

Fathead minnows, *Pimephales promelas*, learn to recognize chemical alarm cues of introduced brook stickleback, *Culaea inconstans*

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Synopsis

In four experiments conducted over a 6-year period, we investigated whether fathead minnows, *Pimephales promelas*, could acquire the ability to recognize chemical alarm cues of introduced brook stickleback, *Culaea inconstans*. A laboratory experiment documented that stickleback-naïve minnows did not exhibit an anti-predator response when exposed to the chemical alarm cues of stickleback. In a laboratory experiment conducted 5 years after the introduction of stickleback to the pond, minnows exhibited an antipredator response to stickleback cues. Moreover, in a field experiment the minnows exhibited avoidance of areas labelled with stickleback alarm cues. Minnows raised from eggs taken from the test pond did not exhibit an anti-predator response to stickleback cues while minnows from the test pond that had experience with stickleback cues did respond to stickleback cues. Our results provide clear evidence that cross-species responses to chemical alarm cues of fishes can be learned. Learned recognition of alarm cues has important implications for predator/prey interactions.

Introduction

Alarm signalling is the situation in which animals encountering a hazard produce a response that makes nearby individuals aware of danger (Smith 1992). The signal(s) can include the sender's escape response or, alternatively, a chemical, auditory or visual cue that may be detected by the receiver (Chivers & Smith 1998). Alarm signals are common in a variety of vertebrates and invertebrates (e.g. mammals: Seyfarth & Cheney 1986, birds: Stefanski & Falls 1972, Aubin 1991, fishes: Smith 1992, amphibians: Chivers et al. 1999, gastropods: Appleton and Palmer 1988, insects: Chivers et al. 1996, Huryn & Chivers 1999).

In aquatic environments, chemical cues are commonly used as alarm signals, whereas in terrestrial environments visual and auditory cues appear to be employed more often (Chivers & Smith 1998, Kats & Dill 1998). Chemical cues may be particularly important in aquatic environments, in areas of high turbidity, dense vegetation or at night.

It is common for prey species that co-occur to recognize each other's alarm cues (Chivers & Smith 1998). Recognizing heterospecific alarm cues should provide receivers with an early warning if they share the same predators. Responses to heterospecific alarm cues are common in primates (e.g. Oda & Masataka 1996, Bshary & Noe 1997), birds (Møller 1992, Aubin 1991), fishes (e.g. Schutz 1956, Smith 1982, Wisenden et al. 1994, 1995, Mirza & Chivers 2001), amphibians (Lutterschmidt et al. 1994, Marvin & Hutchinson 1995, Chivers et al. 1997) and gastropods (Snyder & Snyder 1970).

Some studies have documented that prey species learn to recognize alarm cues from other species. For example, Hauser (1988) documented that infant vervet monkeys, *Cercopithecus aethiops*, learn to respond to alarm calls of starlings, *Lamprotornis superbus*, a species with which they share common predators.

The importance of learning in the recognition of heterospecific chemical alarm cues in fishes has received

little attention. Several of the documented examples of cross-species responses appear to suggest that closely related prey animals are responding to evolutionarily conserved homologous alarm cues (Brown et al. 2000, Mirza & Chivers 2001). For example, Brown et al. (2000) showed that a nitrogen oxide functional group might act as the chief molecular trigger in the alarm systems of fishes in the Superorder Ostariophysi. However, some authors have suggested that cross-species responses to alarm cues may be learned when alarm cues are not homologous.

Chivers & Smith (1994) provided indirect evidence that fathead minnows, *Pimephales promelas*, and finescale dace, *Chrosomus neogaeus*, can learn to identify brook stickleback, *Culaea inconstans*, alarm cues. In a field study, traps marked with brook stickleback skin extract caught fewer and smaller dace and minnows than traps marked with distilled water. Larger fish are typically older and more experienced, suggesting that minnows and dace may have learned to recognize stickleback cues. Chivers et al. (1995) compared the response of fathead minnows that co-occurred with Iowa darters, *Etheostoma exile*, to minnows from a pond lacking darters. Only minnows from the pond containing darters avoided cues of injured darters, and larger fish avoided darter alarm cues more often than smaller fish.

