging and completely avoiding predation are incompatible, but an organism must be capable of balancing these conflicting demands. It is not surprising, then, that many animals are capable of assessing predation risk and using this information to make decisions regarding

foraging, activity patterns, habitat selection, and refuge use (Lima and Dill 1990). A number of researchers have shown that sensory systems, behavioral responses, and signal structure can influence both predation and assessment of predation risk (Lythgoe 1979, Endler 1991, 1993). Our study addresses how complex odor cues can affect the ability of crayfish to effectively forage, and shows how chemical cues can provide the information needed to make important ecological decisions regarding trade-offs between foraging and avoiding predation.

Organisms have many different strategies to avoid predation, including morphological, life history, and behavioral responses (Kats and Dill 1998). One common and effective means of avoiding predation is refuge use. Predation effects on refuge use is demonstrated in many different taxa including fish (Fricke 1987, Petranka et al. 1987, Brown and Smith 1996), insects (Moses and Sih 1998), and snails (Turner 1996). Although seeking refuge is an effective mecha-

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nism for escaping predation, an organism must make important decisions regarding refuge use. Time spent in a shelter is time an organism could have spent foraging. Heavily vegetated areas may offer refuge, for example, but may also have fewer resources than more dangerous areas (Werner et al. 1983). Therefore, how and when an organism uses shelter in dealing with predation risk can be a very important decision. Limited use of shelter could lead to death through predation; however, over use could lead to a loss of fitness through reduction in growth and fecundity (see review in Sih et al. 1988).

The threat of predation may also influence other aspects of an organism's behavior, including when to feed, where to feed, and what to eat (Lima and Dill 1990). Organisms may choose to forage in less profitable areas where there is a reduced risk of predation and they may stay in patches for longer periods. Kohler and McPeck (1989) found that, in the presence of sculpin predators, mayfly larvae reduced the amount of time they spent on the top of substrates (where food is abundant) and reduced their rate of movement while traveling within and between patches. To make decisions regarding these trade-offs, organisms must be able to evaluate their environment to determine the risk of predation and the availability of food resources.

There has been recent recognition of the importance of chemical signals in risk assessment, especially in aquatic systems. Chemical cues have ecological advantages over other sensory cues in providing a means for predator detection in aquatic environments. Visual cues are useful, but they have several drawbacks. Light is often scarce because of turbid or deep water, and vision is only useful at relatively short distances in these environments. In predator avoidance, it is advantageous to detect a predator as far in advance as possible. Tactile cues, although useful, provide little advance warning and generally signal that an attack has begun. Chemical cues can be detected at fairly long distances and thus can provide advance warning even in dark or murky environments. Long-range detection could be helpful in allowing an organism to detect a predator before the predator detects it.

Many organisms can detect a potential predator using chemical cues emanating from the predator (see review in Kats and Dill 1998). Organisms may also exhibit a strong response to

a chemically mediated alarm signal. This damage-released chemical contained in tissues of the prey signals to conspecifics that a predation event may have occurred. Mathis and Smith (1992) found that only a small % of minnows (*Pimephales promelas*) were caught in alarm-baited traps in comparison to the no-odor control traps, and thus minnows exhibited a strong avoidance response to the alarm chemicals. An alarm response was also demonstrated in the crayfish *Orconectes virilis* (Hazlett 1994, 1999). Crayfish exposed to crushed conspecific (alarm) odor exhibited an intermediate posture that signified they were in a state of alert. These crayfish also moved less than those exposed to a food odor but no more than controls did. In addition, they tended to move into shelters when the alarm odor was added. Many species of cambarid crayfish can also detect and respond to predator odors (Hazlett and Schoolmaster 1998).

Avoiding predation is only one part of managing the trade-off between mortality and growth. Although the risk of predation generally reduces foraging behavior, high resource levels promote greater risk taking (Scrimgeour and Culp 1994). Therefore, to optimize its behavior, an organism must be able to assess potential food sources as well as potential predators. A number of different organisms use chemical cues emanating from food sources to detect and locate these sources. Moore and Lepper (1997) found that sea stars could locate food using odor even in the absence of flow. Extensive work has also been done on the orientation of lobsters, crayfish, and blue crabs to food. McLeese (1973) found that lobsters use odor plumes to orient to an upstream food source. A similar behavior pattern was also found in the crayfish *O. rusticus* and *O. virilis* (Moore and Grills 1999, Keller et al., in press). Last, abiotic factors (such as increased turbulence) can severely affect the ability of blue crabs to forage effectively using chemical signals (Weissburg and Zimmer-Faust 1993, Finelli et al. 2000).

