

Morphological and behavioral defenses in dragonfly larvae: trait compensation and cospecialization

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Many animals have two basic traits for avoiding being killed by a predator: behavioral modification and morphological defense. We examined the relationship between antipredator behavior and morphological defense in larvae of three closely related dragonfly species within the genus *Leucorrhinia*. The three species differ with regard to their morphological defense as expressed in the length of the larval abdominal spines. Results showed that longer abdominal spines provided protection against an attacking fish predator (perch) because the probability of being rejected after an attack was significantly higher in the species with the longest abdominal spines. In contrast to other studies, the species with the strongest morphological defense did not show the least behavioral predator avoidance. Instead, the species with intermediate morphological defense showed the least predator behavioral avoidance. The results suggest that the *Leucorrhinia* system is a mixture of trait cospecialization (a positive correlation between antipredator behavior and morphological defense) and trait compensation (a negative correlation between antipredator behavior and morphological defense). Differences in the relationship between morphological and behavioral defense between species might be related to abundance patterns of the three species in lakes with and without fish predators. *Key words*: activity, behavioral defense, morphological defense, Odonata, predation, spines. [*Behav Ecol* 15:614–620 (2004)]

To avoid predation, animals show morphological defenses and behavioral modifications (Edmunds, 1974; Sih, 1987). Behavioral modifications to avoid predation are well studied and include behavior such as reduced activity, increased use of refuge, and selection of less profitable prey (Lima, 1998; Lima and Dill, 1990). Morphological defenses are also well studied and include crypts, armor, spines, and chemicals (Edmunds, 1974; Tollrian and Harvell, 1999). The interaction between morphological and behavioral defense is however less well studied.

Given that species show both morphological and behavioral adaptations to avoid predation, it is interesting to explore how these two traits are related. DeWitt et al. (1999) suggested four functional relationships between such traits: (1) trait codependence, which occurs when traits are mechanically linked (e.g., when behavior is dependent on a certain morphology); (2) trait complementation, when the appropriate behavior depends on morphology; (3) trait cospecialization, where prey use both types of defenses simultaneously (in this case a positive relationship between the two traits is expected); and 4) trait compensation, when there is a negative relationship between traits (e.g., prey with strong morphological defense may show less antipredator behavior).

The underlying assumptions of trait compensation is that it is energetically costly to produce and maintain morphological defense (Lively, 1986; Pettersson and Brönmark, 1997), and that antipredator behavior has a cost in terms reducing the time available for gathering food (Lima, 1998), or that there is a trade-off between morphological and behavioral defense (DeWitt et al., 2000). Under the assumption of a limited amount of energy available to allocate between behavioral and

morphological defenses, a negative relationship between these two kinds of traits is expected. Animals devoting much energy to morphological defense should be expected to behave in a more risky manner to gain more energy. Similarly, animals that are defended should show less behavioral response to predators because they are safer.

More studies exploring the relationship between morphological defense and behavior are needed for two main reasons. First, only two studies (DeWitt et al., 1999; Rundle and Brönmark, 2001) have fully considered the four functional relationships suggested by DeWitt et al. (1999) between morphological and behavioral defense in response to predators. More studies will reveal if any of these relationships have evolved more frequently than have others. Second, no study has investigated the relationship between closely related species. Comparing closely related species is an intermediate complement to the within- and between-species comparisons that have been performed in past studies (see DeWitt et al., 1999, Rundle and Brönmark, 2001).

