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Localized defecation by pike: a response to labelling by cyprinid alarm pheromone?

Received: 11 February 1994/Accepted after revision: 25 September 1994

Abstract Fathead minnows (*Pimephales promelas*) that have never encountered a predatory pike (*Esox lucius*), are able to detect conspecific alarm pheromone in a pike's diet if the pike has recently consumed minnows. It remains unclear how this minnow alarm pheromone is secreted by pike and if a pike is able to avoid being labelled as a potential predator by localizing these cues away from its foraging range. The first experiment determined that minnow alarm pheromone is present in pike feces when pike are fed minnows. Individual fathead minnows exhibited a fright response to a stimulus of pike feces if the pike had been fed minnows, but not if the pike had been fed swordtails, which lack alarm pheromone. Individual minnows also exhibited a fright reaction to alarm pheromone in the water (which contained no feces) housing pike which had been fed minnows, suggesting that alarm pheromone is also released in urine, mucous secretions and/or via respiration. The second experiment determined that test pike spent a significantly greater proportion of time in the "home area" of the test tanks (i.e. where they were fed) but the majority of feces were deposited in the opposite end of the test tank. By localizing their defecation away from the home or foraging area, pike may be able to counter the effects of being labelled as a predator by the alarm pheromone of the prey species.

Key words *Esox lucius* · *Pimephales promelas* · *Schreckstoff* · Predator labelling
Localized defecation

Introduction

Fathead minnows (*Pimephales promelas*) have epidermal club cells which, when mechanically damaged,

release an alarm pheromone [alarm substance (AS), or *Schreckstoff*; Smith 1986, 1992]. Mechanical damage typically occurs when a minnow is attacked or captured by a predator. When detected by conspecifics, AS elicits a stereotypic fright reaction, characterized by increased cover use, freezing, dashing, and/or shoaling (Heczko and Seghers 1981; Lawrence and Smith 1989; Krause 1993; Mathis and Smith 1993a). Both the sender and the receiver of the pheromone receive some benefit associated with alarm pheromone signalling (review Smith 1992). The receiver of an alarm signal has been shown to benefit via increased latency to capture during encounters with predators (Mathis and Smith 1993b). Brown and Smith (1994) have demonstrated a mechanism by which individuals can recognize and shoal preferentially with kin rather than unrelated conspecifics, allowing for the possibility of increased inclusive fitness potential of senders. Secondary predators are attracted to the area in which AS is released (Mathis et al. in press). Senders may directly benefit from the attraction of secondary predators. As a result of predator-predator interference, senders may have an increased probability of escape (D.P. Chivers, G.E. Brown and R.J.F. Smith, unpublished work).

Recently, Mathis and Smith (1993 a, c) demonstrated that minnows that had never encountered a predatory pike (*Esox lucius*) responded with anti-predator behaviour to chemical stimuli from pike if the pike had been foraging on minnows, but not on swordtails (*Xiphophorus helleri*), or breeding male minnows, which lack AS cells (Smith 1973, 1976). Swordtails are non-ostariophysians, and hence lack AS-producing epidermal cells (Mathis and Smith 1993a). From these studies, Mathis and Smith (1993c) concluded that minnows react to the presence of fathead minnow AS in the diet of the pike rather than just the chemical cues or metabolic byproducts of a fish diet.

As a result, pike that forage on fathead minnows can become labelled as a potential predator to minnows

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that may not otherwise recognize the pike as dangerous (Mathis and Smith 1993c). Minnows naive to pike can thus avoid direct encounters with pike and may be able to avoid locations within the stream which carry a high risk of predation. Avoiding such areas would probably increase an individual's survival and fitness potential by reducing predation risk (Lima and Dill 1990). Similar predator labelling has been demonstrated in brook charr (*Salvelinus fontinalis*) (Keefe 1992) and in brook sticklebacks (*Culaea inconstans*) (Gelowitz et al. 1993).

