

LEARNED RECOGNITION OF PREDATION RISK BY
Enallagma DAMSELFLY LARVAE (ODONATA,
ZYGOPTERA) ON THE BASIS OF CHEMICAL CUES

BRIAN D. WISENDEN,* DOUGLAS P. CHIVERS, and
R. JAN. F. SMITH

Department of Biology
University of Saskatchewan
112 Science Place
Saskatoon, SK, Canada S7N 5E2

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Abstract—We studied two populations of damselfly larvae (*Enallagma boreale*): one population cooccurred with a predatory fish (northern pike, *Esox lucius*); the other did not. Damselflies that cooccurred with pike adopted antipredator behavior (reduced activity) in response to chemical stimuli from injured conspecifics, and to chemical stimuli from pike, relative to a distilled water control. Damselflies from an area where pike do not occur responded only to chemical stimuli from injured conspecifics. In a second set of experiments, we conditioned pike-naïve damselflies to recognize and respond to chemical stimuli from pike with antipredator behavior. Damselfly larvae that were previously unresponsive to pike stimuli learned to recognize pike stimuli after a single exposure to stimuli from pike and injured damselflies or pike and injured fathead minnows (*Pimephales promelas*). The response to injured fathead minnows was not a general response to injured fish because damselfly larvae did not respond to chemical stimuli from injured swordtails (*Xiphophorus helleri*), an allopatric fish. Taken together, these data suggest a flexible learning program that allows damselfly larvae to rapidly acquire the ability to recognize local predation risk based on chemical stimuli from predators, conspecifics, and heterospecific members of their prey guild.

Key Words—Injury-released chemical alarm pheromone, alarm signal, antipredator behavior, predator-prey, learned predator recognition, cross-species reactions, prey guild, damselfly, *Enallagma boreale*, fathead minnow, *Pimephales promelas*, northern pike, *Esox lucius*.

*To whom correspondence should be addressed at Center for Ecology, Evolution and Behavior, Morgan School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506-0225.

INTRODUCTION

Chemical stimuli are an important source of information for assessing predation risk for animals living in aquatic habitats, especially at night, in turbid water, or in highly structured habitat when visual information is unavailable (Hara, 1992; Smith, 1992; Dodson et al., 1994).

The chemical ecology of predator-prey interactions involving odonates remains relatively unexplored. Odonate larvae (dragonflies and damselflies) live in structured aquatic habitats and are subject to predation by fish (Morin, 1984; Pierce et al., 1985; Dixon and Baker, 1988; Henrikson, 1988; McPeck, 1990a, b; Johansson and Samuelsson, 1994) including northern pike, *Esox lucius* (Allen, 1939; Lawler, 1965). Juvenile pike readily eat damselflies in the laboratory (personal observation).

Individuals from populations that frequently encounter predators typically exhibit stronger antipredator responses than individuals from populations that rarely experience predators (Giles and Huntingford, 1984; Magurran, 1986; Mathis et al., 1993; Gelowitz et al., 1993; Matity et al., 1994; Chivers et al., 1995a). Population differences in antipredator behavior could result from evolved, genetic differences between populations in response to differing selection pressures, such as the presence or absence of a predator species (e.g., Seghers, 1974; Seghers and Magurran, 1995), or from learned recognition of a predator species by its prey (Chivers and Smith, 1994a). European minnows (*Phoxinus phoxinus*), fathead minnows (*Pimephales promelas*), and brook stickleback (*Culaea inconstans*) learn to associate chemical cues from injured conspecifics with those from a novel predator (Göz, 1941; Magurran, 1989; Mathis and Smith, 1993a; Chivers and Smith, 1994a, b; Chivers et al., 1995b) or from risky habitats (Chivers and Smith, 1995). It is not known whether learned predator recognition occurs in invertebrates.

