

Threat-sensitive predator avoidance by slimy sculpins: understanding the importance of visual versus chemical information

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Abstract: The supposition that prey animals assess and behave flexibly in response to different degrees of predation threat is known as the threat-sensitive predator avoidance hypothesis. We completed a series of field and laboratory experiments to examine whether slimy sculpins (*Cottus cognatus*) exhibit threat-sensitive predator avoidance when exposed to sympatric predatory brook trout (*Salvelinus fontinalis*). In a field experiment we caged small and large trout in similar habitats and found that sculpins avoided areas containing trout that were large enough to pose a threat to them, but did not avoid areas containing trout that were small and hence not a threat. In a series of laboratory experiments we found that sculpins showed threat-sensitive predator avoidance when they could assess the predator visually. However, when only chemical cues from the predator were presented, sculpins responded to the predator regardless of its size. Chemical cues seem to function to warn the sculpin that the predator is in the vicinity, but visual cues are needed in order to accurately assess the risk posed by the predator.

Résumé : L'hypothèse selon laquelle les animaux qui servent de proies évaluent les degrés dans la menace de prédation et y réagissent avec flexibilité s'appelle l'hypothèse de l'évitement des prédateurs en fonction du risque. Nous avons procédé à une série d'expériences en nature et en laboratoire pour déterminer si les Chabots visqueux (*Cottus cognatus*) adoptent un comportement d'évitement des prédateurs en fonction de la menace qu'ils représentent en présence d'Ombles de fontaine (*Salvelinus fontinalis*) sympatriques. Dans une expérience en nature, nous avons mis en cage de petits et de gros ombles dans des habitats semblables et les chabots évitaient les zones contenant des ombles assez gros pour constituer une menace, mais ne cherchaient pas à éviter les zones où se trouvaient des ombles de petite taille qu'ils ne percevaient pas comme menaçants. Dans une série d'expériences en laboratoire, nous avons observé que les chabots avaient un comportement d'évitement des prédateurs lorsqu'ils pouvaient en avoir une perception visuelle. Cependant, lorsqu'ils ne pouvaient percevoir que des indices chimiques, ils réagissaient à la présence des prédateurs, peu importe la taille. Les indices de nature chimique semblent alerter les chabots à la présence de prédateurs dans le voisinage, mais la perception visuelle est indispensable à l'estimation précise des risques associés à ces prédateurs.

[Traduit par la Rédaction]

Introduction

Failure of a prey animal to respond to a predator increases the probability that it will be captured during an encounter with the predator. However, prey that exhibit antipredator behaviour upon encountering nonthreatening predators waste valuable time and energy that would otherwise be available for other activities (Sih 1987; Lima and Dill 1990). Consequently, there should be strong selection pressure to distin-

guish between predators that pose a risk and those that do not. The hypothesis that prey species assess and behave flexibly in response to different degrees of predation threat is known as the threat-sensitive predator avoidance hypothesis (Helfman 1989).

Several studies have examined threat-sensitive predator avoidance in aquatic organisms. For example, Helfman (1989) showed that threespot damselfish (*Stegastes planifrons*) showed more intense antipredator responses to a model trumpetfish (*Aulostomus maculatus*) when the predator model was closer, larger, or in a strike pose. Similarly, Wahle (1992) documented that large American lobsters (*Homarus americanus*) were less likely than small lobsters to seek refuge when encountering predatory sculpins (*Myoxocephalus anaetus*). In another study, Puttlitz et al. (1999) showed that as the size of Pacific treefrog (*Hyla regilla*) tadpoles relative to that of caged salamanders (*Ambystoma macrodactylum*) increased, the antipredator response of the tadpoles decreased. These changes in behaviour closely mirrored changes in actual vulnerability to the predator. Threat-sensitive predator avoidance has also been documented in mayflies (*Baetis bicaudatus*) (McIntosh et al. 1999) and freshwater isopods (Holomuzki and Short 1990), as well as other fishes (Wil-

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liams and Brown 1991; Bishop and Brown 1992; Hartman and Abrahams 2000) and amphibians (Horat and Semlitsch 1994; Kats et al. 1994; Anholt et al. 1996).