If a predator is passively labelled by chemical cues contained within its diet, its overall foraging efficiency may be diminished as a result of increased predator avoidance by prey fish. This is particularly true for pike, an ambush predator. A pike will typically remain under cover, such as aquatic vegetation or overhanging stream banks, and wait until suitable prey approach within its strike range (Hobson 1979; Chapman and MacKay 1984; Savino and Stein 1989). It would be a potential fitness advantage for a pike to employ behaviour patterns that decrease the effects of predator labelling and increase opportunities to forage.

Labelled pike could release AS into the water column through two major pathways; "water" or "feces". AS from prey items could enter via a water pathway through mucous secretions, urine or respiration across the gills, or through a feces pathway if AS occurs within the fecal pellet. If AS is released via some water pathway, it would probably dissipate relatively quickly under natural conditions, hence the pike would be labelled only while it was actually secreting AS. AS within feces would likely not dissipate as quickly, potentially releasing AS slowly over a period of hours or days. If a pike were to defecate within its home area (or foraging range), this area might be labelled as a dangerous habitat. Minnows have been shown to recognize habitats associated with AS on the basis of chemical stimuli (Chivers and Smith in press). Mathis and Smith (1993a, c) could not determine if the alarm pheromone was released via the water or the feces pathway. This distinction is crucial in that if the alarm pheromone is contained in feces, then the possibility exists that the predator may be able to remove the cue via localized defecation.

One way to avoid being labelled as a potential predator would be to defecate away from the region in which foraging bouts are likely to take place. If pike forage on minnows and defecate away from the home area, they could potentially counteract the effects of being labelled as a predator. As a result, they would probably reduce the impact of predator labelling on the benefits of utilizing a sit-and-wait foraging strategy.

We conducted two experiments designed to test whether: (1) AS is present specifically in the feces of a pike that has been maintained on fathead minnows,

and (2) pike localize their defecation away from the home area, perhaps to avoid being chemically labelled as a predator.

Methods

Experiment 1: Do fathead minnows exhibit a "fright reaction" to pike feces?

Test fish

Fathead minnows were collected from Marshy Creek in central Saskatchewan. Marshy Creek drains into Redberry Lake, a large saline evaporation basin with no piscivorous fish species (Mathis and Smith 1993a). Minnows were maintained in the laboratory in a 300-l artificial stream channel at approximately 15°C, on a 14:10 h light : dark cycle for at least 4 months prior to testing. Both minnows and swordtails (see below) were fed once daily with Tetramin flakes. Minnows ($n = 72$) measured (mean \pm SD) 4.92 ± 0.35 cm standard length (distance from the most anterior part of the head to the posterior margin of the last whole vertebral centrum; SL) at testing.

Stimulus preparation

In order to collect stimulus solutions, two pike (19.5 and 18.2 cm SL) were fed equal rations of either fathead minnows or swordtails. Swordtails, which were obtained commercially, were used as a control diet because they do not possess cyprinid alarm pheromone cells (Mathis and Smith 1993a, c). We fed each pike approximately 2–2.5 ml (measured by volumetric displacement in water) of either minnow or swordtail once every 5 days for a total of three feedings.

One hour after the final feeding, the pike were removed from their holding tanks and rinsed with dechlorinated tap water (to remove any remaining prey skin or scales) and returned to identical holding tanks containing fresh, dechlorinated tap water. Eleven hours later (12 h after final feeding), we placed each pike into plexiglas stimulus collection boxes (described in Mathis and Smith 1993a, c), measuring $26 \times 8 \times 8$ (h) cm and containing 1.2 l of fresh dechlorinated tap water.

Twenty-four hours after placing the pike in the collection chambers, we took a 60-ml water sample from each box and replaced this volume with 60 ml of dechlorinated tap water. Twelve hours after this, feces were observed in the collection chambers, and were collected by siphoning as much particulate matter as possible from the collection boxes. We vacuum filtered feces samples through 20 μ m filter paper. All material left on the filter paper was removed and suspended in 60 ml of dechlorinated tap water. Both the water samples (collected before defecation) and the feces samples were divided into twelve 5-ml units and frozen in individual polypropylene bags at approximately -20°C until testing. This procedure was repeated, reversing the pike diets (the pike originally fed minnows was now fed swordtails). This was done to ensure the minnows were not responding to the chemical cues of a specific pike.