In the current study we tested whether fathead minnows can recognize chemical alarm cues of brook stickleback following their introduction. When minnows and stickleback co-occur, they are exposed to many of the same predators (Mathis & Smith 1993) and should benefit by responding heterospecific alarm cues. Previous studies (Mathis & Smith 1993, Chivers & Smith 1994, Brown et al. 1995) provide mixed results regarding whether minnows from populations containing stickleback respond to stickleback alarm cues. No studies have tested whether minnows from locations without stickleback respond to stickleback cues.

We conducted studies to explore the role of experience in response of minnows to stickleback alarm cues. (1) In a laboratory test we confirmed that minnows from a pond that did not contain stickleback did not respond to stickleback alarm cues any differently than they did to a control stimulus (swordtail). (2) We introduced stickleback to the pond, and after 5 years, we retested the minnows for a response to stickleback alarm cues in both laboratory and in field trials. (3) In a final experiment, we raised minnows from eggs collected from a population known to respond to stickleback

cues and tested whether they responded to stickleback alarm cues.

Experiment 1: Response of stickleback-naïve minnows to stickleback alarm cues

Methods

The purpose of this experiment was to determine if fathead minnows, from a population without brook stickleback, respond to stickleback alarm cues. In April 1995, we collected fathead minnows from a 1 ha pond located on the University of Saskatchewan campus (Saskatoon, SK, Canada). The pond is known to contain other fish species, including finescale dace, *Phoxinus neogoeus*, white suckers, *Catostomus commersoni*, and Iowa darters but does not contain brook stickleback. Minnows were transported to our laboratory and maintained in a 350 l stream tank at approximately 13°C on a 14:10 h light:dark cycle, where they were fed daily with commercial fish food. Test fish were fed 1 h prior to the start of testing.

Ten adult stickleback (SL = 6.74 ± 0.27 cm) were sacrificed by a blow to the head (in accordance with the guidelines set by the Canadian Council on Animal Care) and a skin fillet was removed from both sides of each fish producing approximately 45 cm² of skin in total. The skin was placed into 100 ml of distilled water and homogenized using a polytron homogenizer. The sample was filtered through glass wool to remove any solid particles and diluted with 350 ml of distilled water for a total of 450 ml. The extract was divided into sample bags containing 50 ml each and immediately frozen at -20°C. We used the same procedure to produce a control extract from swordtails, *Xiphophorus helleri* (SL = 5.31 ± 0.33 cm). We used swordtail skin extract as a control stimulus to test for an alarm response specific to stickleback and not a general response to injured fish cues. Swordtails are an ideal control because they are easily obtained, similar in size to stickleback, and are allopatric form, and distantly related to minnows (Chivers & Smith 1998).

Observations were completed in 371 glass aquaria filled with dechlorinated tap water. Each tank contained a gravel substrate and a centrally located shelter object consisting of a 10 × 20 cm ceramic tile mounted on three 5.5 cm long cylindrical glass legs. Each tank also contained an airstone near which we attached a 2 m long piece of plastic tubing used to introduce the test

stimuli into the tanks. The injection line allowed the observer to inject test stimuli at approximately 1.5 m from the test aquaria.

Immediately prior to the start of each trial, 60 ml of water was drawn through the stimulus tube and discarded to ensure the tube was clean before each trial. Another 60 ml of water was then drawn, retained, and later used to flush the stimulus into the tank during the trial. Each trial consisted of an 8 min pre-stimulus period followed by injection of the stimulus and an 8 min post-stimulus period. We recorded the time spent under shelter in both the pre and post-stimulus periods. The occurrence of freezing (the cessation of movement where the fish drops to the substrate and remains immobile for a minimum of 30 s) and dashing (very rapid, erratic swimming) were also recorded following injection of the stimulus. We did not test fish that either froze or dashed in the pre-stimulus period. Shelter use, freezing and dashing are known anti-predator responses in minnows (review Chivers & Smith 1998).

