Are behavioural traits in prey sensitive to the risk imposed by predatory fish?

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SUMMARY

1. Behavioural differences among prey species may result from evolutionary adaptations that facilitate coexistence with different predators and influence vulnerability to predators. It has been hypothesised that prey species modify their behaviour in relation to the risk posed by particular predators.

2. We examined the relationship between anti-predator behaviour and predation risk in five species of larval odonates in combination with three predatory fish species (perch, gudgeon and rudd) that differ in foraging behaviour. The odonates, Platycnemis pennipes, Coenagrion puella, Lestes sponsa, Sympetrum striolatum and Libellula depressa, differ with regard to their life cycle and habitat, including water depth, occurrence in temporary ponds and co-existence with fish.

3. The odonate species differed in their response to fish: (i) Two species showed a flexible response. Larval C. puella reduced activity in the presence of fish, regardless of species, whereas L. depressa altered their activity only in the presence of gudgeon. (ii) Independent of fish species, all odonates except L. depressa exhibited spatial avoidance of fish. This was interpreted as a more general anti-predator response. (iii) In some cases the odonates showed no response to predators and their behaviour was thus independent of predation risk.

4. Our results confirm that all odonates responded to the presence of at least some predatory fish, and that some odonate species discriminated between fish species. However, we found no significant correlation between behavioural modifications and predation risk, indicating that anti-predator responses and predation risk depend on the particular predator and the species being preyed on.

Keywords: anti-predator behaviour, behavioural plasticity, chemical cues, predation, predator-prey interactions

Introduction

Predation is known to be a strong selective force (e.g. Kerfoot & Sih, 1987; Reznick et al., 1997; Rundle, Vamosi & Schluter, 2003; reviewed by Vamosi, 2005). The threat sensitivity hypothesis suggests that prey species adjust their anti-predator traits depending on the current threat imposed by potential predators (Sih, 1986). Numerous studies testing this hypothesis have examined behavioural traits, because behavioural adaptations represent an important precontact anti-predator defence. Factors that may influence behavioural decision making of prey species that have been examined (for reviews see also Lima & Dill, 1990; Bernard, 2004) include hunger-level of predators (Abjörnsson et al., 1997), predator type (Eklöv &
Werner, 2000), prey size (Eklöv, 2000) and predator diet (Chivers & Mirza, 2001). Multi-species comparisons, however, are often lacking (Lima, 2002; but see Relyea, 2001a,b).

Vertebrate and invertebrate predators differ in the risk they impose, as both types vary widely in their foraging behaviour and prey detection mode (McPeek, 1990; Reimchen, 1994). However, within these two broad groups, differences in foraging and the threat posed by predators have been found. For instance, anuran larvae exhibit species-specific reactions towards their invertebrate predators and it is unlikely that different prey species always respond in the same way to a particular predator (Relyea, 2001a). Additionally, prey species discriminate among different predators and exhibit predator-specific defences (Relyea, 2001a).

Common behavioural responses among aquatic macroinvertebrates in the presence of a predator are a reduction in activity and spatial avoidance (Sih, 1987; Bernard, 2004). Decreasing activity reduces the probability of encounters with predators (Lima, 1998), but also reduces feeding rate, leading to a reduction in growth and development rate (e.g. Stoks, McPeek & Mitchell, 2003). Many freshwater organisms are able to identify different categories of predator by chemical cues (Dicke & Grostal, 2001). In the mayfly Baetis bicaudatus Dodds, 1923, alterations in behaviour because of different fish predators were found to be proportional to the potential risk (McIntosh & Peckarsky, 2004). However, in a multi-species comparison Relyea (2001b) detected a correlation only between behavioural modifications and predation risk but not between plastic morphological traits and predation risk. Fish are the main predators in many aquatic systems but to our knowledge no study has focused on how different predatory fish species shape the threat-sensitive function of a set of prey species. Investigating the responses of numerous species to a variety of predators may provide a better understanding of the ecology and adaptive nature of plastic anti-predator responses.

Larval odonates are important prey for fish (Rask, 1986). Anti-predator behaviour and vulnerability to fish predation may vary among different odonate species (McPeek, 1990; Stoks & Johansson, 2000). Stoks et al. (2003), for example, reported that differences in the behavioural response and mortality of Enallagma damselfly species caused by invertebrate (aeshnid dragonfly larvae) and vertebrate (Lepomis sunfish) predators depended both on the predator type and on whether it occurred in lakes with or without fish. Additionally, life cycle length and foraging effort of larval odonates can affect their response to predator presence (Stoks & Johansson, 2000). Because odonate species with shorter development times often possess a higher feeding rate and generally high activity (Stoks & Johansson, 2000), these species might not be able to reduce activity and foraging to prevent predation.