Typically, distantly related species are used in these comparative studies because distinct morphological difference among species is evident. Results have shown that species with a less-pronounced morphological defense are more risk averse than those with prominent morphological defense and, hence, show trait compensation (Abrahams, 1995; McLean and Godin, 1989; Rundle and Brönmark, 2001). However, distantly related species also differ in many other traits apart from morphological defense. For example, life history and body shape could contribute to observed differences in behavior as well. The second approach is to compare morphological defense within a species. This is possible in species with induced predator defense and has been used in *Daphnia* (Dodson, 1988; Lüning, 1995), fish (Pettersson et al., 2000), and snails (Rundle and Brönmark, 2001). These studies have shown that individuals with an induced morphological defense show less antipredator behavior compared with that of those without induced morphological defense, again providing support for trait compensation. However,

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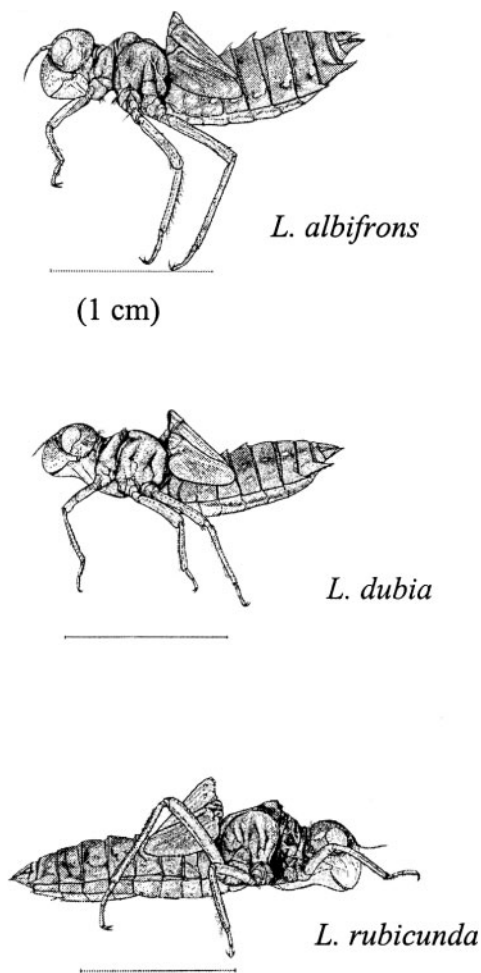


Figure 1
Exuviae (larval skins) of the three *Leucorrhinia* species studied.

because defense can only be induced with predators, the individuals with induced defenses are preconditioned to the presence of predators. Hence, it might be impossible to distinguish if the behavioral response observed is an effect of precondition (learning) to predators or a response caused by morphology per se. An alternative approach is to compare closely related species (e.g., within the same genus) that differ in morphological defense. This comparative method minimizes the risk that other traits (other than the differences in morphological defense) may cause the differences in behavior. It might also reduce the problem of predator preconditioning.

Dragonfly larvae are the top invertebrate predators in many aquatic systems (Benke and Benke, 1975; Macan, 1975) and provide an important food resource for many fish species (Butler, 1989; Rask, 1986;). To avoid fish predation, they show behavioral adaptations and morphological adaptations such as abdominal spines (Corbet, 1999; Nilsson, 1981; Pierce, 1988). A higher activity results in a higher growth rate and higher predation risk in dragonfly larvae (Johansson, 2000; McPeck, 1998; Suhling and Lepkojus, 2001).

Larvae of the genus *Leucorrhinia* (Odonata: Anisoptera) are common members of many Palaearctic boreal lake communities and have similar life cycles (Askew, 1988). Although at least *L. dubia* and *L. rubicunda* larvae show lower abundance in lakes with fish compared with lakes without fish, species within the genera do coexist with fish (Henrikson, 1988, 1993;

Johansson and Samuelsson, 1994). Length of abdominal spines varies greatly among species (Westman et al., 2000) (Figure 1), and in one species (*L. dubia*) there is some indirect evidence that these spines provide protection against predators, because fish have a longer handling time when preying upon long-spined larvae (Johansson and Samuelsson, 1994). However, we have no direct evidence on how effective these spines are in terms of survival of the prey. In addition, we lack information on how the effectiveness of the morphological defense depends on the attack properties of the predator, for example, the direction of an attack. *Leucorrhinia* larvae show behavioral adjustments in the presence of predators, although not as strong as in other species (Henrikson, 1988, Johansson, 1993). Hence, the *Leucorrhinia* system may be appropriate for studying the relationship between morphological and behavioral defenses.