Despite the widespread occurrence of chemosensory responses to predators (reviewed in Kats and Dill 1998), few studies have examined the importance of chemical cues in threat-sensitive predator avoidance. In one study, Kats et al. (1994) documented that newt (*Taricha torosa*) larvae exhibited an ontogenetic shift in response to chemical cues from adult conspecific predators. Small newt larvae showed a strong response to chemical cues, but the response of older larvae was reduced or absent. The loss of the response coincides with the time when the adult newts leave the water. Horat and Semlitsch (1994) demonstrated that two species of frogs (*Rana lessonae* and *Rana esculenta*) showed a greater reduction in activity when exposed to greater concentrations of chemical cues from a predatory pike (*Esox lucius*). In another study, McIntosh et al. (1999) showed that mayflies (*Baetis bicaudatus*) can distinguish between different concentrations of trout odour in natural streams and that the intensity of their response varied according to the relative risk of predation.

Researchers have generally not tested whether the type or quality of information that prey animals can acquire from predators varies with the type of cues presented. From a threat-sensitivity perspective we can ask whether animals are better able to assess relative risk when they are presented with visual versus chemical cues. In one study, Mathis and Vincent (2000) showed that newt (*Notophthalmus viridescens*) larvae distinguished between predatory salamander (*Ambystoma tigrinum*) larvae and nonpredatory tadpoles (*Hyla chrysoscelis/versicolor*), but only when chemical cues were available. When visual cues were presented alone, the prey did not distinguish the degree of threat. Newt larvae responded to both predatory and nonpredatory heterospecifics as if they were predators. In another study, Hartman and Abrahams (2000) showed that fathead minnows (*Pimephales promelas*) exhibited stronger responses to chemical alarm cues when visual cues were limited.

In this study we examined threat-sensitive predator avoidance in slimy sculpins (*Cottus cognatus*), small benthic fish that are found in lakes and streams throughout North America. The sculpins we studied were from a stream in central Maine, where they co-occurred with predatory brook trout (*Salvelinus fontinalis*). Brook trout are common predators on slimy sculpin (Scott and Crossman 1979). Based on our field observations that slimy sculpins appear to avoid areas of the stream that contain large brook trout, we set up a field experiment to test whether sculpins in the wild avoid brook trout that are large enough to pose a significant predation threat. We also conducted a series of laboratory experiments designed to examine the role of visual versus chemosensory information in threat-sensitive predator avoidance.

Field survey

Methods

During the summer of 1998 we conducted a preliminary field survey to examine whether the distribution of sculpins overlapped that of brook trout in Spruce Mountain Brook (central Maine, U.S.A.). We used a Smith-Root backpack electroshocker to sample

all the fish that occurred in 1 × 1 m plots. We sampled a total of 450 plots. Samples were taken in all potential stream habitats.

Results

We captured 710 sculpins in 277 plots and 327 trout in 221 plots. Sculpins and trout were found together in 98 plots. We calculated the average size of sculpins in each plot. We used these averages as well as the information on the largest trout in each plot to construct Table 1, which shows the percentages of plots that contained sculpins of three different sizes, small (<42 mm total length), medium (42–66 mm total length), and large (>66 mm total length), for each of several size classes of trout. Sculpins were more likely to be absent from a plot when it contained large trout than when it contained either small trout or no trout. Moreover, small sculpins were less likely to be found in plots containing large trout than either small trout or no trout. These results suggest that sculpins may actively avoid areas that contain large trout and establish the possibility of threat-sensitive predator avoidance. However, we consider these data to be purely observational. Many factors, including water-flow parameters, substrate type, and food availability, may act alone or interact with predation risk to drive the pattern that we observed. Thus, we opted to use the data to guide our experiments but not to test the hypothesis directly.