Here we test whether the anti-predator behaviour of larval odonates varies among different fish predators and also differs among odonate species. Thus, we chose three fish species that were expected to pose different levels of predation risk with regard to their diet, prey detection mode and/or habitat-use. Additionally, larvae of five odonate species differing in their life cycle, habitat-use and co-occurrence with fish were chosen. Anti-predator behaviours of larval odonates measured in this study were changes in activity and distance from the predator. In a separate experiment, we also examined the survivorship of the odonates in the presence of the different fish species. Based on the threat sensitivity hypothesis we tested the following predictions: (i) prey species vary in their behavioural response to different predatory fish species; (ii) behavioural modifications are directly related to predation risk; (iii) differences in the effectiveness of anti-predator responses of different odonate species determine their ability to co-exist with different predators.

Methods

Study species

Three fish species, differing in their diet, prey detection mode and/or habitat-use, were chosen as predators. Perch (Perca fluviatils L.) is a visual predator that prefers the lower-middle region of the water column and preys on benthic macroinvertebrates (Rask, 1986). Gudgeon (Gobio gobio L.) searches the bottom for benthic invertebrates, hunting both by sight and touch (Vilcinskas, 2004). Rudd (Scardinius erythrophthalmus L.) is a visual predator that swims near the water surface and feeds on aquatic plants and invertebrates (Vilcinskas, 2004). All fish were housed in conspecific groups in 1000 L aquaria.
Larvae of five odonate species, that differ in their life cycles, habitat-use and/or co-occurrence with fish, were selected as prey organisms. *Platycnemis pennipes* (Pallas, 1771) is a univoltine species common in waterbodies with fish. It can be found both on the substratum and within aquatic plants (Martens, 1996). The larvae of *Coenagrion puella* (Linnaeus, 1758) have a life cycle of 1 or 2 years and occur in lakes with or without fish (Banks & Thompson, 1987). *Lestes sponsa* (Hansemann, 1823) has a univoltine life cycle and occurs in fishless ponds with rich vegetation (Jödicke, 1997). Larvae of both, *Coenagrion* and *Lestes* normally take up positions near the water surface (Johansson, 2000). *Sympetrum striolatum* (Charpentier, 1840) is univoltine and lives usually among water plants or algal mats in fishless temporary or perennial ponds (Frobel, 1998). *Libellula depressa* Linnaeus, 1758 is a coloniser of new ponds, which usually do not contain fish, and the larvae are shallow burrowers in the mud (Engelschall & Hartmann, 1998). Larval development of *L. depressa* varies between 1 and 2 years (Weisheit, 1995).

Species are part of a hierarchically structured phylogeny and cannot be regarded as independent samples (Felsenstein, 1985). As larger differences are expected between than within genera (Johansson, 2000), the species selected were from different genera.

**Experimental set-up**

Experiments were conducted in a walk-in climate room with a day/night cycle of 13/11 h, and a constant temperature of 18 °C. For all odonate species, only the penultimate instar (F-1) was sampled from the surrounding of Braunschweig, Germany, between April and August 2003, in the order according to their larval development (also given is head width in mm of the F-1 instar ± SE): *P. pennipes* (April) (2.77 ± 0.8), *C. puella* (May) (2.75 ± 0.3), *L. sponsa* (May to June) (3.01 ± 1.7), *S. striolatum* (June) (4.89 ± 0.7), and *L. depressa* (August) (3.99 ± 1.4).

A total of 1258–1414 individuals per odonate species was sampled and brought into the climate room at least 3 days before being used in experimental trials. About 25 larvae of each species were kept in one bucket filled with 5 L of de-chlorinated water and artificial vegetation. Larvae were fed daphniids every second day. Before trials began, all test aquaria were randomly assigned to a treatment.