We have two main aims with the present study. First, we investigate whether longer spines provide protection against an attacking fish predator, for three species of *Leucorrhinia*. The three species differ in the length of the abdominal spines, with *L. rubicunda* (Linnaeus, 1758) having short spines, *L. dubia* (Van der Linden, 1825) intermediate spines, and *L. albifrons* (Burmeister, 1839) long spines (Figure 1). Second, we analyze the relationship between morphological defense in terms of spines and predator avoidance in terms of activity. The purpose is to investigate which of the four relationships between morphological and behavioral traits outlined by DeWitt et al. (1999) fits best to our study system.

METHODS

Predation experiments

The aim of the predation experiments was to determine whether differences in spine length among species influence survival probabilities after an attack. Preliminary experiments suggested three variables were likely to be important. These were (1) probability of being rejected by the perch predator given an attack from the front, (2) probability of being rejected given an attack from behind, and (3) direction of last attack (front or back attack) before being devoured. In cases in which only one attack occurred, this attack was regarded as the "last attack." Experiments were performed in 100-l aquaria filled with 90 l nonchlorinated tap water. No bottom substrate or structure was used in the aquaria. Each aquarium held four perch, which were allowed to acclimate in the aquaria 2 weeks before the start of the experiment. During this acclimatization period, perch were fed frozen chironomids. Experiments were started by introducing a dragonfly larvae into the middle of an aquarium. We noted the following variables: (1) which fish caught the larvae (individual fish could easily be recognized by size and color patterns), and all attacks that included more than one perch were excluded; (2) whether the first attack on the larvae was from the front or from behind, (3) whether the larva was rejected after the first attack, because most larvae were attacked several times before being devoured; and (4) whether the last attack before being devoured was from the front or behind. A total of 19 perch were used (mean size = 11.2 cm, range = 9.7–13.4 cm). Thus, some perch were used several times, but there was at least a week between trials of reused perch. No perch was used more than three times for each species to reduce learning effects, such as attack direction (see below). Because perch might affect the survival probability of prey (Christensen, 1996), we analyzed the effect of perch size as well.

All larvae used in the predation experiments were measured by their size and spine length by using a dissecting

Table 1
Mean head width (mm) and mean spine length (mm) of dorsal spines on abdominal segment 5 and 6 and of lateral spines on abdominal segment 8 and 9 of the three *Leucorrhinia* species

Species	Head width	D5	D6	L8	L9	<i>n</i>
<i>Leucorrhinia albifrons</i>	5.67 (0.015)	0.47 (0.009)	0.53 (0.008)	0.56 (0.011)	1.06 (0.015)	48
<i>L. dubia</i>	5.19 (0.019)	0.16 (0.014)	0.06 (0.011)	0.40 (0.012)	0.61 (0.017)	57
<i>L. rubicunda</i>	5.78 (0.026)	0.03 (0.008)	0.002 (0.002)	0.28 (0.007)	0.43 (0.010)	44

Values within parentheses are SE. *n* is the number of individuals used for measurement. D5 and D6 indicate abdominal segment 5 and 6, respectively. L8 and L9 indicate lateral spines on abdominal segment 8 and 9, respectively.

microscope. Size was estimated as head width, which is the most reliable measure of overall size in dragonfly larvae (Benke, 1970). Spine length was measured as the distance from the tip of the spine to the base of the spine (see Johansson and Samuelsson, 1994). We measured lateral spines on the abdominal segments 8 and 9, and dorsal spines on segments 5 and 6. Because length of the spines is correlated within an individual (Johansson and Samuelsson, 1994), we only measured these four spines.