Members of a prey guild are species that share habitat and predators. Injury-released chemical cues produced by one species indicate predation risk to all species in the guild (Snyder, 1967). Examples of cross-species responses to injury-released chemical cues among prey guild members are known for gastropods (Stenzler and Atema, 1977) and some fishes (Smith et al., 1991; Mathis and Smith, 1993b; Chivers and Smith, 1994c; Chivers et al., 1995a; Wisenden et al., 1994, 1995a). It has not yet been tested whether animals can learn to recognize novel predator cues by associating them with injury-released chemical cues from heterospecifics.

In this study we quantify foraging activity of damselfly larvae (Odonata, Zygoptera) before and after exposure to test stimuli in order to test four hypotheses. First, we test if damselflies decrease their activity in response to injured conspecifics, a reliable indicator of predation risk. Reduced movement and foraging are common responses of prey animals, including damselflies, to

the presence of predators (Ware, 1973; Heads, 1985; Pierce et al., 1985; Convey, 1988; Dixon and Baker, 1988; McPeck 1990a, b; see reviews by Lima and Dill, 1990; Johnson, 1991). To verify that the response of damselflies to stimuli from injured conspecifics represents antipredator behavior, we exposed damselflies to chemical stimuli from a known predator, northern pike. We used two populations of damselfly larvae, one that cooccurs with pike and one that does not.

The second hypothesis tested in this study is that damselflies that cooccur with pike should decrease foraging activity in response to pike stimuli, whereas damselflies that do not cooccur with pike should not respond to pike stimuli.

Third, we test to see if damselflies respond with antipredator behavior to alarm pheromones from injured heterospecific prey species (fathead minnows) from the same prey guild.

Fourth, we test to see if an antipredator response to a chemical cue can be acquired by learning. We present naive damselfly larvae with a novel predator cue (northern pike) in combination with chemical stimuli either from injured damselflies or from injured fathead minnows.

METHODS AND MATERIALS

In December 1994 we collected damselfly larvae from two locations in south-central Saskatchewan, Canada. Feedlot Pond is located on the University of Saskatchewan campus in Saskatoon and does not contain northern pike. Pike Lake is an oxbow lake of the South Saskatchewan River and contains pike and other species. Damselflies were maintained in 20-liter aquaria at approximately 18°C on a 12L:12D-hr photoperiod and were fed daily with brine shrimp nauplii (*Artemia franciscana*). Damselflies were maintained in the laboratory for a minimum of 2 weeks prior to testing.

All damselfly larvae were keyed to *Enallagma boreale* using Merritt and Cummins (1984) and Walker (1953). Species identification of *Enallagma* based on larval characteristics can be unreliable. Adult male damselflies emerging from the two study sites were collected in June 1995 and identified on the basis of the morphology of male genitalia using Walker (1953). Of 22 male *Enallagma* collected from Feedlot Pond, 15 were *E. boreale* and 7 were *E. cyathigerum*. Of 45 male *Enallagma* collected from Pike Lake, 44 were *E. boreale* and 1 was *E. cyathigerum*. Because the larvae of *E. boreale* and *E. cyathigerum* are morphologically identical (McPeck, 1990b), animals tested in this study could have included some individuals of *E. cyathigerum*. Because cross-species reactions are evident (see results of experiment 2), we believe the possibility that more than one species of *Enallagma* were used in these experiments is unlikely to have affected the conclusions.

Experiment 1: Population Differences. Thirty damselflies from each population were placed individually into 5-liter round opaque plastic containers (diameter, 18 cm) that contained 2 liters of dechlorinated tap water. No substrate or structure was provided. Mean \pm SD length of the 60 damselflies (measured from tip of the head to tip of the abdomen, excluding caudal lamellae) was 17.0 ± 7.2 mm. Experiments began after the damselflies had acclimated to the test chambers for a minimum of 36 hr. Prior to the experiment, we did not feed the damselflies after placing them into the testing chambers. We began by injecting 5 ml of a standard concentration of brine shrimp culture (approximately 1200 shrimp nauplii) into each container. We waited 5 min before conducting observations to allow the damselflies to adjust to the presence of the observer and establish a regular pattern of feeding behavior. We recorded the frequency of three conspicuous behaviors associated with foraging (feeding strikes, head turns, and walking movements) for 5 min before and 5 min after the injection of one of three test stimuli: (1) 10 ml of distilled water (control stimulus), (2) 10 ml of pike stimulus, or (3) 10 ml of water containing stimuli of injured conspecifics.

