

EARLY WARNING IN THE PREDATION SEQUENCE: A DISTURBANCE PHEROMONE IN IOWA DARTERS (*Etheostoma exile*)

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Abstract—The probability of prey avoiding a predator's attack should increase if the predator's presence is detected at an early stage in the predation sequence. In this study, we tested whether threatened Iowa darters (*Etheostoma exile*) release disturbance pheromones that warn conspecifics of the presence of predation threat. Pairs of aquaria were visually isolated from one another, but connected chemically by water circulating between them. Darters in one aquarium were observed before and after darters in the other aquarium were chased with a model predator. In control tests, the model was moved in the same manner but there were no darters in the upstream tank. Darters receiving water from threatened fish increased vigilance behavior and decreased movement. Vigilant fish raised their head above the substratum, propping themselves up on their pectoral fins and/or arching their neck dorsally, pointing the snout upward. Exposure to water from disturbed darters suppressed exploratory behavior and resulted in movement by short rapid hops that ended abruptly in a rigid, alert posture. This study suggests that Iowa darters release a disturbance pheromone that can provide conspecifics with an early warning of predation risk.

Key Words—Disturbance pheromone, alarm signal, predator-prey, predator avoidance, vigilance, Iowa darter, *Etheostoma exile*.

INTRODUCTION

In many situations in aquatic habitats, chemical information is more salient than visual information. For example, visual information may be of little use in highly

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structured habitats, turbid water conditions, or at night. Furthermore, water serves as an excellent medium in which to dissolve and disperse chemical substances (Hara, 1992).

Chemical alarm signals occur in a wide range of aquatic taxa (gastropod mollusks, Atema and Stenzler, 1977; opisthobranchs, Sleeper et al., 1980; anemones, Howe and Sheik, 1975; decapods, Appleton and Palmer, 1988; fishes, Smith, 1992). Many fish have a well developed system of chemical alarm signaling (Smith, 1992). To date, study of alarm pheromones in fishes has focused on substances contained within the epidermis and released only by injury, including the *Schreckstoff* of ostariophysan species (von Frisch, 1938; reviewed in Pfeiffer, 1977; Smith, 1992). Conspecific skin extract invokes antipredator behavior in most ostariophysan fishes tested thus far and in nonostariophysan species such as brook stickleback, *Culaea inconstans* (Mathis and Smith, 1993b), darters (Smith, 1979, 1982), sculpins (Hugie et al., 1991), cyprinodontids (Reed, 1969) and gobies (Smith, 1989; Smith and Lawrence, 1991; Smith et al., 1991). Chemicals released by an injured conspecific serve as a reliable indicator of predation risk. Fathead minnows that have been "warned" by chemical alarm signals are significantly better at surviving in the presence of a predator (Mathis and Smith, 1993a).

Prewarned prey may be able to avoid an encounter with a predator. Prey that are subsequently detected by the predator are better able to avoid an attack by being in a state of readiness. The greater the degree of advance warning of a predator's presence, the greater the advantage to the prey. Therefore, there should be a selective advantage to individuals that can gain information about predation risk from a predator "disturbance" of a conspecific before the encounter escalates to a predator attack.

In birds and mammals, there are examples of visual, auditory, and chemical preinjury alarm signals that occur before prey capture (Caro, 1986b; Caro, 1986a,b; Klump and Shalter, 1984; Müller-Schwarze et al., 1984). In fishes, there are examples of preinjury visual alarm cues (e.g., goby bobbing, Smith, 1989; Smith and Smith, 1989; Sweatman, 1984) and auditory cues (e.g., squirrel fish, *Holocentrus rufus*, Winn et al., 1964; cod, *Gadus callarias*, Brawn 1961). However, among fishes, there are no documented cases of chemical alarm signals sent by uninjured individuals. Rainbow trout (*Oncorhynchus mykiss*) subjected to strong electric shock and other "stressors" release "chemical alarm signals" that increase stress in receivers, but no behavioral responses were measured (Lebedeva et al., 1994). Malyukina et al. (1983) reported that cod (*Gadus morhua*) detect and avoid chemical stimuli from stressed conspecifics. Tester (1963) found that grey sharks (*Caracharhinus menisorrhah*) and black tipped sharks (*C. melanopterus*) were attracted to water from "agitated" and "distressed" groupers (*Epinephelus merra*), and black tipped sharks were attracted to distressed mullet (*Mugil cephalus*). These latter studies suggest that

distressed fish may release distinctive chemical stimuli, but they do not show a link between predation threat and the release of such chemicals or their detection and associated changes in vigilance by conspecifics.