**Odonate activity.** An ‘activity experiment’ was conducted to determine whether odonate species respond differently simply to the presence of different fish predators. Prior to every experimental trial, head width of larval odonates was recorded as a measure of overall size (Benke, 1970). Odonate larvae were placed individually in plastic cups filled with 200 mL of de-chlorinated tap water and fed 10 *Daphnia* 1 day before the activity tests started. Larvae that have reached the end of the last instar stop foraging. Therefore, only larvae that had eaten all the daphniids were used in the experiment. All fish were fed in separate aquaria with dead chironomids and flake food biweekly. Fish were not fed larval odonates. Thus, only predator cues, but not victim cues, from damaged odonates, could affect the behaviour of the larvae within these experimental trials.

For measuring activity we used the well-established method of Johansson (2000). Tests were performed in plastic aquaria (30 × 20 cm, height 20 cm) filled with 10 L of de-chlorinated tap water. To ensure that predators could not capture prey, a small part of each aquarium (11 × 20 cm) was separated as the predator compartment using a transparent polyvinyl chloride (PVC)-plate, with a hole (diameter 7 cm) covered with permeable gauze. This allowed exchange of water between the compartments and ensured that the larvae could receive visual and chemical cues from the predator. Floating plastic rope strands (length 20 cm, diameter 2.5 mm) were fixed on a PVC plate on the bottom. For substratum a 2 cm layer of fine gravel was laid over the PVC plate. A total of 9 × 5 = 45 rope strands were arranged in a 3 × 3 cm square pattern. These rope strands simulated artificial vegetation. The vertical and horizontal position of the larvae was determined by using a 3 × 3 cm grid pattern drawn on the front of each aquarium. The depth was localised with help of the rope strands. To avoid disturbance, sides of the aquaria were covered with black foil. The foil of the front side contained a small slit for observation of larval position.

In the larger compartment one larval odonate, and in the smaller predator compartment one fish (except the control treatment), was introduced 1 h prior to the start of the experiment, thus giving them time to acclimatise. Activity was calculated as the number of position changes per 2.5 h. The position of the larvae was recorded every 10 min, thus the maximum number of positional change was 15. Sample size
per odonate species and fish (perch; gudgeon; rudd; no fish) was for C. puella (51; 49; 46), L. sponsa (50; 50; 49; 49), L. depressa (54; 55; 54), P. pennipes (47; 48; 47; 48), and S. striolatum (36; 27; 30; 32).

To analyse the activity data, a two-way ANCOVA was applied with odonate species and fish species as independent factors and odonate size as a covariate. Pair-wise differences in behaviour among odonate species with different fish predators present were evaluated with Fisher’s Protected Least Significant Difference (PLSD) tests. Fisher’s PLSD test evaluates all possible pair-wise comparisons with a multiple t-statistic implemented in a general way for use with either equal or unequal sample sizes. The analyses were performed in StatView (Abacus Concepts, 1992).

Distance to the predator. Because odonate larvae in our activity experiment were able to detect the predator by visual and chemical cues, it was predicted that larvae would attempt to distance themselves from the predator. We monitored the distance of the head of larval odonates from the fish predator compartment every 10 min when recording positional changes. The means of each individual trial were used for a two-way ANOVA with odonate species and fish species as independent factors. Pair-wise differences in responses among odonate species with different fish predators present were tested using Fisher’s PLSD tests. Odonate size (larval head width) was not included in the model, because no significant effect was detected (ANOVA: $F_{1,903} = 0.198, P = 0.656$).

Mortality. A ‘mortality experiment’ was conducted to examine if the odonate species differ in their vulnerability to the three fish predators. To equalise hunger levels, all fish were starved for 1 week before the experimental trials. A total of 29 perch were used (mean body length ± 1SE: 12.7 cm ± 4.2), 19 gudgeon (9.5 cm ± 1.1), and 40 rudd (13.5 cm ± 4.0). The aquaria used for the predation experiments had an area of 60 × 30 cm and were 30 cm high. Sand was used as a substratum and artificial plants (eight floating strings per aquaria, 30 cm length) provided structure. The aquarium was separated into two compartments (20 × 30 cm and 40 × 30 cm) by a PVC plate with two holes closed by permeable gauze (diameter 7 cm).

One fish predator was introduced into the smaller compartment and 20 odonate larvae of one species into the larger compartment of each aquarium. After acclimatising for 12 h, the PVC plate was lifted and the fish was allowed to prey on the larvae for 3 h. At the end of the experiment, the fish was removed from the aquarium and the surviving odonate larvae counted. Every fish was used only once in an experimental trial with one species, and there was a time span of at least 2 weeks before use with another odonate species. The tests were replicated 16–19 times for each odonate and predator species. Control trials were replicated six times per odonate species. Each day of the experiment only one odonate species was tested, and one control treatment without fish was performed. Losses in the control treatment were subtracted from losses in the fish treatments to account for natural mortality or accidents.