Experiment 1: Field test of threat-sensitive predator avoidance

Methods

We conducted a field experiment to test the hypothesis of threat-sensitive predator avoidance. Specifically, we tested whether the presence of trout of different sizes would alter the spatial distribution of the sculpins in Spruce Mountain Brook in central Maine. We placed wire-mesh cages containing either a single large trout (standard length = 130.7 ± 17.6 mm; mean ± SD), a single small trout (standard length = 59.4 ± 7.6 mm), or nothing into Spruce Mountain Brook. Trout used in the experiment were collected from nearby locations in Spruce Mountain Brook just prior to the tests. The size of the mesh of the cages was such that it prevented any sculpins from entering the cages during the experiment. We set 27 blocks of three mesh cages, each of which was a roughly cylindrical wire-mesh enclosure 43 cm long × 22 cm in diameter. The locations of the small and large trout in the three cages of each block were randomized. All cages in each block were set at the same time in areas of similar habitats, leaving a minimum of 3 m between cages. Three hours after the cages had been set, we removed them and used an electroshocker to capture all sculpins within a 1 × 1 m grid, the center of which was the location of the cage. We measured the length of the sculpins and released them back into the brook.

We calculated the number of small, medium, and large sculpins in each plot. For each size class of sculpins we used a two-way analysis of variance (ANOVA) testing for treatment and block effects. We adjusted our *P* value to 0.0167 using a Bonferroni correction.

Results

A preliminary analysis indicated no significant block effects (all *P* > 0.25), therefore the block and error terms, mean squares, and degrees of freedom were pooled for the remaining comparisons. We found an effect of treatment for the small ($F_{[2,52]} = 9.65$, *P* < 0.001) but not the medium-

Table 1. Percentages of plots containing slimy sculpins (*Cottus cognatus*) of different sizes for each of several size classes of predatory brook trout (*Salvelinus fontinalis*).

	Sculpins				No. of grids
	None	Small (<42 mm total length)	Medium-sized (42–66 mm total length)	Large (>66 mm total length)	
Trout					
None	34.5	22.7	39.3	3.5	229
Small (<80 mm standard length)	32.3	20.5	45.7	1.6	127
Large (≥80 mm standard length)	55.2	11.5	31.35	2.1	96

sized ($F_{[2,52]} = 1.31$, $P = 0.279$) or large ($F_{[2,52]} = 0.491$, $P = 0.620$) sculpins (Fig. 1). Small sculpins avoided large trout but not small trout. These results demonstrate threat-sensitive predator avoidance under natural conditions.

Experiments 2a and 2b: Laboratory test of threat-sensitive predator avoidance using visual cues

Methods

We conducted a series of laboratory trials to test whether sculpins exposed to the sight of a brook trout in an adjacent tank would exhibit an antipredator response of a strength that reflected their vulnerability to the trout.

We collected sculpins and trout from Spruce Mountain Brook and maintained them in tanks in our laboratory at the University of Maine. Sculpins were fed daily with brine shrimp and trout were fed daily with brine shrimp, earthworms, and *Tubifex*. All fish were maintained at room temperature (approximately 19°C) on a 14 h light : 10 h dark cycle.

We set up experimental observation tanks (37 L; 50 × 30 × 25 cm) so that two adjacent tanks were visually separated by a removable barrier. All tanks were filled with fresh well water and each was aerated with a single airstone at the back of the tank. The bottom of each tank was covered with a thin layer of sand. One tank in each pair had a centrally located shelter object consisting of half a broken flower pot.

For expt. 2a we identified 20 small, 20 medium-sized, and 20 large sculpins, and for expt. 2b we identified 20 small and 20 medium-sized sculpins. We placed one fish in each observation tank. Observations were completed after the sculpins had been undisturbed for at least 1 day. Each sculpin was tested twice, once with a predator present and once with a predator absent. During the “predator-absent” trials, the tanks adjacent to the sculpins did not contain a trout. Both the predator-absent and predator-present trials were completed on the same day, with the order of exposure to the two stimuli randomized. Two to 6 h elapsed between trials. In expts. 2a and 2b we used trout with a standard length of 143.8 ± 8.0 (mean ± SD) and 96.5 ± 10 mm, respectively. In expts. 2a and 2b we kept the size of the sculpins the same while reducing the size of the trout used as predators. This allowed us to test whether sculpins would exhibit a response only to those trout that posed a predation threat. Because we had only a limited number of large sculpins, they were used only in expt. 2a.