We observed the response of 15 minnows to each of two different stimuli: (1) skin extract from stickleback and (2) skin extract from swordtails. Tests were conducted after fishes had acclimated for 48 h. Rehnberg et al. (1987) demonstrated that minnows exposed to a frightening stimulus may show a physiological stress response for extended periods (i.e., for hours or days). Consequently, we tested all fish (individually) for a response to the control stimulus (swordtail skin extract) two days before we tested them for a response to the experimental stimuli (stickleback skin extract).

We calculated changes in time spent under shelter (post-stimulus minus pre-stimulus) for each treatment and compared the responses using a Wilcoxon Signed Rank test (Siegel & Castellan 1988). The occurrence of dashing and freezing were compared using a McNemar Change test (Siegel & Castellan 1988). We used one-tailed probability distributions because we predicted that if minnows could recognize stickleback alarm cues then they would increase shelter use and exhibit dashing and freezing behaviour.

Results

There was no significant change in time spent under shelter in response to stickleback *versus* swordtail skin extract ($Z = 0.12$, $N = 14$, $p > 0.45$, Figure 1A). In addition, there was no significant difference in the frequency of dashing ($X^2 = 0$, $df = 1$, $p > 0.99$)

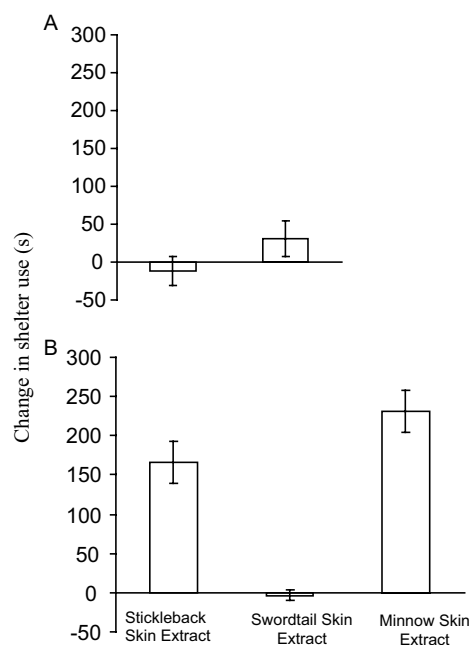


Figure 1. Mean (\pm SE) change in time spent under shelter for fathead minnows following exposure to skin extract of stickleback, swordtails and fathead minnows. (A) shows responses of stickleback-naïve minnows (experiment 1); (B) shows responses of stickleback-experienced minnows (experiment 2).

or freezing behaviour ($X^2 = 0$, $df = 1$, $p > 0.99$) between the two treatments. These results indicate that minnows naïve to stickleback do not recognize stickleback alarm cues as an indicator of predation risk.

Experiment 2: Acquired recognition of stickleback alarm cues by fathead minnows: a laboratory test

Methods

The purpose of this experiment was to determine whether fathead minnows from the test pond could acquire the ability to recognize stickleback alarm cues following the introduction of stickleback. In May 1995, following experiment 1, we collected 2008 brook stickleback from Bradwell Reservoir in south central Saskatchewan, and released them into the test pond. Minnows from the test pond were collected in the winter of 1999 for use in experiment 2.

We used a similar experimental procedure as in experiment 1. However, instead of testing the response

of the same minnows to cues of swordtails (control) and stickleback (experimental), each fish was tested only once. Moreover, we added fathead minnow alarm cues as a third treatment in order to compare the intensity of any response to heterospecific alarm cues against the response to conspecific alarm cues. Our sample size was 20 for each of the three treatments. Skin extracts were prepared as in the first experiment. We used the skin from 10 swordtails (SL = 3.34 ± 0.54 cm), 7 stickleback (SL = 4.90 ± 0.42 cm) and 5 minnows (SL = 5.30 ± 0.51 cm). In all cases we added the appropriate amount of distilled water to the skin extract we collected to create a stimulus with a concentration of 1.0 cm^2 per 10 ml of distilled water.