Crayfish (*Orconectes virilis*) and hermit crabs (*Calcinus laevimanus*) respond to "disturbance pheromones" from conspecifics with antipredator behavior (Hazlett, 1985, 1990b). In addition, individuals of *O. virilis* respond to disturbance pheromones produced by other species of crayfish (*O. rusticus*, *Cambarus diogenes*), leeches (*Macrobdella decora*), newts (*Notophthalmus viridescens*), rock bass (*Ambloplites rupestris*), and the Iowa darter (*Etheostoma exile*) (Hazlett, 1985, 1989; 1990a).

If Iowa darters produce chemical stimuli when stressed (but not injured) to which crayfish respond, it follows that Iowa darters, themselves, may be able to detect these chemicals and respond with antipredator behavior. We conducted a laboratory experiment to investigate whether Iowa darters respond to chemical stimuli produced by disturbed conspecifics. We predicted that test individuals would increase vigilance behavior and suppress conspicuous behavior (movement) in response to chemical cues produced by sender conspecifics that were chased by a model predator in a separate, visually isolated aquarium.

METHODS AND MATERIALS

Two variations of this experiment were conducted at separate times by different investigators using fish from two different populations.

Experiment 1. We captured Iowa darters by seine in Eagle Creek, a tributary of the North Saskatchewan River, at a site approximately 50 km west of Saskatoon, Saskatchewan. Mean \pm SE total lengths (TL) of a subsample of 15 females and 10 males were 43.1 ± 0.09 mm TL and 44.0 ± 0.11 mm TL, respectively. They were held in the laboratory at 15°C and fed a mixture of frozen brine shrimp and live food, including cladocerans, copepods, and mosquito larvae.

We placed pairs of 37-liter aquaria (50 \times 30 \times 25 cm high) end to end, separated by a small space and an opaque barrier. We used eight pairs in rotation. We connected the tanks by siphons at the abutting ends. Water was pumped from the distal end of the receiver tank into the distal end of the sender tank so that water flowed continuously through the siphons from senders to receivers. Flow rates averaged 1.2 liter/min. Each tank contained a substratum of several centimeters of silica sand.

Data were collected in May 1992 during daylight hours. Three darters (receivers) were placed in the receiver tank at least three days before the observation day. In experimental trials, 12 darters were placed in the sender tank at least three days before observation to ensure that they were well adjusted to the

laboratory setting. Both senders and receivers need to be in an undisturbed state for observers to detect a behavioral response to chemical cues (Hazlett, 1989; Smith, 1979). We buried a predator model in the sand of the sender's tank at least three days prior to the observations. The model was a fish lure 15 cm long and 2.5 cm high with hooks removed. A metal disc was glued to the underside of each model with silicone cement. The disc provided a heavy, stable platform to prevent the model from rolling or lifting off the substrate during the trial. The model was attached to monofilament line that led from the tank to the observation location. There was always live food present in both tanks on the observation day, and we fed the fish to satiation on the day before the observations. Darters do not respond to conspecific skin extract when they are hungry (Smith, 1981). Fish were used only once as receivers but were occasionally used more than once as senders. We drained and washed tanks between observations.

We quietly observed fish from about 1.5 m from the receiver tank. For 15 min before the fish model stimulus, we recorded the number of moves and head-up posture. In addition, we noted the time during which at least one of the three receivers was in the head-up posture. We then pulled the model out of the sand in the sender tank and moved it a short distance at 30-sec intervals for 5 min. No observations were made during this period. The above behaviors were similarly recorded for 15 min following exposure of the senders to the model predator. We conducted 10 experimental trials in which senders were present in the upstream tank. In 10 control trials, the upstream tank contained no sender fish, but we manipulated the model in the same manner as in experimental trials. This controlled for any stimuli produced by the movement of the model.

Iowa darters normally rest on the bottom. A move was scored each time a fish changed its location. A head-up posture was scored if a darter was stationary on the substratum with either the anterior part of its body propped up by its pectoral fins or if it arched its neck dorsally, pointing its snout upwards, or both. Head-up behavior is a component of the fright reaction of Iowa darters (Smith, 1982). Iowa darters are small, elongate benthic fish. Their body shape and habit leave these fish with a limited vantage point from which to view the surrounding area for predators and to sample water-borne chemical cues above the boundary layer (Moore and Atema, 1991; Moore et al., 1994). Head-up behavior would thus appear to be a cryptic, low-risk form of vigilance behavior.