Testing protocol

Individual minnows were tested in 12 identical 37-l glass aquaria at approximately 18°C under a 14:10 L:D cycle. Each tank contained an object to provide the fish with cover (9.8×20.0 cm ceramic tile mounted on three 5.5-cm-long cylindrical glass legs). We arbitrarily selected minnows from our stock population and placed them in the test tanks for a 48-h acclimation period prior to testing.

We observed each minnow for a 16-min observation period. Each observation period consisted of an 8-min “pre-stimulus” period and an 8-min “post-stimulus” period. During each period, we recorded the time spent under the cover object as well as the occurrence of two additional behaviours; “dashing” and “freezing”. Dashing is defined as very rapid, apparently disoriented swimming and freezing is defined as remaining motionless on the substrate of the tank for at least 30 s. Increased cover use and the occurrence of dashing and freezing behaviours have been characterized as stereotypic responses by minnows to conspecific alarm pheromone (Lawrence and Smith 1989) and pike stimuli (Chivers and Smith 1994a,b).

An airstone was fixed to the back wall of the tank and an additional length of Tygon tubing was attached to the airstone, to allow for the injection of stimulus solutions from a distance of approximately 3 m. Prior to injecting the stimulus, we removed and discarded 60 ml of water from the tubing (to remove any stagnant water remaining in the line). We removed another 60 ml of water and retained this; then 5 ml of stimulus were injected into the line and after 8 min we injected the second 60 ml of water, forcing the stimulus into the tank. Because the stimulus is injected near the airstone, it was quickly distributed throughout the tank. Distilled water control observations were conducted between 0800 and 1100 hours. During the control trials, 5 ml of dechlorinated tap water was used as the stimulus solution. Experimental observations were conducted 2 h after the completion of the distilled water control observations (between 1300 and 1500 hours). The order of treatments (distilled water control vs. experimental) was not randomized since upon detecting alarm substance, minnows show evidence of escalated stress for an extended period of time (Rehnberg and Smith 1990). Minnows were randomly assigned to one of four treatment conditions: (1) minnow diet pike water (FHM-W), (2) minnow diet pike feces (FHM-F), (3) swordtail diet pike water (SWT-W), and (4) swordtail diet pike feces (SWT-F). A total of 18 minnows were tested for each stimulus solution (i.e. nine minnows for each pike donor for each condition). Each minnow was tested only once.

Statistical analyses

We calculated the difference between time spent using cover for pre- and post-stimulus periods for both control and experimental trials and compared these using a Mann-Whitney *U*-test (Siegel 1956). If the minnows are responding to the pike-derived stimulus with a fright reaction, we would observe a significant increase in cover use in the experimental trials compared to the control trials. To determine if minnows were responding to conspecific alarm substance or simply to the smell of a fish diet, we compared the response to stimulus from pike fed on minnows and pike fed on swordtails for each treatment (i.e. FHM-W vs. SWT-W and FHM-F vs. SWT-F) using a Mann-Whitney *U*-test. We tested for differences in the presence or absence of dashing and freezing behaviours using a Fisher’s exact probability test (Siegel and Castellan 1988). To control for any effect of pike (i.e. stimulus donor) identity, we compared similar diets for each pike using cover use as the dependant variable (i.e. pike A FHM-F vs. pike B FHM-F) using a Mann-Whitney *U*-test.

Experiment 2: Do pike localize their defecation away from their home area?

Test fish

Juvenile northern pike were collected using seine nets from Eagle Creek, a small tributary stream of the North Saskatchewan River in central Saskatchewan. Pike were held in the laboratory in a 300-l artificial steam tank at approximately 15°C under a 14:10 h L:D cycle for at least 2 months prior to testing. During this period,

pike were fed one or two fathead minnows once every 5 days. Ten pike (mean \pm SD = 14.1 \pm 1.71 cm SL) were used for this study.