Behavioral experiments

The aim of the behavioral experiments was to estimate activity differences among *Leucorrhinia* species in the presence and absence of a fish predator. Although all three species coexist in lakes in northern Sweden, it was not possible for us to find enough larvae for the experiments from a single lake. Consequently, we had to sample larvae from two lakes, which allowed us to make pairwise between-species comparisons.

In May 2001 we sampled last instar *L. dubia* and *L. albifrons* larvae from lake Mjösjön, and *L. dubia* and *L. rubicunda* larvae from lake Täftebölesjön. These lakes are situated within a radius of 10 km from Umeå, Northern Sweden, and contain several fish species, including perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), and pike (*Esox lucius*). Dragonfly larvae in their last instar stop feeding and reduce activity close to emergence. We therefore avoided using individuals with swollen wing pads, which are signs of an approaching emergence. In addition, we checked feeding in larvae placed in a small water-filled plastic cup (height, 55 mm; diameter, 85 mm) with 10 *Daphnia magna* 1 day before the experiments. Larvae that did not eat all 10 *Daphnia* were not used for activity estimates. As predators we used perch, *Perca fluviatilis* L., which were collected in lakes in the vicinity of Umeå. Perch is a natural predator on odonate larvae (Rask, 1986). Fish were held in large plastic tanks or large aquaria when not being used, and they were fed frozen chironomids and live damselfly larvae.

Activity experiments were performed in plastic aquaria (30 × 20 cm; height, 20 cm) filled with 10 l nonchlorinated tap water. Artificial vegetation was created by fixing small white floating plastic rope strings (length, 20 cm; diameter, 2.5 mm) to a PVC-plate mounted in the bottom of each aquaria. The bottom substrate consisted of a 2-cm layer of fine gravel. The rope strings were arranged in a 3 × 3-cm square pattern, giving a total of 9 × 5 = 45 rope strings in each aquaria. Larval position was determined by using a 3 × 3-cm grid pattern that was drawn on the front of each aquaria. Each aquarium was divided into two compartments (size, 11 × 20 and 19 × 20 cm) by a transparent Plexiglas partition. To allow water circulation between the compartments, nine holes (diameter, 2 mm) had been made in the partition. The small compartment was used to hold a predator and the large to hold a *Leucorrhinia* larva. Water temperature was 20 ± 1°C,

and light was provided by fluorescent light tubes with lights on and off at 0400 and 2100 h, respectively.

Activity was estimated in the presence and absence of predators. One hour before the start of an activity experiment, one predator (when required) was introduced into the small compartment and thereafter one larva into the large compartment. Because of transparency and perforation of the Plexiglas partition, the larva could get both visual and chemical cues from the perch predator. The position of the larvae was recorded every 10 min from 1000–1300 h. Maximum number of moves (position changes) was thus 18. Distance moved was not analyzed because it is well correlated with number of moves (position changes) in odonate larvae (Johansson, 2000). Trials were replicated 23–25 times for each species and predator treatment. A total of eight perch predators (size range = 9.7–12.0 cm) were used; thus, some perch we used up to four times, but there was always at least a 3-day interval. Perch were combined randomly in experiments with respect to *Leucorrhinia* species and perch size.

Data analysis

Behavior was analyzed with two-way ANOVAs using species and predator treatment as factors. Because *L. dubia* larvae were used from both lakes, we also performed a two-way ANOVA on behavior of this species using lake origin and predator treatment as factors. Because spine lengths of larva are correlated (Johansson and Samuelsson, 1994), differences among species in length of larval spines were analyzed with a MANOVA. Size differences between larvae was analyzed with a one-way ANOVA. We merged data on size and spine length of *L. dubia* larvae from the two lakes in our analyses of size and spine differences among species. The differences in size and spine length among *L. dubia* populations from fish lakes is negligible compared with differences among species and does therefore not affect our results with regard to size and spine length differences among species (Johansson and Samuelsson, 1994), and see also SE of larval size and spine length in Table 1.