Experiment 2. We collected adult and subadult darters (TL of subsample = 48 ± 1.5 mm, $N = 4$) from a 1-ha pond on the University of Saskatchewan campus using minnow traps and a seine net. This population originated from the South Saskatchewan River in 1959. Darters in the laboratory holding tanks were provided with live cladocerans, mosquito larvae, and copepods ad libitum, supplemented occasionally with frozen brine shrimp.

We set up six pairs of 37-liter aquaria in the same manner as described for

experiment 1. The mean \pm SE rate of flow was 2.9 ± 0.06 liters/min ($N = 6$ paired tanks). Food coloring added to the far end of upstream tanks was visible in the downstream tank to a human observer within 35 ± 7.7 sec ($N = 6$). Live food was always present in both tanks during the trials and for at least 1 hr before observations began.

Data were collected in June and July 1994 during daylight hours. We placed three receiver darters into the downstream tank. For experimental trials ($N = 9$), we placed 12 sender darters into the upstream tank. For control trials ($N = 10$), no darters were added to the upstream tank. All receiver fish were naive to the experiment and used only once as receivers. Some sender and receiver fish were used as senders in subsequent trials. Tanks were drained and washed between trials.

We videotaped all trials. Each trial lasted 35 min. At 10-sec intervals for 15 min, we scored the number of receiver fish with their head elevated above the substratum. After 15 min, a previously concealed model predator emerged from under a piece of black plastic in the upstream tank. In control trials the upstream tank contained no fish, but in experimental trials it contained sender darters. The model predator was similar to the one used in experiment 1. The model was attached to monofilament line through a system of pulleys, which enabled us to manipulate its position remotely (6 m from the receiver fish). The predator model moved from one end of the tank and back again every 15 sec, for 5 min. We then recorded the number of receiver fish in the head-up posture every 10 sec for 15 min.

Statistical Analyses. For statistical comparisons, we tested three behaviors (head-up posture, duration of time when at least one of three receivers was in head-up posture, and move frequency). We used the total frequency of each behavior exhibited by all three receivers in each trial to produce a single, independent datum before and after stimulus presentation per trial. We used Wilcoxon signed-rank tests (Siegel and Castellan, 1988) to compare darter behavior before and after model stimulus in the number of receiver fish performing head-ups for experimental and control trials separately.

RESULTS

Experiment 1. Darters significantly increased (Wilcoxon $T^+ = 47$, $P = 0.048$, two-tailed, $N = 10$) the frequency of their head-up postures from 15.7 ± 3.6 (mean \pm SE) per 15 min before presentation of the predator model to 24.7 ± 3.7 per 15 min after model presentation, during which they were exposed to water from threatened conspecifics (Figure 1). In control trials, darters performed 17.7 ± 3.8 head-ups in the 15 min before the model emerged from the sand compared to 19.1 ± 3.2 during the final 15 min of each trial, which were

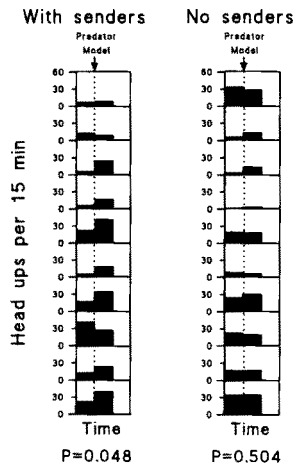


FIG. 1. Frequency of head-up posture by three receiver darters for 15 min before and after presentation of a model predator in an adjacent but visually isolated aquarium. Each cell represents a single trial. In experimental trials (left-hand column) sender darters were present in the adjacent aquarium with the model. In control trials (right-hand column) no sender fish were in the adjacent tank with the model. Below each column, significance of change between pre- and postpredator head-up frequency (Wilcoxon signed-rank test).

not significantly different (Wilcoxon $T^+ = 23.5$, $P = 0.504$, two-tailed, $N = 8$ excluding ties).

The duration of time in which at least one of the three receiver darters performed a head-up behavior significantly increased (Wilcoxon $T^+ = 33.5$, $P = 0.032$, two-tailed, $N = 8$ excluding ties) in experimental trials from 3.2 ± 0.8 min before the model was presented to 5.2 ± 0.8 min after sender darters were exposed to the model predator, but remained virtually unchanged (5.2 ± 0.5 vs. 4.7 ± 0.5 min) in control trials (Wilcoxon $T^+ = 13$, $P = 0.546$, two-tailed, $N = 8$ excluding ties, Figure 2).