During each trial an observer was positioned approximately 1.5 m from the tank. For 10 min the observer recorded the number of short moves (including all that were <2 body lengths) and the number of long moves (including all that were >2 body lengths) made by the sculpins. In addition, shelter use was recorded at 30-s intervals. After 10 min, the barrier between the pair of tanks was removed and the sculpins were observed for an additional 10 min.

During the post-stimulus period, we also recorded short moves, long moves, and shelter use.

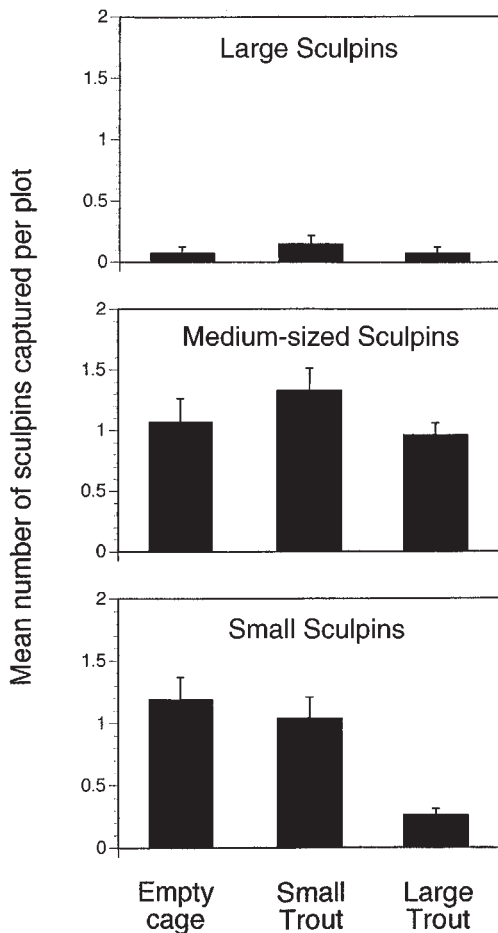
For all trials we calculated the change (post-stimulus minus pre-stimulus) in number of short moves and long moves for sculpins in both the predator-absent and predator-present trials. Our previous work had shown that slimy sculpins decrease activity when exposed to a predation threat (Bryer et al. 2001). Shelter use was rare and hence was dropped from the analysis. We conducted a series of paired *t* tests to determine whether each size class of sculpins responded differently in terms of change in short moves or long moves in the predator-absent versus predator-present conditions. We then used independent *t* tests to compare among the size treatments the change in numbers of short and long moves made by the sculpins following exposure to the brook trout. For expt. 2a, the familywise error rate was assessed and controlled using the modified Bonferroni test following Keppel (1982). The modified Bonferroni test specifies that corrections to the familywise error rate be introduced only when the number of comparisons exceeds $k - 1$, where k is the number of treatments (Keppel 1982). In total, there were 3 treatments in this experiment. Since the analysis was restricted to 3 preplanned comparisons based on specific a priori predictions, the probability of rejection (P) was set at 0.033 for each comparison (Keppel 1982). For expt. 2b, a modified Bonferroni correction was not needed because we completed only one preplanned comparison between small and medium-sized sculpins. In this and subsequent tests we used one-tailed tests because we predicted that fish would decrease, not increase, activity upon exposure to the predator. Furthermore, we predicted that smaller sculpins would show a more intense response than larger fish (Mathis et al. 1993; Chivers and Smith 1998).

Results

In expt. 2a, small and medium-sized sculpins exhibited a significantly greater reduction in both short and long moves in the predator-present condition than in the predator-absent condition ($P < 0.05$ for all comparisons; Fig. 2). Large sculpins failed to respond differently in terms of short or long moves in the presence versus absence of the predator. Direct comparisons between treatments in terms of changes in number of short moves revealed a significant difference between small and large ($P = 0.002$) and between medium-sized and large ($P = 0.005$) sculpins but not between small and medium-sized ($P = 0.092$) sculpins. Direct comparisons between treatments in terms of changes in number of long moves revealed P values of 0.036 (small vs. large sculpins), 0.008 (medium-sized vs. large sculpins), and 0.22 (small vs. medium-sized sculpins).