Data on attacks by perch on larvae, rejected or devoured, are dichotomous. We therefore modeled the variance in these response variables in generalized linear models, using binomial error distributions and logit link functions (Crawley, 1993). Our model contained species as the variable and fish size and larval size as covariates. The effects of species, fish size, and larval head width were tested in log-likelihood ratio tests comparing the deviance of a model including all factors with a model excluding the one being tested. The interaction species × head width and species × fish size were tested by comparing the deviance of a full model with a model excluding the interaction term (Crawley, 1993). Because we were not interested in the fish size × head width and fish size × head width × species interactions, we did not include these in our analysis. The dichotomous data were analyzed

Table 2

(a) Number of larvae and percentage of larvae rejected after the first attack by perch on the three different *Leucorrhinia*-species when attacked from front or from behind

	Rejected		% rejected
	yes	no	
Frontal attacks			
<i>L. albifrons</i>	6	23	20.7
<i>L. dubia</i>	2	33	5.7
<i>L. rubicunda</i>	4	14	22.2
Attack from behind			
<i>L. albifrons</i>	19	0	100.0
<i>L. dubia</i>	20	2	90.9
<i>L. rubicunda</i>	17	9	65.4

(b) Number of larvae devoured after last attack from behind and from the front and percentage of larvae devoured from behind

	Behind	Frontal	Devoured from behind (%)
<i>L. albifrons</i>	0	42	0.0
<i>L. dubia</i>	2	51	3.9
<i>L. rubicunda</i>	12	31	27.9

with GLIM 3.77 and all other data with StatView 5.0. We did not consider to evaluate a lake effect in the predation experiment because we could see no reason why the variables analyzed should differ between lakes. We were only interested in a morphological species effects, which is not influenced by which lake the larvae originated from.

RESULTS

Larval size and spine length

Last instar larva differed in size among species (ANOVA; MS = 5.17, $F_{2,146} = 253.2$, $p < .001$) (Table 1). *L. rubicunda* was significantly larger than *L. albifrons*, which in turn was significantly larger than *L. dubia* (all $p < .001$, Tukey's test). Larval head width was not correlated with any spine length in any of the species ($p > .05$ in all comparisons; *L. rubicunda*: r range = -0.286 – 0.173 , *L. albifrons*: r range = -0.060 – 0.066 , *L. dubia*: r range = 0.057 – 0.236). We found a significant difference in spine length among species (MANOVA; Wilk's $\lambda = 0.026$, $F_{8,286} = 184.2$, $p < .001$) (Table 1), with *L. albifrons* having the largest spines, and *L. rubicunda* the smallest spines. In summary, these results show that species differ in final instar larval size with *L. rubicunda* being the largest and *L. dubia* the smallest. These larval size difference are not mirrored in the size of larval spines because *L. albifrons* had the largest spines and *L. rubicunda* the smallest.

Predation experiments

Survival probability, that is, the probability of being rejected (spat out), was affected by the direction of perch attacks (Tables 2 and 3). When attacked from the front, only a few larvae were rejected after the first attack, and there was no significant difference with regard to species or covariates (test of full model; $\chi^2 = 11.06$, $df = 8$, $p = .20$) (Tables 2 and 3). In contrast, significant effects were detected when larvae were attacked from behind (test of full model; $\chi^2 = 25.22$, $df = 8$, $p = .0015$) (Tables 2 and 3). Although the long-spined species,

Table 3

Results of generalized linear models of the attack direction (front/behind) on probability of being rejected by the attacking perch, and the direction of the last attack (front or back) by perch on the *Leucorrhinia* larvae species

Source	Deviance	LLR	df	p
Attack front	68.27	—	81	—
Attack behind	59.84	—	66	—
Species	—	13.27	2	.001
Head-width	—	1.34	1	.24
Fish size	—	8.85	1	.003
Species \times head width	—	1.74	2	.41
Species \times fish size	—	3.23	2	.20
Direction last attack	90.60	—	137	—
Species	—	19.10	2	.0001
Head width	—	0.01	1	.92
Fish size	—	4.90	1	.03
Species \times head width	—	0.30	2	.86
Species \times fish size	—	1.70	2	.43

Larval head width and fish size are used as covariates in the model. LLR is the value of the log-likelihood ratio test.