We compared the change (post-stimulus minus pre-stimulus) in time spent under shelter using a Kruskal-Wallis one-way analysis of variance on ranks (Siegel & Castellan 1988). The occurrence of dashing and freezing was analyzed with a Fisher Exact Probability test.

Results

There was an overall significant difference in time spent under shelter among the three treatments (KW = -28.90 , $df = 2$, $p < 0.001$, Figure 1B). Post-hoc multiple comparisons among treatments showed that there was no difference in shelter use between the stickleback and minnow treatments but both differed from the swordtail treatment. Fathead minnows exposed to minnow extract dashed more frequently (and tended to freeze more frequently) than those exposed to swordtail cues (Table 1). Similarly, minnows that were exposed to stickleback extract showed a tendency to dash more frequently than those exposed to swordtail extract (Table 1).

Table 1. Comparisons of the occurrence of dashing and freezing by fathead minnows exposed to either swordtail, stickleback, or fathead minnow skin extract (Fisher exact test).

Treatment	Dashing	P-value	Freezing	P-value
Swordtail	0	0.053	0	0.500
Stickleback	4		1	
Swordtail	0	0.010	0	0.053
Fathead	6		4	
Stickleback	4	0.53	1	0.200
Fathead	6		4	

Experiment 3: Acquired recognition of stickleback alarm cues by fathead minnows: a field test

The purpose of this experiment was to determine whether fathead minnows from the test pond would avoid traps labelled with stickleback alarm cues. This experiment was conducted in the summer of 2000, 5 years after stickleback were introduced into the test pond.

Methods

We used the same general methodology as in experiments 1 and 2 to produce the swordtail and stickleback skin extracts. The skin from 6 adult swordtails (3.42 ± 0.32 cm) and 7 adult stickleback (4.2 ± 0.29 cm) was added to the appropriate amount of distilled water to create a stimulus with a concentration of 1.0 cm^2 per 10 ml of water. We attached 2 sponges ($2 \times 2 \times 2$ cm) onto each of 34 stainless steel wires. We added 5 ml of stickleback skin extract (experimental) to each of the sponges on 17 of the wires and added 5 ml of swordtail skin extract (control) to each of the sponges on the remaining 17 wires.

We attached the wires that contained the stimulus sponges to the inside of 34 minnow traps (17 traps had sponges labelled with stickleback cues and 17 traps had sponges labelled with swordtail cues). The minnow traps were roughly cylindrical wire enclosures (43 cm long \times 22 cm wide) with an inverted funnel located at each end. The two sponges in each trap were positioned such that they were approximately 4 cm from each trap entrance. Pairs of traps (consisting of one control and one experimental trap) were placed into the water along the edge of the pond approximately 10 m apart. Pairs of traps were placed into the water at 5 min intervals until all 17 pairs were set. The order of placement of the control and experimental traps along the pond edge was determined randomly for each pair.

Trap pairs were removed from the water at 5 min intervals, starting 2 h after the first pair was set. All fish found in the traps were removed, identified to species, and counted. We used a Wilcoxon Signed Rank test to compare the number of minnows captured in traps marked with swordtail extract compared with the number of minnows captured in traps marked with stickleback extract. A one-tailed test was used because we predicted that fathead minnows would be

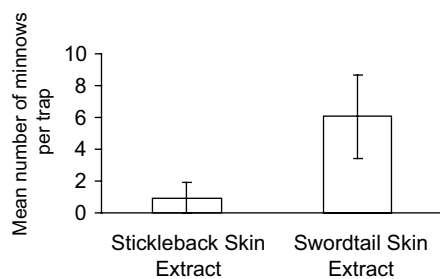


Figure 2. Mean (\pm SE) number of fathead minnows captured in traps marked with skin extract from stickleback or swordtails.

captured significantly less often in experimental traps than control traps.