Data from the predation experiment were analysed with a two-way ANOVA. The covariates fish length and odonate size were excluded from the model, because an ANCOVA failed to detect either a significant influence on survival alone (fish length: $F_{1,249} = 0.642, P = 0.424$; odonate size: $F_{1,249} = 0.619, P = 0.432$) or a significant interaction between the two variables ($F_{1,249} = 0.860, P = 0.355$). Prior to statistical analysis, mortality data were transformed using the angular transformation (Sokal & Rohlf, 1997). The analysis was followed by pair-wise Fisher’s PLSD tests. A Pearson correlation matrix was conducted to analyse the relationship between mean activity and predation risk (mortality). In a second Pearson correlation, we analysed the relationship between modifications in activity-level and predation risk: net change in the activity of the odonate species (activity of species 1 with predator 1 – activity of species 1 without predator 1) was compared with mortality (mortality of species 1 with predator 1) for all odonate and predator combinations.

Results

Odonate activity

A significant interaction between odonate species and fish treatment confirmed that odonate species respond differently towards predatory fish species (Table 1; Fig. 1). Neither of P. pennipes, L. sponsa, or S. striolatum changed their activity levels in different predator treatments, whereas C. puella and L. depressa reacted to the presence of fish (Fig. 1). Coenagrion puella
decreased its activity in the presence of all the fish species tested (all Fisher’s PLSD: P < 0.02; Fig. 1). By contrast, L. depressa responded to the presence of gudgeon only by increasing its activity (P = 0.007, all other Fisher’s PLSD: P > 0.15; Fig. 1).

Comparing all five species over all treatments (Table 1), P. pennipes exhibited the lowest activity level (all Fisher’s PLSD: P < 0.001; Fig. 1). Apart from L. depressa being more active than L. sponsa (P = 0.04), no other pair-wise differences in the mean activity were found (all Fisher’s PLSD: P > 0.10; Fig. 1).

Distance to the predator

The interaction term between odonate species and fish species was not quite significant (Table 2; Fig. 2).

Larval P. pennipes exhibited differences only between rudd treatments and the control, taking up a position more distant to the fish compartment (Fig. 2).

There were no differences between odonate species and mean distance to the predator (Table 2). Odonate species showed significant responses by occupying positions away from the caged fish (all Fisher’s PLSD: P ≥ 0.07; Fig. 2).

Mortality

A significant interaction between fish treatment and odonate species reveals that fish species differed in their impact on different species of odonates (Table 3; Fig. 3). Larvae of C. puella faced the greatest losses to perch predation, followed by gudgeon, whereas rudd

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**Table 1** Results of a two-way ANCOVA testing for differences in mean activity among the studied odonate species and effects of different fish species/no fish. Odonate size (larval head width) was used as an independent variable.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>d.f.</th>
<th>F-ratio</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Odonates</td>
<td>955.177</td>
<td>4</td>
<td>26.813</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Fish</td>
<td>66.457</td>
<td>3</td>
<td>2.487</td>
<td>0.059</td>
</tr>
<tr>
<td>Odonates × fish</td>
<td>256.514</td>
<td>12</td>
<td>2.400</td>
<td>0.005</td>
</tr>
<tr>
<td>Odonate size</td>
<td>31.198</td>
<td>1</td>
<td>3.503</td>
<td>0.062</td>
</tr>
<tr>
<td>Error</td>
<td>8024.174</td>
<td>903</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 2** Results of a two-way ANOVA testing differences in mean distance (cm) to predator compartment among the studied odonate species and effects of different fish species/no fish.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>d.f.</th>
<th>F-ratio</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Odonates</td>
<td>131.110</td>
<td>4</td>
<td>1.837</td>
<td>0.120</td>
</tr>
<tr>
<td>Fish</td>
<td>907.788</td>
<td>3</td>
<td>16.963</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Odonates × fish</td>
<td>347.458</td>
<td>12</td>
<td>1.623</td>
<td>0.079</td>
</tr>
<tr>
<td>Error</td>
<td>16 125.836</td>
<td>904</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
caused the smallest losses (all Fisher’s PLSD: $P \leq 0.008$) (Fig. 3). For larval *L. sponsa*, *S. striolatum* and *L. depressa* no significant differences in mortality were found between predation by perch and rudd (all Fisher’s PLSD: $P > 0.30$), but gudgeon caused significant lower mortality (all Fisher’s PLSD: $P \leq 0.006$; Fig. 3). In contrast, mortality of larval *P. pennipes* was unaffected by fish species (all Fisher’s PLSD: $P > 0.2$; Fig. 3).