A feeding strike was scored every time a damselfly extended and retracted its prementum (feeding apparatus that bears mandibles). A head turn was recorded whenever a damselfly shifted its head position by an arc of more than 22.5° ($1/4$ of a 90° arc) in any direction. A walking movement was a short walk that entailed the lifting of a tarsus (foot) and planting it in a new location. Bouts of walking not separated by more than 1 sec were counted as a single "move." Typically, damselflies used short walks of one to several steps while feeding on brine shrimp. Moves greater than one body length ($N = 1$ in 900 min) and undulatory swimming ($N = 6$ in 900 min) were rare.

We tested 30 individuals from each population of damselflies, 10 in each of the three treatment conditions (control, pike, and conspecific). For each trial we calculated the change in the number of feeding strikes, head turns, and walking movements by subtracting the number performed before exposure to the stimulus from the number performed after exposure to the stimulus. For each damselfly population (and in subsequent experiments) we used separate Kruskal–Wallis one-way analysis of variance tests to compare the significance in the change in each foraging behavior (Siegel and Castellan, 1988). These analyses were followed by post hoc nonparametric multiple comparisons with alpha level adjusted for nonindependent pairwise comparisons (Siegel and Castellan, 1988). One-tailed statistical tests were used because we predicted that damselflies would reduce the frequency of conspicuous behavior in response to water containing stimuli from pike or injured conspecifics.

We prepared the conspecific stimuli by crushing two damselflies (one from each population), with a mortar and pestle and then adding 20 ml of distilled water. We used 10 ml from each 20-ml solution of conspecific stimulus to test one damselfly from each population. In all cases the conspecific stimulus was used within 15 min of preparation.

To ensure that damselflies in our study did not respond to stimuli in the pike's diet (Mathis and Smith, 1993a; Brown et al., 1995), we fed the pike a diet of swordtails for three feedings (once every 5 days) prior to collecting the stimulus. Approximately 12 hr after the final feeding, the pike (fork length, 18 cm) was placed into a clear plastic collection chamber (26 × 8 × 8 cm) that contained 1200 ml of dechlorinated tap water. The collection chamber was aerated but not filtered. After 3 days the pike was removed from the chamber and the pike stimulus water was frozen at approximately -20°C until needed. Previous studies have shown that the use of multiple pike to generate pike stimulus is no better than using a single pike (Gelowitz et al., 1993).

Experiment 2: Learned Recognition of a Novel Predator Cue. Damselfly larvae were collected from Feedlot Pond in December 1994, transferred to laboratory aquaria, and maintained at 18°C on newly hatched brine shrimp for at least a week before being used in experiments. Three days before the experiment began, one damselfly larva was placed into each of 30 5-liter plastic containers filled with 2 liters of dechlorinated tap water. On Day 1 of the experiment, each larva was tested for its response to one of three sets of paired stimuli: (1) 10 ml of pike stimulus combined with 5 ml of water containing injured conspecific damselflies, (2) 10 ml of pike stimulus combined with 5 ml of skin extract from fathead minnows, or (3) 10 ml of pike stimulus combined with 5 ml of distilled water (Control). Damselfly stimulus was made by crushing two damselflies in 10 ml of distilled water to produce two 5-ml aliquots for two trials. Pike stimulus was prepared as described for experiment 1. Fathead minnow skin extract was prepared by killing two minnows by a blow to the head and making 25 vertical superficial cuts on each side of the body using a razor blade. Each fish was rinsed with 5 ml of distilled water. We prepared stimulus from pairs of fish and used the resulting 10 ml of rinse water as stimulus for two trials. Thus one minnow was used per trial. The stimulus was used immediately. The mean \pm SD standard length of fish used as stimulus was 3.4 ± 0.2 cm.