Results

We captured a total of 119 fathead minnows and 161 stickleback in this experiment. Significantly fewer fathead minnows were captured in traps marked with stickleback skin extract than in traps marked with swordtail skin extract ($Z = 1.82$, $n = 13$, $p = 0.034$, Figure 2). Stickleback showed a non-significant trend toward avoiding stickleback traps ($Z = 1.38$, $n = 11$, $P = 0.083$). For stickleback our sample size was reduced to 11 since 6 trap-pairs failed to capture stickleback.

Experiment 4: The role of experience in acquired recognition of stickleback alarm cues by fathead minnows

The purpose of this experiment was to determine if the acquired recognition of stickleback alarm cues is a learned or, alternatively, a genetically-based behaviour promoted over 5 years of selection. We compared the response of minnows from the test pond experienced with stickleback alarm cues to lab-reared minnows inexperienced with stickleback cues. Stickleback-naïve minnows were raised from eggs collected from the test pond in the summer of 2000. Our laboratory population of naïve minnows originated from 8 different broods but we do not know how many test fish came from each brood. The experienced fish were collected in the winter of 2000.

The experimental protocol for this experiment was nearly identical to that used in Experiment 1, except we tested both naïve and experienced minnows. Due to the limited availability of fish at the time of

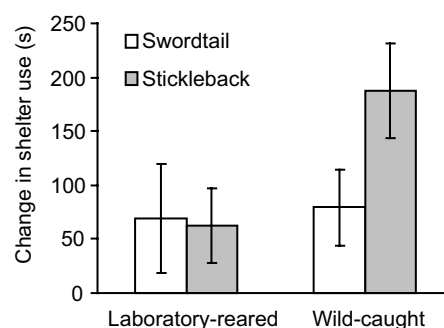


Figure 3. Mean (\pm SE) change in time spent under shelter following exposure to chemical stimuli from swordtails and stickleback by minnows that were laboratory-reared (naïve to stickleback) or wild-caught (experienced with stickleback).

testing, we tested 12 wild-caught experienced minnows and 11 laboratory-reared naïve minnows. Experienced and stickleback-naïve test fish were of similar size when tested (SL: naïve minnows = 4.1 ± 0.54 cm, experienced minnows = 4.4 ± 1.00 cm).

Results

There was no significant difference between treatments for change in time spent under ($Z = -0.561$, $n = 11$, $P > 0.25$, Figure 3) for laboratory-reared minnows. In contrast, wild-caught minnows showed a significantly stronger increase in shelter use following exposure to the stickleback extract in comparison to the swordtail skin extract ($Z = -2.490$, $n = 12$, $P = 0.007$, Figure 3). Dashing and freezing were exhibited less frequently in this experiment than in the previous experiment with experienced fish. There were no significant treatment differences in the frequency of dashing or freezing behaviour between the two treatments for either wild-caught or laboratory-reared minnows (McNemar Change test, $P > 0.10$ for all comparisons).

Discussion

The results of our study indicate that fathead minnows from a population without stickleback do not respond to stickleback alarm cues with antipredator behavior. However, our laboratory and field experiments show that minnows from the test population acquired recognition of stickleback alarm cues following the introduction of stickleback. Testing the response of minnows collected as eggs allowed us to conclude that acquired recognition was the result of learning and was not an

evolved response. These data are among the first to provide clear evidence that cross-species responses to chemical alarm cues of fishes must be learned in at least some instances. Minnows should receive a survival benefit by responding to alarm cues from brook stickleback (Mathis & Smith 1993). Although mixed associations of fish are common (Nursall & Pinsent 1969), few studies have examined the costs or benefits of these associations (Pitcher 1986). Our study illustrates a possible benefit for mixed species aggregations of fishes.