Test tank

Three identical 500-l glass aquaria [183 \times 49 \times 56 (h) cm] were used as testing tanks. We divided the tanks into seven compartments by drawing gridlines on the exterior of the tank with a marking pencil. The first compartment was 38 cm in width and each of the remaining six compartments was 24 cm in width. The larger compartment was designated as the “home area” and contained rocks and artificial plants which extended to within 15 cm from the water surface. In addition, opaque plastic covers were placed over the “home area” to provide shading. The floor of the entire tank was covered with silica sand to a depth of 4 cm. Water temperature in the testing tanks was approximately 18°C, and tanks were maintained on a 14:10 L:D cycle.

Experimental protocol

Trials lasted 1 week, and each trial consisted of 5 days of acclimation (days 1–5) and 2 days of testing (days 6 and 7). An individual pike was placed into a test tank on the morning of day 1. During day 1–5, we fed the pike one fathead minnow each day (mean \pm SD volume = 1.41 \pm 0.27 ml, measured by volumetric displacement in water). Prior to feeding, the minnows were killed with an overdose of MS 222 and the body cavity injected with approximately 0.5 ml of ultra-violet fluorescent dye (Tracer Glo). Since pike do not readily consume dead prey (Huntingford 1984), we presented the minnows on the end of a fine-gauge stainless-steel wire. The use of the wire allowed us to manipulate the minnow and induce the pike to eat it. The wire was placed in the base of the caudal fin and could be easily pulled free once the pike bit the minnow without disturbing the pike. The minnows were always presented in the home area.

At the end of day 5, we removed (with a siphon) all feces visible in the tank. On day 6, we began recording two measures: (1) proportion of time spent in each area of the tank (area use) and (2) location of feces. We quantified area use by recording the location of the pike once every 10 s for a 10-min observation period every hour for 8 h on days 6 and 7. Observations began at 0830 hours each day.

The location of the feces was quantified after the final area use observation each day. We recorded (and removed with a siphon) the number of fecal pellets in each compartment of the test tank. Fecal pellets within 1 cm of each other were recorded as a single pellet. After recording the location of feces on day 7, we removed the pike and carefully drained the tank so as not to disturb the substrate. We used a UV light to check for any fecal pellets which may have partially dissolved or been covered with sand. We recorded the presence of fluorescent dye as a fecal pellet, using the same 1 cm criterion.

Statistical analysis

We employed a one-way analysis of variance (ANOVA) to determine if there was a significant difference in the amount of time spent or the number of fecal pellets in each of the seven areas of the test tank (home plus six additional areas). We compared the percent of time versus the percent of total feces in each of the seven areas of the tank using paired *t*-tests corrected for increasing alpha using a modified Bonferroni procedure (Keppel 1982). If pike were localizing their defecation away from their home area, we would predict that there should be a significant difference between the percent time and percent feces scores in each area.

Results

Experiment 1

Pike identity did not have a significant effect on the use of cover by fathead minnows in any of the four stimulus conditions (pike A versus pike B, FHM-W, $z = -1.72$, $P > 0.05$; FHM-F, $z = -0.66$, $P > 0.05$; SWT-W, $z = -0.31$, $P > 0.05$; SWT-F, $z = -0.39$, $P > 0.05$ two-tailed Mann-Whitney U -test). As a result, data from both pike were combined for further analyses.

Minnows exposed to FHM-W stimulus significantly increased their use of cover ($z = -2.82$, $P \leq 0.003$) while minnows exposed to SWT-W did not increase their time spent under cover ($z = -0.59$, $P = 0.28$; Fig. 1). Similarly, minnows presented with FHM-F also significantly increased their use of cover ($z = -4.43$, $P \leq 0.0003$) and those exposed to SWT-F exhibited no significant increase in cover use ($z = -0.063$, $P = 0.476$; Fig. 2).