In expt. 2b we found a significant difference in short moves ($P = 0.047$, but not long moves, $P = 0.063$) between the predator-present and predator-absent condition for small sculpins (Fig. 3). There was no significant difference in short

Fig. 1. Numbers (mean + SE) of small, medium-sized, and large slimy sculpins (*Cottus cognatus*) captured in areas with cages holding small brook trout (*Salvelinus fontinalis*), large trout, or nothing. Cages were set for 3 h. Fewer small sculpins were captured in areas with large trout (see the text for details).



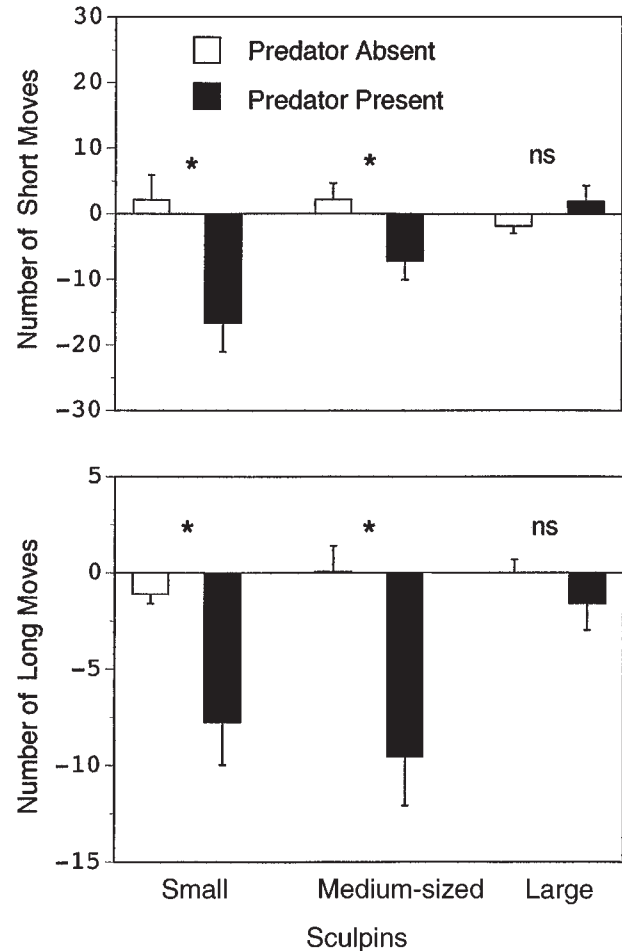
or long moves between the predator-present and predator-absent condition for medium-sized sculpins ($P > 0.05$). Direct comparisons between small and medium-sized sculpins revealed a significant difference in terms of changes in number of short moves ($P = 0.028$) but not changes in number of long moves ($P = 0.34$). The results of these experiments show that sculpins exhibit threat-sensitive predator avoidance when exposed to only the sight of a brook trout in an adjacent tank.

Experiment 3: Laboratory test of threat-sensitive predator avoidance using chemical cues

Methods

We conducted a series of laboratory trials to test whether sculpins exposed to chemical cues from a brook trout would exhibit an antipredator response of a strength that reflected their vulnerability to the trout. Our previous work established that chemical cues from brook trout elicit an anti-predator response from sculpins (Bryer et al. 2001). The trout used in this experiment were obtained from the Enfield State Fish Hatchery (Enfield, Maine). Trout were maintained on a diet of commercial pellets and brine shrimp.