We began each trial by injecting 5 ml of live brine shrimp into the center of the container. After 5 min, we recorded the frequency of foraging behavior for 5 min using the same criteria as described for experiment 1. After 5 min, we gently introduced one of the test solutions of paired stimuli into the container and monitored foraging behavior for another 5 min. At the end of Day 1, we emptied each container and replaced the water with fresh dechlorinated tap water.

We repeated the same procedure the next day using the same damselflies. The protocol was similar to the first day except that no additional stimuli accompanied the 10 ml of pike stimulus.

Mean \pm SD length of the 10 damselfly larvae used for each treatment in this experiment was as follows: damselfly, 14.3 ± 0.9 mm; fathead minnow, 15.2 ± 0.9 mm; and distilled water (control), 15.2 ± 1.3 mm.

Experiment 3: Specificity of Response to Fish Alarm Cues. In this experiment, we exposed damselflies to skin extract of swordtails (*Xiphophorus helleri*) to test if the response to fathead minnow skin was specific to fathead minnows or a general response to chemical stimuli from injured fish. Swordtails are tropical fish, allopatric to the damselflies used in this experiment, and thus unfamiliar to the test animals. Swordtails are phylogenetically unrelated to fathead minnows and lack the specialized epidermal alarm substance cells present in fathead minnows (Smith, 1992).

The experimental protocol was similar to the first two experiments. We used damselflies from Feedlot Pond (where pike are absent). One damselfly was placed into each of 30 5-liter containers 3 days before the experiment began. At the start of a trial, 5 ml of live brine shrimp were added to the center of the container. After waiting 5 min, we recorded the number of feeding strikes, head turns, and walking movements for 5 min. Then we added one of three stimuli: (1) 15 ml of chemical stimuli from an injured conspecific damselfly, (2) 15 ml rinse of chemical stimuli from an injured swordtail, or (3) 15 ml of distilled water. The frequency of foraging behaviors was recorded for another 5 min. Mean \pm SD length of the 10 damselfly larvae used for each treatment in this experiment was as follows: damselfly, 16.3 ± 0.9 mm; swordtail, 15.6 ± 1.6 mm; and distilled water, 16.2 ± 1.9 mm.

Damselfly stimulus was prepared as described for the first experiment except 30 ml were used instead of 20 ml to prepare stimulus for each set of two trials. Swordtail skin extract was prepared by killing each fish by a blow to the head, making 25 vertical cuts on each side of its body, and rinsing with 15 ml of distilled water. One swordtail was used per trial. Mean \pm SD standard length of the 10 swordtails used in the experiment was 4.0 ± 0.28 cm.

RESULTS

Experiment 1: Population Differences. For damselflies that do not cooccur with pike, there was a significant effect of the treatments on feeding strikes [Kruskal-Wallis (KW) = 8.68, $P < 0.02$], head turns (KW = 13.50, $P < 0.01$), and walking movements (KW = 14.26, $P < 0.001$). Damselflies reduced their frequency of feeding strikes, head turns and walking movements in response to conspecific stimuli relative to pike stimuli or distilled water (Figure 1; $P < 0.05$ for all comparisons). There was no significant difference in the change in feeding behavior between the distilled water and the pike stimulus treatments ($P > 0.15$ for all comparisons). Slight increases occurred in control trials because some brine shrimp that settled during the first 10 min were resuspended upon introduction of the test stimulus thus stimulating foraging activity.