These studies all characterized an organism's response to a single odor cue. In natural systems, such as streams, organisms are flooded with a complex mixture of different chemical cues simultaneously (e.g., mate pheromones, food stimuli, predator cues, and information about other conspecifics). Conflicting chemical signals can drastically modify behavior in crus-

taceans (Hancock 1974, Chapman and Smith 1979, Hazlett 1996, 1999, Hazlett and McLay 2000). All these studies showed that it is critical for an organism to extract relevant information provided by multiple cues to make the correct behavioral decisions. Measuring the distribution of chemical signals in the behavioral areas and comparing this distribution with subsequent behavior can further these studies. Our study specifically addresses 2 distinct hypotheses: 1) Can crayfish orient to food sources effectively with conflicting chemical stimuli present, i.e., an attractive chemical source and a nonattractive chemical source? and 2) If crayfish can locate odor sources in complex chemical environments, what aspects of their orientation strategies are affected by conflicting chemical cues? Answers to these questions should lead to a broader understanding of natural behaviors in complex sensory environments.

Methods

Organisms

All animals were collected and experiments were done during the summer (11–26 July 1998) in northern Michigan. The crayfish (*Orconectes virilis*) used were collected at night near a sandy bay in Burt Lake (northern lower Michigan), and had a carapace length between 25 mm and 35 mm (mean = 29.5 mm \pm 0.222 SE). This size range represents adult *O. virilis* crayfish in Burt Lake (T. A. Keller, personal observations). Crayfish were housed outside in plastic tubs supplied with continuously flowing river water and ample shelter. Crayfish were starved for 48 h prior to testing to control for hunger level. Twenty animals were used for each of the 4 experimental groups, and each animal was only used once. Perch (*Perca flavescens*) were captured from Douglas Lake, humanely euthanized, and used as the food odor stimulant (University of Michigan vertebrate permit #7236).

Design and protocol

A 2 \times 2 factorial design with 2 odor treatments and 2 shelter treatments was used to determine how crayfish use complex odors to assess their environment and make foraging decisions, and how shelter availability impacts these decisions. This design resulted in 4 exper-

imental groups: 1) alarm and open shelters 2) alarm and filled shelters 3) no alarm and open shelters, and 4) no alarm and filled shelters. All treatments had a food-odor stimulus. Odor treatments consisted of food odor alone and food odor plus alarm odor. Previous research has shown that *O. virilis* do not exhibit orientation behavior without a food odor present. Therefore, it was unnecessary to include an odorless control (Moore and Grills 1999, Keller et al., in press). Crushed conspecific odor simulates an act of predation and causes an alarm response in crayfish, which consists of a retreat to shelter and a cessation of movement (Hazlett 1994). Given this response, it was unnecessary to include an alarm-only control. Alarm and food odor together produce a complex odor with conflicting information: attraction for the food and aversion to the crushed conspecific. Responses to the food odor alone served as the control response to be compared with the behavior resulting from the complex odor signal. The 2 shelter treatments included open clay pot halves that provided shelter, and filled clay pot halves that did not provide shelter.

Three adjacent flumes were constructed at the University of Michigan Biological Station's Streams Research Facility. The flumes (250 cm \times 50 cm \times 15.3 cm) were created from cinder-blocks lined with 3 mm clear plastic sheeting, and the floor was covered with sand for substrate. The portion of the flume accessible to the crayfish was 177 cm long. Water from the Maple River was delivered into 3 separate 208 L head tanks and then gravity fed into the flumes (Fig. 1). Three collimators, pieces of plastic fluorescent light covers ("egg crating", 1.69 cm² ID holes) wrapped in fiberglass mesh (1 mm² ID holes), were placed in each flume to dampen turbulence created by the water being delivered into the flume (Moore et al. 1991). Water exited the far end of the flume through plastic crating and drained back into the Maple River. The average flow rate in the middle of the flumes was 4.2 cm/s (\pm 0.06 SE). This rate was measured by observing the time it took a positively buoyant particle (8 cm diameter) to travel 1 m in the flume.