The mortality of odonates because of fish predation differed significantly between the odonate species (Table 3). Larval *P. pennipes* experienced the lowest mortality; followed by *L. depressa*, *S. striolatum* and *C. puella*, whereas *L. sponsa* suffered the highest mortality (all significant differences in Fisher’s PLSD: $P \leq 0.01$; Fig. 3). No significant correlation was found between mean activity and mortality ($P = 0.285$), nor was the correlation between net activity and mortality significant ($P = 0.616$).

### Discussion

Modifications in odonate behaviour were not generally related to the threat imposed (predation risk). Rather, odonates exhibited predator- and species-specific strategies towards predatory fish. Larval odonates may only react either to a particular fish species or in a similar manner to all fish, and can either demonstrate modifications in all or only one or a few anti-predator traits. The outcome of our study reveals that prey-predator interactions are dependent on the ability of a predator to search, capture, and consume prey as well as on the ability of prey species to deal with predators in a manner that is related to their life history.

Our results confirm that mortality varies among prey species depending on the predator species present. It has been shown in previous studies that different prey species vary in their vulnerability towards predation, because of behavioural differences (Sih, 1986; McPeek, 1990). Accordingly, different predator species may also vary in their risk they impose because of different foraging modes (McPeek, 1990; Relyea, 2001b; Stoks et al., 2003). The detected differences in mortality were not caused by size or seasonal effects affecting fish behaviour. Neither fish length nor odonate size had a significant influence in the analysis. Additionally, the diet of fish may change seasonally according to prey abundance, but no general changes in feeding spectrum occur within size classes of fish (Guti, 1993). Finally, the behaviour of fish was not affected by spawning periods during the experiment.

The highest mortality because of fish was experienced by *L. sponsa*. This odonate species prefers near-surface microhabitats, which are less complex and of higher predation risk (Johansson, 2000). *Coenagrion puella* suffered the highest mortality from perch, whereas *L. sponsa* was taken equally by rudd and perch. Rudd prefers feeding in dense submerged vegetation closer to the water surface, which is the preferred habitat of *L. sponsa* and *C. puella*. Mortality in *C. puella* was lowest in the presence of rudd, although larvae did not differentiate in behaviour between fish species. Hence, this odonate species seems to be better adapted to

### Table 3 Results of a two-way ANOVA testing differences in predator induced mortality among the studied odonate species with three different fish predator species. Data were transformed by angular transformation.

<table>
<thead>
<tr>
<th>Source</th>
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<th>d.f.</th>
<th>F-ratio</th>
<th>P-value</th>
</tr>
</thead>
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<tr>
<td>Odonates</td>
<td>20.181</td>
<td>4</td>
<td>103.734</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Fish</td>
<td>3.394</td>
<td>2</td>
<td>34.892</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Odonates × fish</td>
<td>4.056</td>
<td>8</td>
<td>10.423</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>12.257</td>
<td>252</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Fig. 3* Percentage of larval mortality caused by three different fish predators. Initial prey number per aquarium was 20 larvae of one species and one predatory fish. Fish had 3 h to prey on larvae. Error bars are shown (±1 SE).

Multiple predator effects on prey behaviour 81

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coexistence with rudd than perch. Gudgeon was the least successful predator of all the fish species. Surprisingly, gudgeon preyed more successfully on *L. sponsa* and *C. puella*, although gudgeon usually hunt close to the bottom. Additionally, gudgeon uses a more tactile detection mode to find prey. However, the gudgeon is not entirely restricted to tactile prey-detection and is also able to see prey that are not directly on the bottom.

In the analysis of distance from the predator the odonates showed a more generalised response to predatory fish: odonate species were more distant to the fish compartment when fish were present, with the exception of larval *L. depressa*. Sih (1987) mentioned two ways of avoiding encounters with predators: (i) staying away from predators or (ii) avoiding detection when close to predators. Our results suggest that the majority of larval odonates adopted the former method for avoiding predation. Prey may determine the location of a predator by chemical gradients (Brodin, Mikolajewski & Johansson, unpublished data). Therefore, increasing the distance to a predator in order to reach a safer, physically complex microhabitat should be a common anti-predator behaviour.