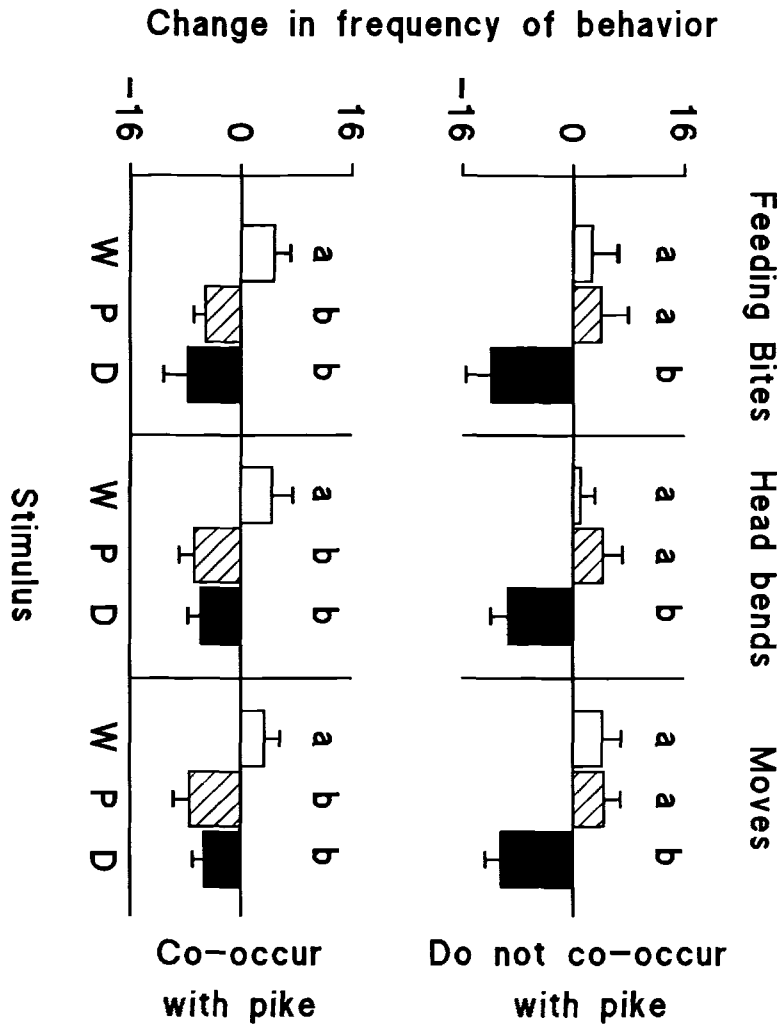


FIG. 1. Mean (\pm SE) change in frequency of feeding strikes, head turns, and walking movements by damselflies that cooccur with pike and those that do not, following exposure to a control of distilled water (W; open bars), pike stimulus (P; hatched bars), or injured conspecific damselflies (D; solid bars). For each behavior, bars with different letters are significantly different from others in that population (KW post hoc multiple-comparison test, $P < 0.05$).

For the population that cooccurs with pike, there was a significant overall effect of the treatments on feeding strikes (KW = 9.58, $P < 0.01$), head turns (KW = 7.98, $P < 0.02$), and walking movements (KW = 12.51, $P < 0.01$). Damselflies reduced their frequency of feeding strikes, head turns, and walking movements in response to conspecific or pike stimuli relative to distilled water (Figure 1; $P < 0.05$ for all comparisons). There was no significant difference between the response to conspecific and pike stimuli ($P > 0.15$ for all comparisons).

Experiment 2: Learned Recognition of a Novel Predator Cue. Chemical stimuli presented to damselflies along with pike stimuli had a significant overall effect on feeding strikes on Day 1 (conditioning trials) of the experiment (KW = 12.43, $P < 0.01$), head turns (KW = 9.23, $P < 0.01$), and walking movements (KW = 9.79, $P < 0.01$). Damselflies performed significantly fewer feeding strikes ($P < 0.05$), head turns ($P < 0.05$), and walking movements ($P < 0.01$) after exposure to stimuli from pike plus injured damselfly than after exposure to stimuli from pike plus distilled water (Figure 2). Exposure to fathead minnow skin extract along with pike stimuli resulted in a significant decrease in the frequency of feeding strikes, head turns, and walking movements compared to control trials (Figure 2; $P < 0.05$ for all comparisons). There were no significant differences between the damselfly and the minnow treatments ($P > 0.30$).