Pike diet also influenced the frequency of dashing and freezing behaviour. Significantly more minnows exhibited dashing behaviour when exposed to FHM-W versus SWT-W stimulus (50% vs. 11.1%, Fisher's exact probability = 0.03) and FHM-F versus SWT-F stimulus (66.7% vs. 0%, Fisher's exact probability = 0.0001). Similarly, significantly more minnows froze when exposed to FHM-F than SWT-F stimulus (33.3% vs. 0%, Fisher's exact probability = 0.0009). Insufficient freezing events occurred in the FHM-W and SWT-W trials to allow statistical comparison, though in each occurrence the freezing was observed only in the FHM-W trials. These results suggest that AS is present in both the "water" and feces of a pike which has recently been given a diet of minnows and that this is a sufficient stimulus to elicit a fright reaction by individual fathead minnows. We did not con-

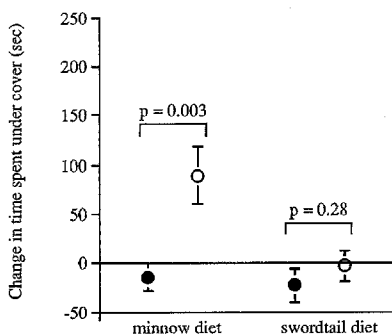


Fig. 1 Mean (\pm 1SD) time (S) spent under cover by individual fathead minnows ($n = 18$ per stimulus condition) when presented with distilled water control stimuli (closed circles) and pike "water" experimental stimuli (open circles) for minnow and swordtail diet treatments. See text for details

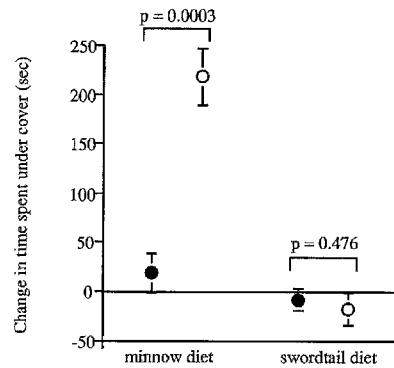


Fig. 2 Mean (\pm 1SD) time (S) spent under cover by individual fathead minnows ($n = 18$ per stimulus condition) when presented with distilled water control stimuli (closed circles) and pike feces experimental stimuli (open circles) for minnow and swordtail diet treatments. See text for details

duct direct comparisons between FHM-W and FHM-F because we were unable to control for the volume of AS in each stimulus condition.

Experiment 2

Pike spent a significantly greater proportion of time in the home area and the area adjacent to it ($F_{(6, 63)} = 44.46$, $P \leq 0.0001$; Fig. 3). Conversely, direct visual inspection and UV fluorescence showed that pike tended to defecate significantly more often in the two areas furthest away from the home area (areas 5 and 6; $F_{(6, 63)} = 48.45$, $P \leq 0.0001$; Fig. 3). Individual comparisons demonstrate that there is a significant difference in the amount of time spent and the amount of feces in the home area and area 1 ($t = 6.78$, $P \leq 0.01$; $t = 3.46$, $P \leq 0.05$ respectively) and areas 5 and 6 ($t = -5.70$ and -7.36 , $P \leq 0.01$ respectively; Fig. 3) supporting the hypothesis that pike are localizing their defecation away from their home area.

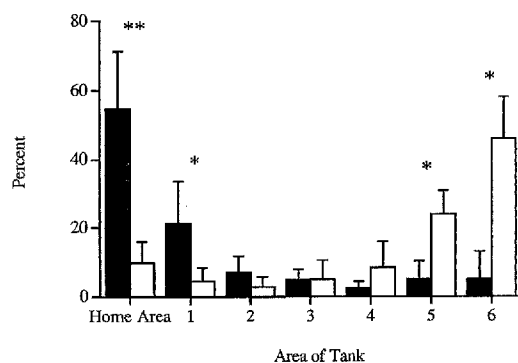


Fig. 3 Mean (\pm 1SD) percent of time spent (closed bars) and percent of feces (open bars) in each area of the tank. * $P < 0.05$, ** $P < 0.01$, for the comparison of % time vs. % feces in each area of the tank. See text for details

Discussion

The results of experiment 1 demonstrate that pike-naive fathead minnows exhibit a stereotypic fright response to the feces of pike fed fathead minnows but not to the feces of pike fed swordtails. By responding to the AS excreted by pike, minnows naive to pike are able to learn of the presence of a potential predator (i.e. Mathis and Smith 1993c). This ability has obvious potential benefits to the individual minnow's survival and fitness (Mathis and Smith 1993b). No effect of pike identification was found, confirming the previous results of Mathis and Smith (1993a, c) and Gelowitz et al. (1993).