Start pots were created to keep the crayfish in one location while acclimating to the stream. These pots were constructed of a half clay pot (11.6 cm long \times 11.6 cm wide \times 6.2 cm radius) fastened to a Plexiglas base with a sliding Plex-

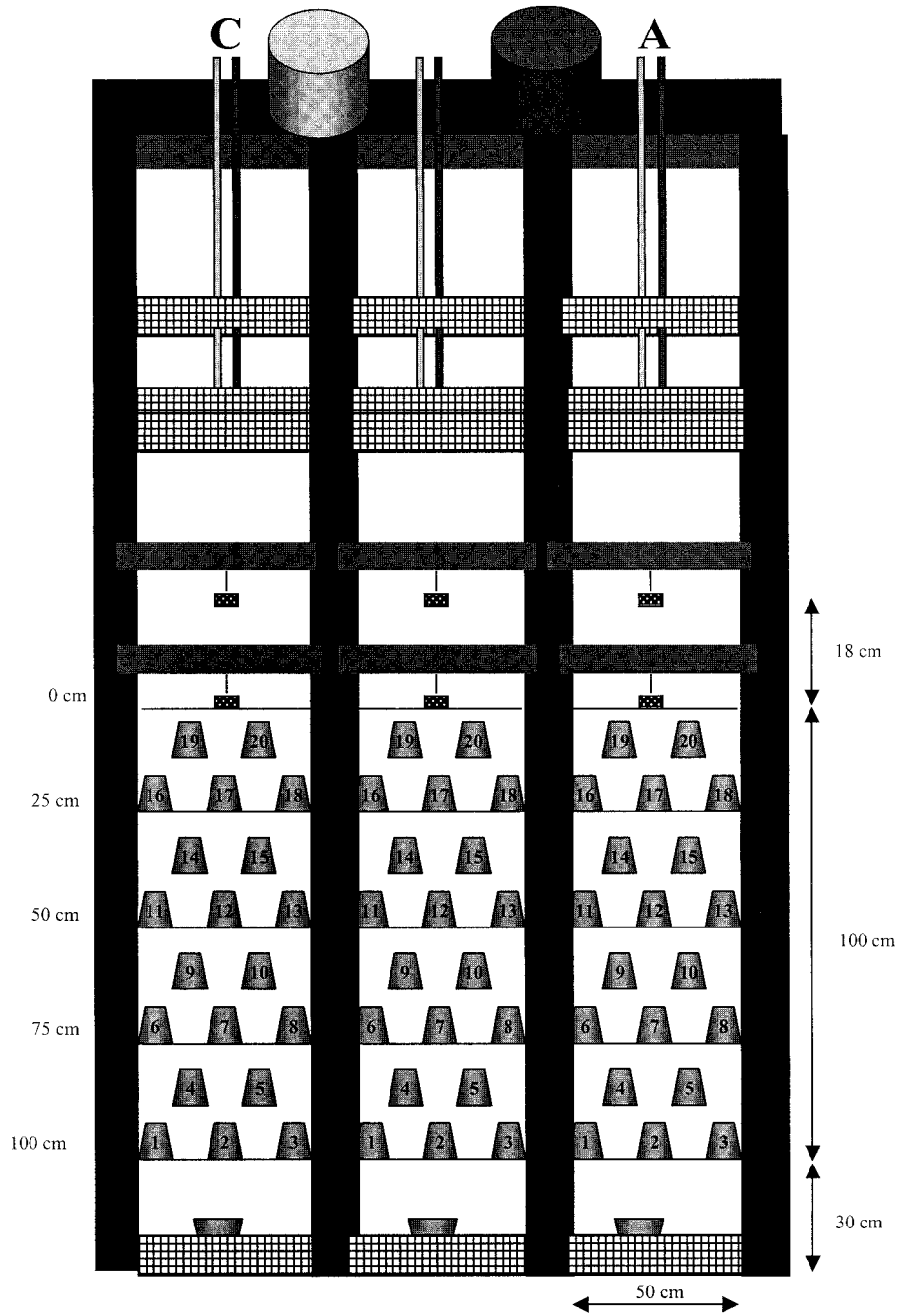


FIG. 1. Artificial stream set-up used in odor experiments. The cylinders at the top represent the alarm (A) and control (C) stimuli. Delivery tubes are shaded to match the cylinders. The numbered trapezoids represent both center and side shelters. (Side shelters = those numbered 1, 3, 6, 8, 11, 13, 16, and 18.)

iglas door covering the opening. The start pot faced upstream and was located 115 cm from the most downstream food odor source. Water could move freely in and out of the start pot.