When the same damselflies were subsequently presented with pike stimuli alone on Day 2 (test trials), there was a significant difference among groups in the frequency of feeding strikes (KW = 9.25, $P < 0.01$), head turns (KW = 9.05, $P < 0.02$), and walking movements (KW = 17.43, $P < 0.001$). Pairwise comparisons between groups showed that for each behavior, activity was significantly lower for damselflies previously exposed to stimuli from pike plus injured damselfly or pike plus injured minnow compared to control trials ($P < 0.05$). There was no significant difference between damselflies previously conditioned with stimuli from injured damselflies and damselflies previously conditioned with fathead minnow skin (Figure 2; $P > 0.30$). Therefore, damselfly larvae that were previously unresponsive to pike stimuli learned to recognize pike stimuli after a single exposure to stimuli from pike and injured damselflies or pike and injured fathead minnows.

Experiment 3: Specificity of Response to Fish Alarm Cues. There was a significant overall effect of the test stimuli on the frequency of feeding strikes (KW = 13.8, $P < 0.01$), head turns (KW = 19.3, $P < 0.001$), and walking movements (KW = 15.0, $P < 0.001$). After exposure to injured damselflies, the frequency of all three behaviors was significantly reduced ($P < 0.05$ for all comparisons) in comparison with either distilled water or swordtail skin extract (Figure 3). There was no significant difference in damselfly behavior between the distilled water and the swordtail treatments ($P > 0.30$ for all comparisons).

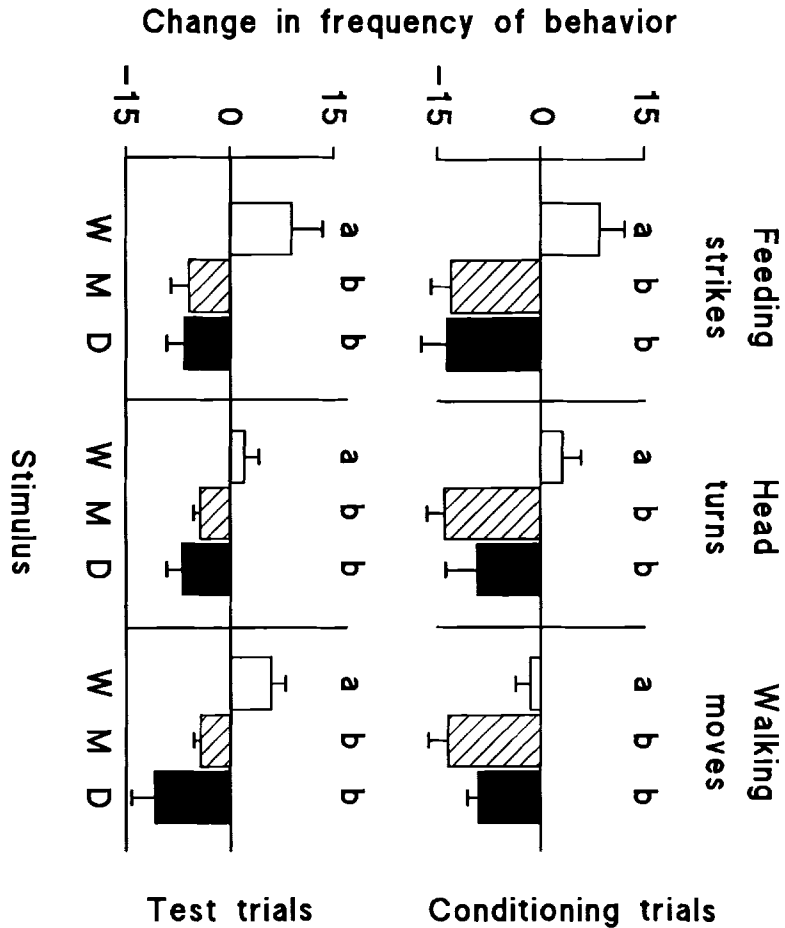


FIG. 2. Right: Mean (\pm SE) change in frequency of feeding strikes, head turns, and walking movements for damselflies presented with chemical stimuli from pike and distilled water (W; open bars), pike and injured fathead minnows (M; hatched bars), or pike and injured conspecific damselflies (D; solid bars). Left: Mean (\pm SE) change in frequency of feeding behaviors for the same damselflies when presented later with chemical stimuli from pike alone. Bars denote conditioning stimuli described above. For each behavior, bars marked with different lowercase letters are significantly different from others in that set of trials (KW post hoc multiple-comparison test, $P < 0.05$).