Prey activity was not directly related to predation risk, as we found no significant correlation between mean activity of the odonates and mortality. Furthermore, there were no significant correlations between modifications in activity (net activity) and predation risk. In general, a direct relationship between predation risk and the magnitude of prey response may be expected (Sih, 1987; Lima, 1998). Accordingly, Relyea (2001b) found that the magnitude of phenotypic responses across prey species was correlated with predation risk. However, the proportion of traits that are related to predation risk is low compared with the totality of phenotypic responses. Differences in behavioural plasticity may also be related to historical differences in the predators with which each prey species coexists (West-Eberhard, 1989). For example, *P. pennipes*, a species from streams with fish, showed an equally low activity-level in both the presence and absence of fish. Given that anti-predator traits are expected to be fixed when predation risk is continuously high (Sih, 1987), the activity-level of *P. pennipes*, which always co-occurs with fish, appears to be an example of a fixed behavioural trait (Steiner *et al.*, 2000).

Flexible traits, in contrast, are predicted when predation occurs heterogeneously over time or space (Sih, 1987). For *C. puella*, which may occur with or without fish, our findings confirmed that larvae of this species can exhibit flexible, activity-based adaptations to fish presence. Larval *L. depressa* changed activity only in the presence of the benthic gudgeon. In this case, prey and predator prefer the same microhabitat. Surprisingly, gudgeon induced a higher activity in larval *L. depressa*. As gudgeon are semi visual/tactile predators, they are able to find even motionless or buried prey by searching with their barbels, resulting in high risk of encounters with gudgeon even for buried *L. depressa* larvae. An increase in foraging activity shortens time of development (Pickup & Thompson, 1984; Johansson *et al.*, 2001) and, therefore, time spent in the habitat shared with the potential predator. *Lestes sponsa* and *S. striolatum* exhibited a fixed high activity, which is probably an adaptation to their habit of breeding in temporary, fishless waters. Because a high foraging activity leads to a fast development rate (Pickup & Thompson, 1984; Johansson *et al.*, 2001), the costs of reduced foraging activity in the presence of predators may be too high for these species.

Similar responses of aquatic prey species to their predators have been documented in other systems. McIntosh & Peckarsky (2004) demonstrated a flexible anti-predator response in a larval mayfly depending on predation risk. Mayflies were able to detect and distinguish between chemical cues of predatory fish. However, conspecific mayflies were fed to predators during the experiment. Thus, the differentiated response to fish species was suggested to depend on varying concentrations of ‘victim cues’ related to the consumption rates of the predators. In damselflies it is known that the strength of the anti-predator response depends on whether the predators have consumed con- or heterospecifics before the tests (Brodin, Mikolajewski & Johansson, unpublished data). Because the fish in the current study were not fed with odonates, cues detected by our study species were neither victim cues nor did the predator faeces contain any odonate stimuli. Our results confirm that some odonates are able to detect predators visually and/or chemically and respond appropriately (e.g. Koperski, 1997; Stoks & Johansson, 2000; Mikolajewski & Johansson, 2004). We demonstrate for the first time that discrimination is not due to victim cues or
fish faeces containing odonate chemicals but to the predators themselves. Furthermore, odonate larvae can differentiate among fish species to some extent, assuming species-specific predation risk for different fish species. Our findings are in accordance with those of Relyea (2001b), who demonstrated that anti-predator responses of prey to different predator species generally are not related to risk, but depend on prey and predator species, as predation risk is prey- and predator-specific.

In our study we show that odonates may undergo a significant change in activity in the presence of fish. Additionally, only a few experiments (Relyea, 2001a,b) with multiple prey and predator species have been conducted to reflect the complexity of anti-predator behaviours. We suggest that the ability to reduce activity in the presence of predators will depend on the characteristics of the prey species, especially the length of the life cycle and ability to co-occur with fish. In contrast, increasing the distance to a predator is likely to be a more generalised response in larval odonates and may depend on the structural complexity of the environment in which the different odonates live (e.g. Thompson, 1987). Generally, our results confirm those of previous studies illustrating that prey species differ in their anti-predator traits with respect to prey and predator species biology.

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References


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