Three previous studies have tested whether fathead minnows respond to alarm cues of brook stickleback. In a laboratory study, Mathis & Smith (1993) observed no significant difference in response by minnows, experienced with stickleback, to stickleback and swordtail alarm cues. In a subsequent field experiment, Chivers & Smith (1994) caught fewer minnows in traps marked with stickleback cues than traps marked with a control extract. While providing tentative evidence that minnows avoid stickleback alarm cues, the same result could occur if minnows were attracted to stickleback captured in control traps. Brown et al. (1995) showed that minnows, experienced with stickleback, recognize stickleback alarm cues in the diet of a pike (*Esox lucius*), and avoided areas containing such cues.

The results of our current study provide insights into previous conflicting results. If minnows must learn to recognize stickleback cues, then the recognition by individuals in any population must be a consequence of the potential opportunities to learn. The degree of overlap in microhabitat use between these species and the degree to which they share predators are likely important variables to consider when examining whether there are sufficient opportunities for animals to learn to recognize each other's alarm cues. Likewise, the relative density of the two prey species may be an important variable to consider because the greater the number of heterospecifics the greater the opportunity for acquired recognition. Species abundance, microhabitat overlap, the dietary overlap of predators, and the relative density of prey animals varies across short and long-term spatial and temporal scales. Future studies need to consider these variables when explaining the presence or absence of cross-species responses. We know little about the mechanisms by which learned recognition of heterospecific alarm cues occur (but see Mirza & Chivers 2001). Future studies should address the mechanisms by which prey learn to recognize heterospecific alarm cues.

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References cited

- Appleton, R.D. & A.R. Palmer. 1988. Water-borne stimuli released by predatory crabs and damaged prey induced more predator-resistant shells in a marine gastropod. *Proc. Nat. Acad. Sci. U.S.A.* 85: 4387–4391.
- Aubin, T. 1991. Why do distress calls evoke interspecific responses? An experimental study applied to some species of birds. *Behav. Process.* 23: 103–111.
- Brown, G.E., J.C. Adrian, Jr., E. Smyth, H. Leet & S. Brennan. 2000. Ostariophysan alarm pheromones: Laboratory and field tests of the functional significance of nitrogen oxides. *J. Chem. Ecol.* 26: 139–154.
- Brown, G.E., D.P. Chivers & R.J.F. Smith. 1995. Fathead minnows avoid conspecific and heterospecific alarm pheromones in the feces of northern pike. *J. Fish Biol.* 47: 387–393.
- Bshary, R. & R. Noe. 1997. Red colobus and Diana monkeys provide mutual protection against predators. *Anim. Behav.* 54: 1461–1474.
- Chivers, D.P. & R.J.F. Smith. 1994. Intra and interspecific avoidance of areas marked with skin extract from brook sticklebacks (*Culaea inconstans*) in a natural habitat. *J. Chem. Ecol.* 20: 1517–1524.
- Chivers, D.P. & R.J.F. Smith. 1998. Chemical alarm signaling in aquatic predator-prey systems: A review and prospectus. *Écoscience* 5: 338–352.
- Chivers, D.P., B.D. Wisenden & R.J.F. Smith. 1995. The role of experience in the response of fathead minnows (*Pimephales promelas*) to skin extract of Iowa darters (*Etheostoma exile*). *Anim. Behav.* 50: 665–674.
- Chivers, D.P., B.D. Wisenden & R.J.F. Smith. 1996. Damsel fly larva learn to recognize predators from chemical cues in the predator's diet. *Anim. Behav.* 52: 315–320.
- Chivers, D.P., J.M. Kiesecker, E.L. Wildy, M.T. Anderson & A.R. Blaustein. 1997. Chemical alarm signaling in terrestrial salamanders: Intra- and interspecific responses. *Ethology* 103: 599–613.
- Chivers, D.P., J.M. Kiesecker, E.L. Wildy, L.K. Belden, L.B. Kats & A.R. Blaustein. 1999. Avoidance response of post-metamorphic anurans to cues of injured conspecifics and predators. *J. Herp.* 33: 472–476.