Orconectes virilis search and locate food odor sources separated in space faster than when odor sources are placed together (Keller et al., in press), so 2 separated odor sources (blocks of fish gelatin) were used in all of the trials to maximize the orientation response. Gelatin blocks (4 cm × 2 cm × 1 cm) were chosen to ensure a standardized delivery of odor and to mimic naturally decaying carrion sources on which crayfish readily feed (Momot 1995). The gelatin was made with 45 g of yellow perch, 0.71 L of water, and 28 g of unflavored dried gelatin. The gelatin blocks were suspended in fiberglass mesh bags, 2 cm above the substrate, and 130 cm and 145 cm from the outflow (Fig. 1).

Alarm odor was generated immediately before each trial. Two chelae were removed from an *O. virilis*, weighed, and chopped in 4 places each. Chela pieces were placed in a mesh bag and suspended in a container with 3 L of river water. Alarm odor was gravity fed into the flume through tubing throughout the trial at a rate of 0.2 L/min. Alarm odor was delivered 2.5 cm above the substrate and ~1 cm downstream from the last collimator. In the food-only treatments, untreated river water was delivered similarly to serve as a control.

Shelter availability was manipulated using 20 clay pot halves (8.4 cm diameter, 8.7 cm long). They were numbered and arranged with the open ends facing downstream 1 m downstream from the food odor source. Control pots were filled with concrete to provide similar structure and flow regime without providing shelter. Control pots were arranged identically to the open pots.

The trials were run between 2000 h and 0300 h because *O. virilis* is more active at night (Hazlett et al. 1979). An observer was positioned at the outflow facing upstream and recorded movements. To aid visibility, a 25 W red light was positioned at the outflow and illuminated the flume. Crayfish do not see red light, so the effect of light on their behavior was minimized. Crayfish were confined to the start pot for a 30-min acclimation period. After acclimation, a 2nd person hung both food odor sources in the flume, while the observer simultaneously removed the door to the start pot. The trial com-

menced once the door to the start pot was lifted. The alarm odor or the odorless water control was introduced 1 min after the trial started so we could observe the effect of the alarm signal on organisms that were actively orienting towards a goal. Trials were ended when either the crayfish grasped 1 of the food sources with its chelae or after 15 min elapsed. Up to 12 experimental trials were conducted during any given night. Treatments were randomized and observations were made by different people to reduce bias. The individual flumes were randomly daily assigned to either open or filled shelters. The odor treatments also were randomly assigned to each trial. The rate and volume of water flow through the flumes ensured that all odors from previous trials were removed before the subsequent trial began.

Several measures of crayfish behavior were obtained. Emergence time refers to the elapsed time from the start of the trial to when the crayfish 1st exited the start pot. Search time is the period from when the crayfish initially emerged from the start pot until the end of trial. Time in shelters refers to the total time crayfish spent in shelters, including the start pot but excluding the emergence time.

Dye tracing suggested that the alarm odor was mainly distributed down the center of the flume whereas the food odor was not, so we were interested in whether these patterns would affect which shelters crayfish spent time in. Therefore, we quantified the average time they spent in shelters along the sides and center of the flume. To identify any effect alarm odor concentration had on crayfish behavior, we plotted search time versus the mass of chela alarm material used to generate the alarm signal.

Measuring chemical signals

We used standard IVEC (In Vivo Electrochemistry Computer System; Medical Systems Corp., Greenvale, New York) recording procedures to quantify the distribution of aquatic chemical signals (Moore et al. 1989, Moore and Atema 1991, Moore et al. 1994). A graphite-epoxy capillary electrode was used (Gerhardt et al. 1984) with a tip diameter of 3 μm at a sampling rate of 10 Hz using the IVEC-10. Each 100 ms epoch for the 10 Hz sampling rate was composed of a 50 ms epoch at +0.55 v (oxidation) followed by a 50 ms epoch at 0.0 v (reduction).

The recording electrodes were sampled every 50 ms: analog-to-digital conversions of the samples were done at 4 kHz, and data were averaged for the 50 ms time epoch. Further details of recording and digitizing are explained in Moore et al. (1989). Electrodes were calibrated in solutions of dopamine prepared in natural stream water and exhibited linearity over a concentration range of 0 to 36 μM (coefficient of determination, $r^2 > 0.99$).

A 0.5 M dopamine, 0.05 M ascorbic acid (antioxidant) solution was used to track the food odor signal. Dopamine solution was delivered at the rate of 1 mL/min through 2 air stones (ASR-02 Aquarium 1.11 cm cylinder bubble stone) using a Manoset[®] syringe pump. In dye trials, the emission of chemicals from the air stones mimicked those coming off the gelatin. One air stone was placed in each of hanging mesh bags as described earlier. To simulate the alarm odor, the same dopamine solution was gravity fed into the flume as in the behavioral trials.