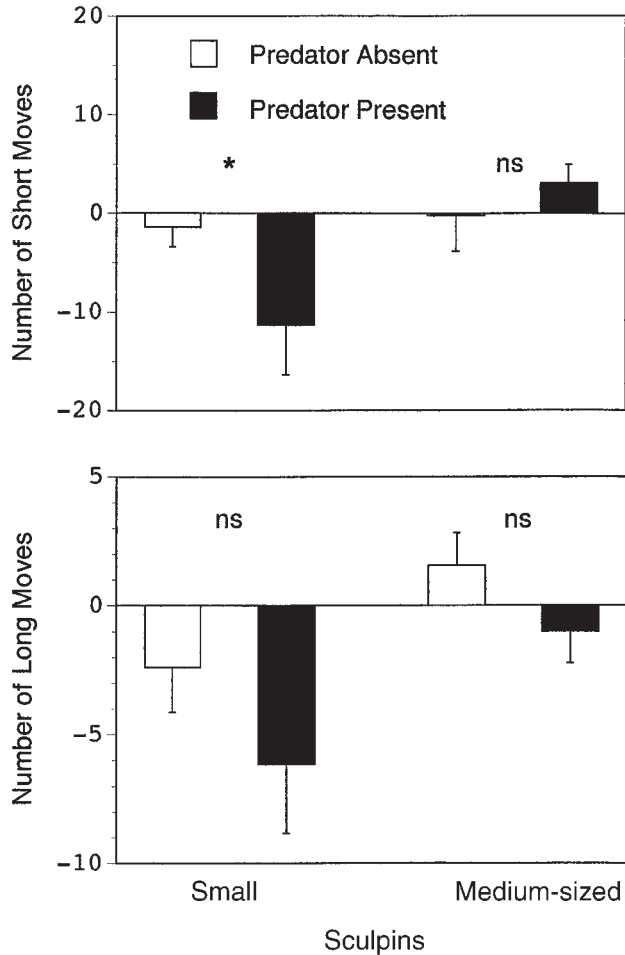
Fig. 2. Changes (mean + SE) in numbers of short moves and long moves by small, medium-sized, and large sculpins following removal of the barrier in the presence versus absence of a predatory brook trout. (* denotes a significant difference in change in activity in the presence versus absence of the predator; ns, not significant; see the text for details.)



We used the same general methodology as in the previous laboratory experiment. We observed the numbers of short moves and long moves performed by individual sculpins for 10 min. We then introduced chemical stimuli from either small or large trout or a blank control and then observed behaviour for an additional 10 min. Stimuli were injected into the observation tanks through airline tubing located approximately 1.5 m from the tank. We conducted a total of 180 trials. The three different size classes of sculpins (small, medium, and large) were exposed to the three different stimuli (control water, chemical stimuli from large trout, and chemical stimuli from small trout). For all combinations, a sample size of 20 was used.

We prepared the trout stimulus in the following manner. A single large trout was placed in a 37-L glass collection chamber and left undisturbed for approximately 24 h. The chamber was aerated but not filtered. Trout were not fed in the collection chambers. We used 60 mL of stimulus for each trial. Five different trout (standard length = 211.5 ± 8.2 mm; mean \pm SD) were used to prepare the large-trout stimulus. To prepare the small-trout stimulus we used several small trout (standard length = 75.2 ± 9.8 mm) whose total mass matched that of the large trout. Hence, we exposed sculpins to the odour of either a single large trout or several small trout that had the same mass as the large trout.

Fig. 3. Changes (mean + SE) in numbers of short moves and long moves by small and medium-sized sculpins following removal of the barrier in the presence versus absence of a predatory brook trout. (* denotes a significant difference in change in activity in the presence versus absence of the predator; ns, not significant; see the text for details.)



We calculated the change (post-stimulus minus pre-stimulus) in numbers of short and long moves by sculpins exposed to control water or stimuli from small or large trout. We used these values to perform a two-way ANOVA examining for effects of treatment (i.e., trout size), sculpin size, and interactions between treatment and sculpin size.