Damselflies did not appear to recognize chemical stimuli from swordtail skin as an indicator of danger, and thus it is not likely that the response to fathead minnow skin extract in experiment 2 represented a general response to stimuli released from injured fish.

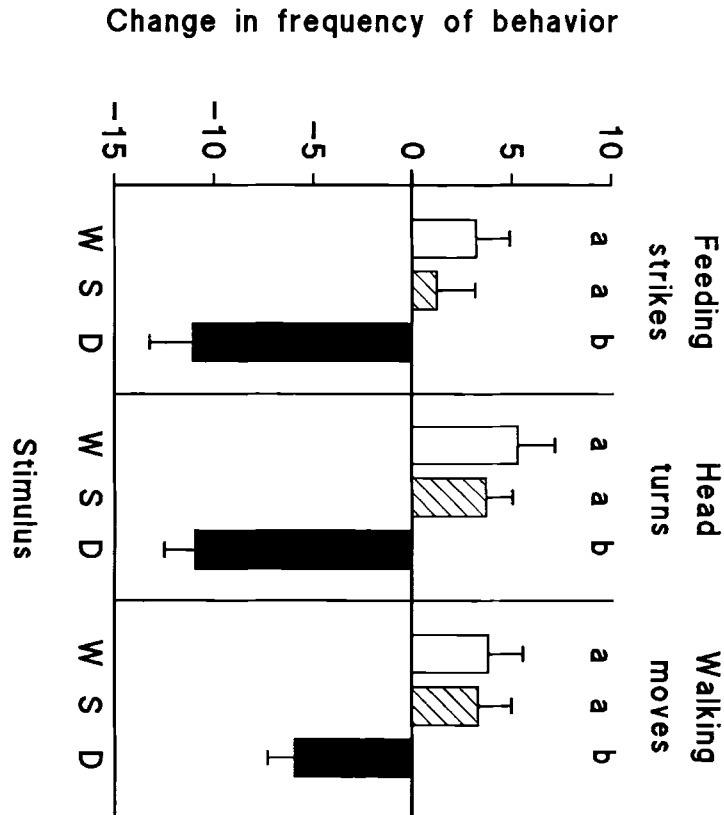


FIG. 3. Mean (\pm SE) change in frequency of feeding strikes, head turns, and walking movements for damselflies presented with distilled water (W; open bars), chemical stimuli from injured swordtails (S; hatched bars), or chemical stimuli from injured conspecific damselflies (D; solid bars). For each behavior, bars marked with different lowercase letters are significantly different (KW post hoc multiple-comparison test, $P < 0.05$).

DISCUSSION

To our knowledge this is the first study to demonstrate that a member of the order Odonata responds to injured conspecifics with an antipredator response. Damselflies from both populations decreased activity in response to stimuli from injured conspecifics alone. We do not know if the antipredator response to stimuli from injured conspecifics is species-specific or if it is a general response to damaged odonate or insect tissue. Because we prepared the stimulus from whole damselflies, we do not know whether or not conspecifics are sensitive only to stimuli from a particular part of the damselfly body. In ostariophysan

fishes such as fathead minnows, specialized epidermal club cells contain alarm pheromone (Smith, 1992). In mud snails (*Nassarius obsoletus*), the foot, viscera, and blood all elicit an alarm reaction from conspecifics (Atema and Stenzler, 1977).