For all the electrochemical recordings, the IVEC probe was placed 4.5 cm above the substrate, which is well within the sampling range of the lateral antennules of a crayfish. Recordings were taken at 60 cm from the source at 5 cm and 15 cm from the left and right wall, and in the center of the flume (Fig. 1). One 4-min recording was made at all of these locations to measure how the alarm and control odors dispersed. Similar measurements were taken at these positions to determine the spatial and temporal dynamics of the food odor stimuli. IVEC recordings were made with open and filled pots for alarm and food source delivery. Measurements were never made while simultaneously delivering both the alarm odor and the food odor because of the inability of the IVEC to distinguish among sources.

Statistical analyses

Effects of treatments on emergence and search time were analyzed using a 2-way analysis of variance (ANOVA). Post-hoc comparisons were conducted with the Tukey HSD test (which corrects for the number of comparisons). The effect of the alarm on time spent in shelters was analyzed using a 2-tailed t -test. A χ^2 test was used to analyze data on the number of organisms that successfully found the source and

the number of organisms that responded to different amounts of chela alarm material.

Crayfish in the treatments containing alarm odor (with and without open shelters) that reached the food source in <120 s were omitted from the data set because it took the alarm chemicals at least 120 s to reach the most downstream portion of the flume, as demonstrated by dye trials. This period included the 1-min delay (time prior to chemical release) plus the 1-min advection time needed for the chemical to travel from the source to the end of the flume. Animals that immediately emerged from the start pot and found the source in <120 s were exposed to the food odor but had insufficient exposure to alarm signal for it to have an effect on their foraging behavior, as determined from the amount of time it took for the alarm signal to reach the end of the flume (explained above). Thus, 11% (5 out of 45 animals) of alarm experimental trials were deleted. Additional trials were conducted to maintain identical sample sizes ($n = 20$) for each of the treatment groups.

Results

The alarm odor had a significant effect on the foraging behavior of the crayfish. Crayfish in the food-only treatments were significantly more successful in reaching the food source than animals in the alarm + food treatments (χ^2 , $p < 0.004$, Fig. 2A). Also, the search time of the crayfish in the food-only treatment was significantly shorter than that of the food + alarm groups (2-way ANOVA, $p < 0.001$, Fig. 2B). As expected, the emergence time of crayfish did not differ across trials (2-way ANOVA, $p > 0.78$). Neither search time (2-way ANOVA, $p > 0.42$) nor the rates of success (χ^2 , $p > 0.078$) differed with shelter availability.

However, the alarm odor affected how crayfish used the shelters. In the open pot treatment, the alarm + food animals spent significantly more time in shelters than did the control animals (2-tailed t -test, $p < 0.004$, Fig. 3). In the alarm + food: open category, the crayfish spent significantly more time per shelter in the side shelters than the center shelters (Tukey HSD, $p < 0.0002$, Fig. 4). However, in the food-only treatment there was no difference in the time spent between side shelters and center shelters (Tukey HSD, $p > 0.99$). The time spent per side