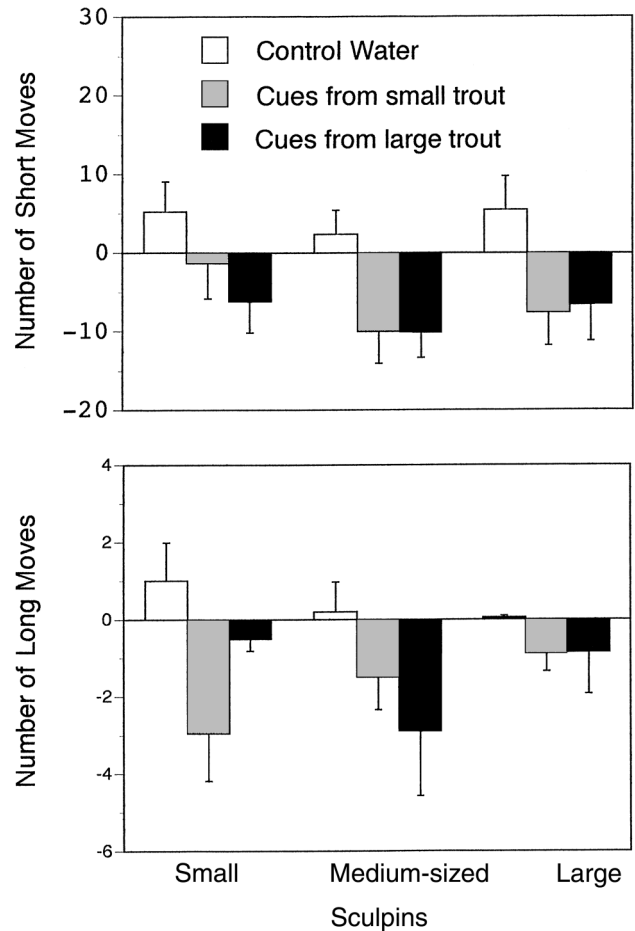
Results

We found significant treatment effects for both short ($F_{[2,171]} = 7.970, P < 0.001$) and long moves ($F_{[2,171]} = 4.509, P = 0.012$; Fig. 4). However, there were no effects of sculpin size (short moves, $F_{2,171} = 1.223, P = 0.297$; long moves, $F_{[2,171]} = 0.648, P = 0.524$) nor were there any interactions between sculpin size and treatment (short moves, $F_{[4,171]} = 0.235, P = 0.918$; long moves, $F_{[4,171]} = 1.439, P = 0.223$).

Discussion

Our experiments demonstrated that slimy sculpins can exhibit threat-sensitive predator avoidance when exposed to only visual cues, but not only chemical cues, from a predat-

Fig. 4. Changes (mean + SE) in numbers of short moves and long moves by small, medium-sized, and large sculpins following addition of chemical stimuli from small brook trout or large brook trout or a blank control.



tory trout. The ability to exhibit threat-sensitive predator avoidance has important implications. By responding to predators that pose a threat, but not to those that do not, sculpins can avoid wasting valuable time and energy that could be directed towards other activities (Lima and Dill 1990).

In our preliminary field survey we observed that sculpins were more likely to be absent from plots containing large trout than from plots containing small trout, and that small sculpins were less likely to be found in plots containing large trout than from plots containing small trout or no trout. These results indicate that sculpins may have been exhibiting threat-sensitive predator avoidance. However, conclusions based on the field-survey data should be drawn cautiously. Other factors, such as a preference for a particular water depth, water speed, type of substrate, or available food, could act alone or interact with predation risk to drive the pattern that we observed. Nevertheless, the results of our field experiment clearly demonstrate that sculpins can exhibit threat-sensitive predator avoidance under natural conditions. In the field experiment we found that small sculpins avoided cages that contained large trout but did not avoid cages that held small trout. Similarly, neither medium-sized nor large sculpins avoided cages with small or large trout in

the field. These results indicate that responses to trout are not generalized, but instead are graded to reflect the degree of threat posed by the predator. Our data emphasize the importance of measuring individual behaviour when attempting to understand distributional patterns.