An alarm response was observed to the "water" of a pike fed fathead minnows. This would provide another possible cue by which prey species could recognize predators, but this cue would likely dissipate relatively quickly in moving water (e.g. Vogel 1981). Conversely, AS deposited in feces may be released into the water column over an extended period. The duration of release of AS from feces is unknown and is the subject of current investigations.

The observation that AS is contained in both pike "water" and pike feces provides a possible basis by which minnows can gain information about potential predation risk via predator inspection visits. By sampling chemosensory cues, individual minnows may be able to assess the relative risk of a particular predator or of a particular habitat or area.

The results of experiment 2 strongly demonstrate that pike are able to counter the effect of chemically labelled feces by localizing their defecation away from their home/feeding area. Pike were observed to spend the majority of their time in the home area or the adjacent area, while the majority of their feces was observed in the farthest end of the tank (areas 6 and 7). While the area use data were being recorded, several pike were observed to swim from the home area to area 7, defecate and immediately return to the home area. By defecating away from the home area, pike potentially remove one source of predator-labelling cues. To our knowledge, this is the first example of localized defecation in a fish species.

Over 90% of a pike's diet typically consists of fish (Scott and Crossman 1973). Of these, minnows and other ostariophysian fishes are common food items (Lawler 1965; personal observations). Thus the potential for benefits associated with localized defecation are considerable.

A number of alternative hypotheses could explain the observed localized defecation. Initially, pike may be defecating away from the home area for sanitary reasons. By localizing defecation away from the home area, pike may be reducing the risk of parasite or pathogen transfer or infection. This has been demon-

strated in a variety of avian and mammalian species (Poole 1985).

Secondly, localized defecation has been shown to serve as territory markings for both the territorial individual itself and for conspecifics (Mykytowycz 1968; Shorey 1976; Poole 1985). By defecating at strategic points around the territory, an individual could mark its territorial boundaries for itself (i.e. it knows where its own territory ends) and for conspecifics (i.e. others know where its territory begins). By doing so, individuals could avoid the costs associated with active territorial defence and/or repeated territorial disputes (e.g. Getty 1987). There is insufficient understanding of pike territoriality to determine if localized defecation can or does serve as a territorial marker. It remains unclear if northern pike actively defend foraging or home ranges.

A third possible function of localized defecation is to allow for the recognition of group members. African raccoon dogs (*Nyctereates procyonoides*) use common latrine areas in order to allow the exchange of individual and group identity cues (Yamamoto 1984). Unfamiliar individuals are rejected from the social group unless they have been exposed to feces from the group specific defecation site. Again, it is unlikely that such a selection pressure would operate in pike, since pike are generally considered to be solitary foragers (Savino and Stein 1989) and are known to be highly cannibalistic (Lawler 1965).

It has been shown that AS released by a minnow during a predation event may serve to attract secondary predators (Smith 1992; Mathis et al. in press). This second predator could either compete with the primary predator for the captured food item, or could attack the primary predator as a prey item. Similar hypotheses have been suggested for the evolution of distress calls in various avian species (Perrone 1980; Högstedt 1983; Koenig et al. 1991). Avoidance of secondary predator interference may serve as a possible selection pressure for localized defecation. By localizing a source of AS away from its home range, the pike avoids potential conflicts with secondary predators.

These hypotheses are not necessarily mutually exclusive. A single selection pressure or a combination of selection pressures may act in selecting for and maintaining localized defecation behaviours in predatory northern pike. The data do suggest, though, that because minnows can recognize and respond to AS in pike feces, it may be to the predators' advantage to defecate away from the home range. How the presence of pike feces affects the distribution of minnows under natural conditions remains unknown.

Acknowledgements The authors wish to thank Dr. Brian Wisenden and Penelope G. Pearse for their comments on earlier versions of this manuscript. Financial support was provided by a Natural Sciences and Engineering Research Council (NSERC) of Canada Postdoctoral Fellowship to G.E.B. an NSERC Postgraduate

Fellowship to D.P.C. and an NSERC operating grant and University of Saskatchewan research support to R.J.F.S.

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Communicated by G. M. Klump