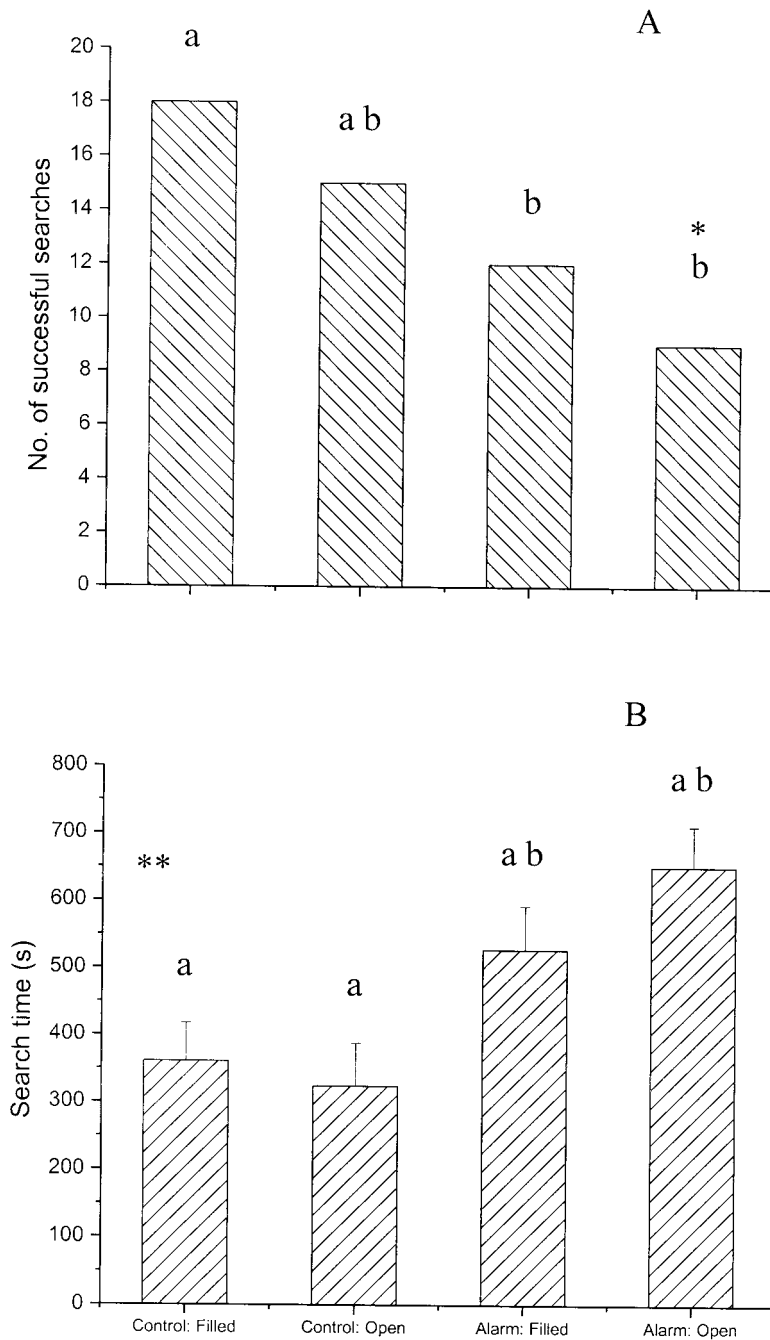


FIG. 2. Effect of alarm odor on foraging success and efficiency. A.—Number of crayfish in each group that found the food source. Asterisk indicates a significant difference between alarm and control treatments (χ^2 , $p < 0.004$). Differing letters (i.e., a, b) indicate a significant difference of $p < 0.05$. B.—Mean (+SE) search time: time from emergence from start pot until end of trial. Double asterisk indicates a significant difference between alarm and control treatments (2-way ANOVA, $p < 0.001$). Differing letters (i.e., a, b) indicate a significant difference (Tukey HSD, $p < 0.05$). $n = 20$ for all groups.

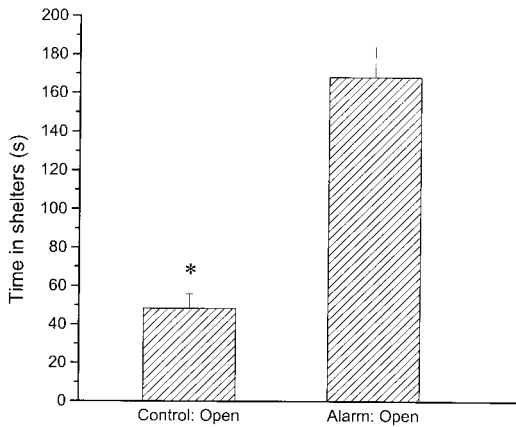


FIG. 3. Mean (+SE) time spent in shelters minus initial time spent in start pot. Asterisk indicates a significant difference between alarm and control treatments (2-tailed *t*-test, $p < 0.004$). $n = 20$ for all groups.

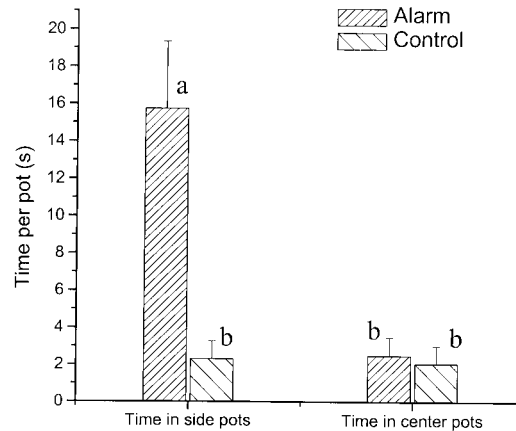


FIG. 4. Mean (+SE) time spent in side shelters vs center shelters. Time is normalized per shelter. Differing letters (i.e., a, b) indicate a significant difference (Tukey HSD, $p < 0.001$). $n = 20$ for all groups.

pot also differed between the food and the food + alarm animals (Tukey HSD, $p < 0.0002$).