- Hauser, M.D. 1988. How infant vervet monkeys learn to recognize startling alarm calls: The role of experience. *Behaviour* 105: 187–201.
- Huryn, A.D. & D.P. Chivers. 1999. Contrasting behavioral responses by detritivorous and predatory mayflies to chemicals released by injured conspecifics and their predators. *J. Chem. Ecol.* 25: 2729–2740.
- Kats, L.B. & L.M. Dill. 1998. The scent of death: Chemosensory assessment of predation risk by prey animals. *Écoscience* 5: 361–394.
- Lutterschmidt, W.I., G.A. Marvin & V.H. Hutchison. 1994. Alarm substances by a plethodontid salamander (*Desmognathus ochrophaeus*): Conspecific and heterospecific 'Schreckstoff'. *J. Chem. Ecol.* 20: 2751–2759.
- Marvin, G.A. & V.H. Hutchison. 1995. Avoidance response by adult newts (*Cynops pyrrhogaster* and *Notophthalmus viridescens*) to chemical alarm cues. *Behaviour* 132: 95–105.
- Mathis, A. & R.J.F. Smith. 1993. Intraspecific and cross-superorder responses to chemical alarm signals by brook stickleback. *Ecology* 74: 2395–2404.
- Mirza, R.S. & D.P. Chivers. 2001. Are chemical alarm signals conserved within salmonid fishes? *J. Chem. Ecol.* 27: 1641–1655.
- Møller, A.P. 1992. Interspecific response to playback of birds song. *Ethology* 90: 315–320.
- Nursall, J.R. & M.E. Pinsent. 1969. Aggregations of spot-tail shiners and yellow perch. *J. Fish. Res. Bd. Can.* 26: 1672–1676.
- Oda, R. & N. Masataka. 1996. Interspecific responses of ring-tailed lemurs to playback of antipredator alarm calls given by Verreaux's sifakas. *Ethology* 102: 441–453.
- Pitcher, T.J. 1986. *The Behaviour of Teleost Fishes*. Croom Helm, London. 294–337 pp.
- Rehnberg, B.G., R.J.F. Smith & B.D. Sloley. 1987. The reaction of pearl dace (Pisces: Cyprinidae) to alarm substance: Time-course of behavior, brain amines, and stress physiology. *Can. J. Zool.* 65: 2916–2921.
- Schutz, V.F. 1956. Vergleichende Untersuchungen über die Schreckreaktion bei Fischen und deren Verbreitung. *Z. Vergl. Physiol.* 38: 84–135.
- Seyfarth, R.M. & D.L. Cheney. 1986. The assessment by vervet monkeys of their own and another species alarm calls. *Anim. Behav.* 34: 754–764.
- Siegel, S. & N.J. Castellan. 1988. *Nonparametric Statistics for the Behavioral Sciences*. 2nd edn., New York: McGraw-Hill. 86, 206 pp.
- Smith, R.J.F. 1982. Reaction of *Percina nigrofasciata*, *Ammocrypta beani* and *Etheostoma swaini* (Percidae: Pisces) to conspecific and intergeneric skin extracts. *Can. J. Zool.* 60: 1067–1072.
- Smith, R.J.F. 1992. Alarm signals in fishes. *Rev. Fish Biol. Fish.* 2: 33–63.
- Snyder, N.F.R. & H.A. Snyder. 1970. Defenses of the Florida apple snail *Pomacea paludosa*. *Behaviour* 40: 175–215.
- Stefanski, R.A. & J.B. Falls. 1972. A study of distress calls of song, swamp and white-throated sparrows (Aves: Fringillidae). II. Interspecific responses and properties used in recognition. *Can. J. Zool.* 50: 1513–1525.
- Wisenden, B.D., D.P. Chivers, G.E. Brown & R.J.F. Smith. 1995. The role of experience in risk assessment: Avoidance of areas chemically labelled with fathead minnow alarm pheromone by conspecifics and heterospecifics. *Écoscience* 2: 116–122.
- Wisenden, B.D., D.P. Chivers & R.J.F. Smith. 1994. Risk sensitive habitat use by brook stickleback (*Culaea inconstans*) in areas associated with minnow alarm pheromone. *J. Chem. Ecol.* 20: 2975–2983.