The trout that we used in the field study were wild trout that had been collected just prior to the experiment. We do not know the diet of these fish. In some predator-prey systems the diet of the predator has been shown to be an important determinant of the strength of the antipredator response (reviewed in Chivers and Mirza 2001). Prey may respond more strongly to cues from predators fed conspecifics of the prey than to cues from the same predators fed another diet. This means that avoidance of large trout, but not small trout, could be partially mediated through the effects of diet cues if large trout had eaten sculpins and small trout had not. However, Bryer et al. (2001) have shown that sculpins from Spruce Mountain Brook respond to brook trout cues regardless of the diet of the trout, and that the intensity of the responses of the sculpins does not vary with changes in the diet of the trout.

In our laboratory experiments, where we exposed sculpins to only the sight of the predator, we obtained results similar to those in the field experiment. In expt. 2a, both small and medium-sized sculpins, but not large sculpins, responded to the trout. When we decreased the size of the predator in expt. 2b, we found that medium-sized sculpins no longer responded to the predator, while small sculpins continued to respond. Our experimental design did not allow us to determine whether the responses of sculpins to the sight of a large trout represented a generalized response to any large fish or a specific response to predatory brook trout. However, no other fish species are found in Spruce Mountain Brook, hence an antipredator response to any large fish would be adaptive.

When we exposed sculpins of different sizes to only chemical cues from the predator, we found no evidence of threat-sensitive predator avoidance. The sculpins showed a clear antipredator response to cues from the trout. However, sculpins of all size classes responded to the trout cues, regardless of the size of the trout. The lack of a differential response may indicate that trout odour does not differ predictably with size. In some ways we may consider that sculpins are wasting their time and energy responding to chemical cues from small trout that pose no threat. However, responding to a nonthreatening predator is likely less costly than failing to respond to a predator that poses a threat. Additional studies should address the different roles played by chemical and visual cues in risk assessment in other predator-prey systems.

We should emphasize that chemical cues from trout probably provide important information that allows sculpins to reduce their risk of predation. Chemical cues would warn the sculpins that there is a trout in the vicinity. This information is valuable even if information regarding the actual threat posed by the trout is lacking. It may be common for a sculpin to be alerted to the presence of a trout before the trout is seen. In this way chemical cues may provide early warning of the presence of the predator (Chivers and Smith 1998; Kats and Dill 1998). Fine-tuning of risk assessment would then require the prey to see the predator.

Additional studies are needed if we are to understand the role of chemical cues in threat-sensitive predator avoidance. Horat and Semlitsch (1994) and McIntosh et al. (1999) have documented that tadpoles and mayflies show stronger antipredator responses when the concentration of chemical cues from predators is increased. Our experiment was designed differently than these studies. We did not manipulate the concentration of predator cues. We attempted to keep the concentration of cues constant by using an equal mass of small and large trout to produce the stimulus. If sculpins can distinguish the degree of threat according to the odour of different-sized predators, they should have responded differentially to the two types of trout cues, even though these were at the same concentration. We found no evidence of a differential response to the two size classes of trout. It is possible that sculpins would have exhibited a stronger antipredator response if we had increased the perceived threat by increasing the concentration of cues as opposed to increasing the perceived threat by manipulating the size of the predator that produced the cues. Additional studies should be carried out to test whether other species (including mayflies and tadpoles) can distinguish between predators of different sizes that pose different degrees of threat as opposed to simply detecting a difference in the concentration of cues.

Most studies of threat-sensitive predator avoidance have shown that prey animals exhibit stronger antipredator responses as the perceived degree of threat increases. Increasing the level of risk can be accomplished by using several types of experimental manipulations. The most common approach has been to alter the size and (or) age of either the predator or the prey (e.g., Helfman 1989; Wahle 1992; Kats et al. 1994). Other possible approaches include altering the habitat to make the prey more difficult to capture or making alternative prey available so as to direct predation away from the preferred prey. Future studies should verify that changes in behavioural responses of prey to different degrees of threat accurately mirror changes in actual vulnerability to predation (Puttlitz et al. 1999). A knowledge of the evolutionary history of the coexistence of predator and prey should allow us to predict how tightly coupled changes in behaviour will mirror changes in vulnerability.

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