Electrochemical recordings showed that the dopamine tracer was present in high concentrations down the center of the flume but occurred in very low concentrations or was absent along the sides of the flume, 60 cm from the source for both the food and alarm trials (Figs 5 and 6).

Discussion

The results illustrate the importance of complex chemical cues in shaping ecological behaviors such as foraging. It is imperative to determine the information available to organisms to

understand the sensory mechanisms associated with foraging in complex sensory environments. Chemical signals in aquatic ecosystems can serve as a particularly important source of sensory information. Organisms can use this information to orient to an attractive stimulus (e.g., cues from food or mates; Farkas and Shorey 1972, McLesse 1973, Moore and Lepper 1997) or to avoid an aversive stimulus (e.g., cues signaling predators or danger; Parker and Shulman 1986, Fricke 1987, see review in Kats and Dill 1998). Our study demonstrates that the spatial distribution of complex odor mixtures provides important information to organisms, which alters their behavior and shapes the natures of ecological interactions.

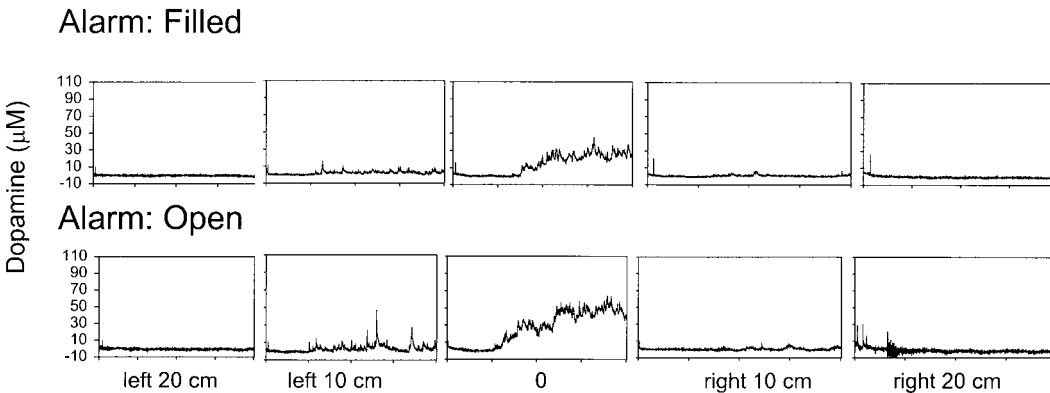


FIG. 5. Four-minute IVEC recordings of the alarm odor taken at 60 cm from the most downstream food source. Major tick marks represent 60-s intervals. The X-axis indicates the distance from the center of the flume.

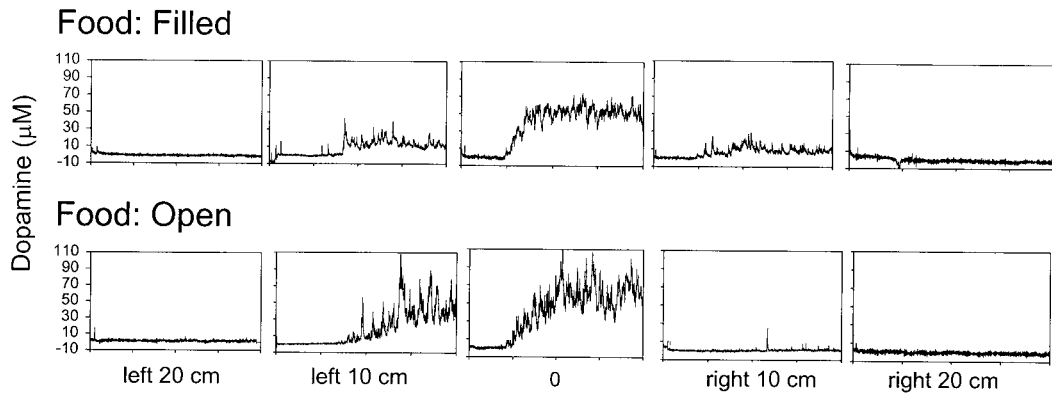


FIG. 6. Four-minute IVEC recordings of the food odor taken at 60 cm from the most downstream food source. Major tick marks represent 60-s intervals. The X-axis indicates the distance from the center of the flume.