Predator recognition is of obvious survival value. Early recognition of predation risk allows animals to adopt cryptic behavior and decrease the chances of their being detected and attacked by a predator (Snyder, 1967; Hews, 1988; Mathis and Smith, 1993c; Lima and Dill, 1990; Wisenden et al., 1995b). Upon recognition of the pike cue, damselflies reduced movements associated with feeding; as a consequence, there was an increase in crypsis.

Motion attracts predators. Movement by *Chaoborus* larvae more than doubles the maximum distance at which they can be detected by white crappie (*Pomoxis annularis*) (Wright and O'Brien, 1982). Three-spine (*Gasterosteus aculeatus*) and 10-spine (*Pungitius pungitius*) stickleback preferentially attack larval damselflies in motion, especially in the absence of structured refuge (Convey, 1988). Once detected by predacious fish, *Enallagma* damselflies rarely escape (McPeck, 1990b).

In the first experiment, pike stimuli caused damselflies that cooccur with pike to decrease conspicuous behaviors associated with feeding, whereas damselflies that do not occur with pike did not respond. Although *E. boreale* are vulnerable to predation by centrarchids (McPeck, 1990b), naive *E. boreale* do not respond to their presence (McPeck, 1990a). *Enallagma boreale* are excluded from lakes that contain sunfish (*Lepomis gibbosus*, *L. macrochirus*), probably due to predation pressure from these fishes (McPeck, 1989; 1990a, b). Our study sites do not contain centrarchids, suggesting that *E. boreale* are able to coexist with pike and the other fish species that occur at our study sites.

Data from experiments 1 and 2 show that damselfly larvae learned to recognize pike as predators on the basis of chemosensory cues when pike odor was presented simultaneously with chemical alarm cues. To our knowledge, this is the first demonstration of learned predator recognition in an insect. These data suggest a robust learning mechanism by which damselflies can acquire knowledge of predation risk across their geographical distribution, regardless of the types and abundance of predators present in any one locale. An important aspect of this learning is that it occurred after a single presentation and therefore minimized the cost of acquiring this information (Johnston, 1982; Menzel et al., 1984). Repeated naive encounters with a predator would greatly increase the risk of predation.

Experiment 3 established that the response to fathead minnow skin was not a general response to injured fish, suggesting that damselflies use injury-released chemicals from heterospecifics to assess predation risk. To our knowledge, this is the first demonstration of learned predator recognition based on cues from an injured heterospecific from a different phylum and reinforces the concept of

shared information relating to predation risk among members of a prey guild (Snyder, 1967). Presumably, damselfly larvae used in this experiment had at some point in their lives in Feedlot Pond transferred the association between conspecific alarm cues and predation risk to cues from an injured minnow. In this study, we demonstrated that damselflies were able to transfer an association between injured minnow skin and predation risk to an association between chemical stimuli from pike and predation risk.

Our data were collected from two populations, one with and one without pike. We cannot extrapolate from a single population in each condition to make general statements about all damselfly populations that may or may not cooccur with pike. However, these data serve to illustrate that population differences in predator recognition can result from experience, and not strictly as the result of an evolved, genetic trait. Because we did not train damselflies from Pike Lake, a study of laboratory reared damselflies from the Pike Lake population would be needed to determine if the antipredator response to pike stimuli in this population is genetically based or a learned response.

We cannot say from these data how long damselfly larvae may retain the learned recognition of pike stimuli. The response observed in this study resulted from a single exposure of a predatory cue paired with known indicators of predation risk. Presumably, the pairing of predator cues with stimuli from injured conspecifics occurs frequently in nature, which would serve to reinforce recognition of predator cues. Recognition of predator cues could in turn be used by damselfly larvae to extend the range of recognized chemical cues that indicate risk. This could be achieved by pairing predator cues with injury-released chemicals from heterospecific members of its prey guild, for example, the *Enallagma boreale/cyathigerum* species complex, or phylogenetically distant species such as fathead minnows.

Future research should be directed toward tests of the generality of this phenomenon among aquatic taxa and evolutionary constraints on the classes of stimuli that can be associated with predation risk (Chivers and Smith, 1994b).

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