L. albifrons was always rejected on the first attack when attacked from behind; *L. rubicunda*, the short-spined species, was rejected in 65% of the attacks from behind. *L. dubia*, which is intermediate in spine length, was rejected in 90% of the attacks. All larvae that were rejected after an attack were alive as determined by movements of legs and jet propulsion.

The direction of the last perch attack before being devoured differed significantly among the species (test of full model; $\chi^2 = 29.20$, $df = 8$, $p = .0003$) (Tables 2 and 3). *L. albifrons* was never devoured when attacked from behind. In contrast, *L. rubicunda* was devoured in 28% of the attacks from behind. Only 4% of *L. dubia* were devoured after an attack from behind (Table 2).

Size of larvae (head width) did not affect the attack variables significantly (Table 3). Fish size, however, had a significant effect on attacks from behind and direction of being devoured. Larger fish rejected fewer larvae when attacked from behind, and they were less selective compared with small fish as to whether the last attack was from the front or behind. No significant effects of fish size were found when fish attacked larvae from the front (Table 3).

Behavioral experiments

Lake origin had a significant effect on the larval behavior of *L. dubia* (Table 4), suggesting that larvae from different lakes might behave differently. We therefore treated each lake separately in our analysis. In lake Mjösjön, *L. albifrons* larvae were less active than were *L. dubia* larvae (Table 4 and Figure 2). This is in agreement with the cospecialization prediction, which is that *L. albifrons* should be less active because this species has longer spines than does *L. dubia*. In lake Täftebölesjön *L. dubia* larvae were more active than were *L. rubicunda* larvae (Table 4 and Figure 2), which is in agreement with the trait compensation prediction.

The presence of a perch predator reduced activity of both species from lake Mjösjön (Table 4 and Figure 2). A significant interaction term in the ANOVA, with the long-spined species decreasing behavior more than the short-spined species, should support the trait compensation mechanism. Because no interaction term was evident from the ANOVA, we found no support for trait compensation, which predicts that *L. albifrons*, which had longer spines than

Table 4

Differences in number of moves between the species *L. albifrons* and *L. dubia* from lake Mjösjön and *L. rubicunda* and *L. dubia* from lake Täftebölesjön and, difference between individuals of *L. dubia* from the two different lakes

Source	Mean square	df	F ratio	p
Lake Mjösjön				
Species	231.70	1	21.85	<.001
Treatment	88.04	1	8.30	.005
Species × treatment	7.34	1	0.30	.41
Error	10.60	88		
Lake Täftebölesjön				
Species	104.26	1	22.92	<.001
Treatment	12.15	1	2.67	.10
Species × treatment	8.04	1	1.84	.18
Error	4.55	92		
<i>L. dubia</i> from two lakes				
Lakes	108.70	1	10.20	.002
Treatment	84.17	1	7.90	.006
Lake × treatment	8.52	1	0.80	.38
Error	10.66	88		

Results of two-way-ANOVAs testing. Treatment is presence and absence of fish.

does *L. dubia*, should reduce activity to a lesser extent in the presence fish. Larvae from lake Täftebölesjön did not show a strong reduction in activity in response to the presence of a perch predator (Table 4 and Figure 2). There was, however, a trend for a reduction in activity in the presence of perch in *L. dubia* larvae ($p = .059$, Tukey's test) (Figure 2). Again, the absence of a significant interaction term does not support trait compensation, which predicts that the long-spined species (*L. dubia*) should reduce its activity less in the presence of fish compared with the short-spined species (*L. rubicunda*).