In control trials, the number of moves per 15 min by the three receiver fish significantly increased (Wilcoxon $T^+ = 47.5$, $P = 0.044$, two-tailed, $N = 10$) from 97.7 ± 23.5 to 116.8 ± 20.9 after the model presentation. However, in experimental trials, move frequency did not change between the experimental treatments (115.8 ± 13.6 vs. 101.7 ± 11.1 , Wilcoxon $T^+ = 35.5$, $P = 0.146$, two-tailed, $N = 9$ excluding ties, Figure 3).

Experiment 2. The number of receiver darters observed in the head-up posture significantly increased when exposed to water containing chemical cues of disturbed conspecifics (Figure 4). Overall, the number of individuals in the

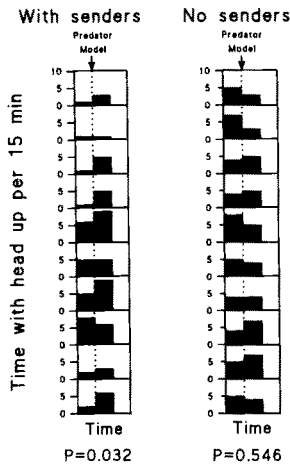


FIG. 2. Time, in minutes, in which at least one of the three receiver darters maintained a head-up posture before and after presentation of a model predator in the adjacent tank in the presence or absence of sender fish. Figure format as described for Figure 1.

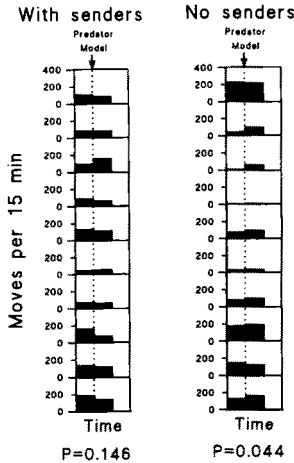


FIG. 3. Move frequency by three receiver darters before and after presentation of a model predator in an adjacent tank with or without sender fish. Figure format as described for Figure 1.

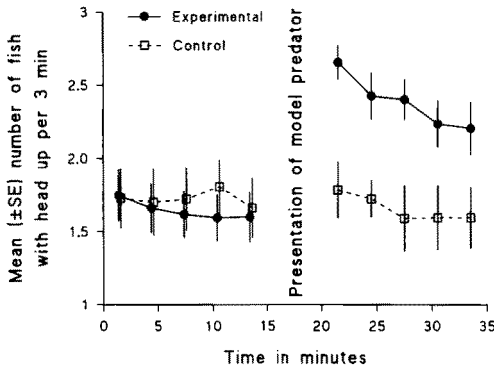


FIG. 4. Mean (\pm SE) number of fish exhibiting the head-up posture during each 3-min interval of the 15-min prepredator period and the 15-min postpredator period, separately. Data were not recorded during the 5-min interval while the model predator was active in the upstream tank.

head-up posture in the experimental trials increased from 1.64 ± 0.15 to 2.38 ± 0.15 (Wilcoxon $T^+ = 44$, $P = 0.008$, two-tailed, $N = 9$ excluding ties). In control trials, the average number of receivers in the head-up posture was 1.72 ± 0.21 before the model predator, and 1.66 ± 0.16 for the 15 min afterwards (Wilcoxon $T^+ = 22$, $P = 0.625$, two-tailed, $N = 10$).

Although we did not quantify the frequency of moves in the second experiment, we noted qualitative changes in fish movement during the postpredator period. Receiver fish in experimental trials changed position on the tank bottom with short rapid hops ending abruptly in a rigid, alert posture. These hops never took the fish very far above the substratum and the hops were separated by long intervals of motionlessness. In one extreme case, a fish buried itself in the sand during the 5-min interval when the model was being manipulated in the upstream tank and did not emerge until 6 min into the postpredator period. During the postpredator period, the behavior of control fish was similar to control and experimental fish in the prepredator period. Control fish moved about slowly, often swimming up into the water column and then gliding back to the tank bottom.

DISCUSSION

In both replications of this experiment, Iowa darters responded to water that had first passed over threatened conspecifics by increasing the frequency and duration of their head-up (vigilance) behavior. In a head-up position, darters

would likely be better able to view the surrounding area and sample chemical information.