Our findings support previous work that demonstrated crayfish use the chemical stimuli of an odor plume to locate a food source in a structurally complex habitat (Moore and Grills 1999, Keller et al., in press). Crayfish exposed to food odor alone also found the source at a higher success rate (82.5%) than those of previous studies (77% in Moore and Grills 1999, 66% in Keller et al., in press.), which may be attributed to the fact that the experiment was run at night when crayfish are more active (Hazlett et al. 1979). The use of 2 odor sources in all trials may also have affected the success rate.

Response to alarm signals

Like many other organisms (Mathis and Smith 1992, Hazlett 1994), crayfish in our study responded strongly to alarm chemicals. The addition of the avoidance signals caused crayfish to exhibit a number of common and effective antipredator behaviors similar to those in other organisms, including a decrease in foraging (Burrows and Gibson 1995, Brown and Smith 1996, Moses and Sih 1998), an increase in refuge use (Stein and Magnuson 1976, Fricke 1987, Petranks et al. 1987), and avoidance of the alarm odor (Mathis and Smith 1992, Mitchell and Hazlett 1996).

Many studies have documented how alarm chemicals affect foraging (see above), but few have characterized how alarm cues affect the mechanisms involved with foraging and orientation to a food source. Organisms need to balance the conflicting demands of foraging and avoiding predation (Werner and Gilliam 1984,

Werner and Anholt 1993). Decreased foraging success indicates that crayfish may be able to assess risk using chemicals and modify risky behaviors such as foraging. Foraging success may decline because it is incompatible with several predator avoidance strategies, such as seeking refuge or reducing movement (McPeck 1990). The behavioral response seen in our study appears to be intermediate between complete cessation of foraging and a fully developed foraging response (e.g., as seen in the food only treatments). These results are indicative of a risk-sensitive trade-off between predator avoidance and resource gain. A similar type of behavioral response is found in many other organisms (see review by Lima and Dill 1990). Chemical cues can play a very important role in these decisions for crayfish.

The addition of alarm chemicals to a food odor plume did not cause the crayfish to remain downstream from the alarm source in the start pot as predicted from a simple response to the alarm signal. Instead, the crayfish likely detected both chemicals, and responded by avoiding the negative stimulus (by moving laterally out of the alarm odor plume), yet still moved toward the attractive stimulus (by moving upstream). This behavior may be the safest way for the crayfish to balance these conflicting demands. However, this strategy also takes them out of the center of the food plume, which contains information they need to locate the food and the alarm odor sources. Movements to areas outside of the food odor plume can partially explain the decrease in foraging success. The crayfish may also continue upstream outside of the

alarm odor plume because the alarm chemical serves as an attractant to other predators. Moving downstream may bring them into contact with another predator, whereas moving laterally outside of the plume is more likely to avoid predators all together.

Impact of shelters on alarm responses

We also found that shelter availability had no effect on the response of animals in the alarm treatment. It is possible that crayfish have different strategies to deal with potential predators, depending on whether or not shelter is present; however, these strategies do not affect success rate or foraging efficiency. The presence of these strategies may not be surprising because environmentally stable strategies should successfully balance foraging gains with predator avoidance and thus have similar success rates.

Relation to natural signals

Although our study was conducted in artificial flumes, the results should be similar to the natural environment. Flume size was smaller than many crayfish environments but the experimental setup eliminated some potential consequences of a smaller environment. First, we showed that the flume was wider than the odor plumes through IVEC recordings and dye tracings. Therefore, crayfish were able to move themselves both upstream and laterally out of the odor plume. Second, crayfish were forced to orient around obstacles as they would in nature because of the array of shelters present in the flume. This configuration also prevented the animals from following the walls directly upstream to the food source. Also, the crayfish could not locate the food source by simply following the perimeter of the flume because both food sources were suspended from above the stream and not attached to a wall. Third, the amount of alarm stimulus used was most likely conservative because we only used the chelae of a conspecific. More alarm chemical would be released if a predation event occurred and an entire conspecific was consumed.

Our study further illustrates the importance of chemical signals in aquatic systems for both locating food and avoiding predators, and shows that complex odors influence habitat use as well as foraging efficiency and success. The

content, concentration, and distribution of complex chemical signals are a very important part of risk assessment mechanisms and provide the necessary information to facilitate ecological interactions.

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