We are reasonably confident that the disturbance signal was transmitted by a chemical cue. The two test tanks containing sender and receiver individuals were visually isolated and separated by a small space. Mechanical vibrations caused by movement of the model were present in both experimental and control trials. However, it is conceivable (we think remotely so) that darters may emit an alarm sound that could travel through the water in the siphon hose connecting the two test tanks. Further experiments are needed before this alternative modality can be excluded completely.

Motionlessness, or freezing, is a component of darter antipredator behavior (Radabaugh, 1989; Rahel and Stein, 1988; Smith, 1979). Darters exposed to water from threatened conspecifics did not decrease their frequency of movement. However, they did not increase movement as the control fish did (Figure 3). Movement by control fish may have been stimulated by the model's activity in the adjacent tank, perhaps stirring up particles and odors in the sand substratum. Thus, increased movement by control fish may represent exploratory behavior. The suppression of a similar increase in experimental fish may reflect a trade-off between information-gathering and cost of conspicuous behavior when under risk of predation.

Disturbance pheromones do not require injury and thus indicate a lower level of predation threat to receivers than injury-released pheromones. In crayfish, this is reflected by a behavioral response of lower intensity (Hazlett, 1985). In this study, response to disturbance pheromone did not include freezing behavior, characteristic of the response of darters to skin extract (Smith, 1979) or predators (Radabaugh, 1989) or of crayfish to conspecific hemolymph (Hazlett, 1994).

In nature, the release and detection of disturbance pheromones could occur before the predator detects the prey, hence the emphasis on crypsis. Head-up behavior is a relatively cryptic method of gathering information about predation risk. Decreased movement is a form of crypsis. Disturbance pheromones themselves may be a cryptic warning signal if the origin of a chemical signal is more difficult to localize than a visual or auditory signal, thus minimizing the signaler's conspicuousness to predators.

Hazlett (1989, 1990a) speculated that the disturbance pheromone in crayfish is ammonia, excreted under duress in urine or through the gills during periods of increased (metabolic) activity. The same may be true for Iowa darters. However, prestressed Iowa darters lose their ability to produce disturbance pheromones (Smith, 1979), suggesting that the pheromone supply can be exhausted. This evidence suggests that disturbance pheromone may be urinary in origin, rather than a metabolite excreted continuously from the gills.

The disturbance signal may not necessarily be an intentional warning to other fish but rather a normal physiological response to stress to which other individuals have become attuned. Urine released by nonthreatened individuals would constitute a false alarm. Some level of experience may be required for darters to associate predation threat with a sudden pulse of nitrogenous metabolites. In this study we compared the behavior of the recipient fish before and after the stimulus and thus controlled for any response of recipients to background level of urine released by nonstressed sender fish.

The evolution of a disturbance signal would involve selection pressures similar to the evolution of injury-released alarm signals (Smith 1992). There are greater possibilities for the signal sender to benefit from postsignal effects of a disturbance signal, because the sender of such a signal has a better chance of survival than a sender of injury-released pheromones. A possible postsignal benefit to the sender may be to induce group crypsis, which would reduce the chance of detection by the predator, thus benefiting both the signaler and receivers (Dawkins, 1976). Signal-senders may benefit by warning and increasing the survival of group members because retaining group members may reduce future predation risk to the sender (Smith, 1986). Reducing predator success in the signaler's home range may discourage future hunting in the region (Trivers, 1971). A disturbance alarm signal may also serve as an attack deterrent by informing the predator that prey are alerted to its presence and that further hunting is unlikely to succeed (Caro, 1986a,b).

From what is known about injury-released alarm pheromones, we predict that fish may be able to use disturbance pheromones to acquire predator recognition (Chivers and Smith, 1994a,c; Magurran, 1989) and avoid risky areas (Chivers and Smith, 1995) and may respond to disturbance pheromones produced by heterospecifics with which they share habitat and predators (Chivers and Smith, 1994b; Mathis and Smith, 1993b). Crayfish respond to disturbance pheromones from a range of heterospecifics (Hazlett, 1990a). Documenting the existence of disturbance pheromones increases the scope of chemosensory information in predator-prey relationships in fishes. Disturbance pheromones provide conspecifics, and possibly heterospecifics within the same prey guild, with an early warning of predation threat in advance of prey capture and hence earlier than the release of injury-released alarm pheromones. This should increase the probability that prey can avoid an encounter with a predator by either fleeing the area or employing crypsis. Increased vigilance will result in improved chances of escape should a predator initiate an attack.

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