In summary, these results suggest that spine length of the three species is not correlated with general activity, because *L. dubia*, which was intermediate in spine length, had a higher activity than did both the long-spined *L. albifrons* and the short-spined *L. rubicunda*. We did not find any support for the commonly observed pattern that well-armored species (long-spined) should have a lower reduction in activity in the presence of predators than less-armored species (short-spined).

DISCUSSION

Because longer spines provided protection against an attacking fish predator, the *Leucorhina* system is a good complement to other approaches suited for testing the functional relationships. As far as we know, the present study is one of few studies (for another example, see De Witt et al., 1999) to explore the four suggested functional relationships between morphological defense and behavioral avoidance in closely related species. Spines provided protection from predation, and decreased activity reduces the probability of encounters with predators. Because neither of these traits requires the other to function in *Leucorhina* larvae, trait codependence seems as an unlikely defense mechanism in the present study. Similarly, neither of the traits requires the other to be effective, and therefore, also trait complementation seems unlikely as a defense mechanism. The results were not consistent trait compensation, the general hypothesis that morphological defense results in less antipredator behavior.

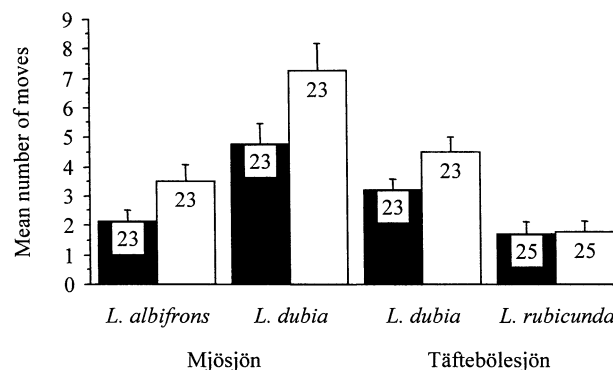


Figure 2

Mean number of moves by larvae of three *Leucorhina*-species from lakes Mjösjön and Täftebölesjön studied in the laboratory. White bars are without predators and black bars with predators. Error bars are SE, and number in the bars are n values.

Although many other studies have found support for this hypothesis (Abrahams, 1995; McLean and Godin, 1989; Rundle and Brönmark, 2001), the longer-spined *L. albifrons* did not show less strong antipredator behavior than did the short-spined species in the present study. This was true for activity in the presence/absence of fish as well as for the antipredator response.

Our results suggest that the *Leucorhina* system we studied shows a mixture of trait cospecialization and trait compensation. Had we only studied the species pair *L. albifrons* and *L. dubia*, a positive relationship between activity and spine length would have been found, which corresponds to trait cospecialization. The species with the better morphological defense (*L. albifrons*) showed the strongest antipredator behavior. In contrast, had we studied the species pair *L. rubicunda* and *L. dubia*, a negative relationship, which corresponds to trait compensation would have been found. The species with poor morphological defense showed stronger antipredator behavior. Currently, we have no explanation for the pattern observed, but our working hypothesis is related to species abundance of *Leucorhina* in relation to fish presence/absence in lakes. Fish do influence abundance of many aquatic organisms (Wellborn et al., 1996), and comparative studies on other species that differ in their abundance in lakes with and without fish might be rewarding with regard to our understanding of the patterns and evolution of the relationship between morphological defense and antipredator behavior.

In our study area, we have found *L. albifrons* in only two lakes, which both contain fish, and we have never found it in a lake without fish, even though we have sampled 34 lakes. In contrast, *L. dubia* and *L. rubicunda* have much lower abundance in lakes with fish compared with lakes without fish (Johansson and Samuelsson, 1994, Johansson F, unpublished data). The average abundance from standardized sweep net samples in lakes with fish ($n = 7$) is 1.8 and 2.5 for *L. dubia* and *L. rubicunda*, respectively, and the corresponding figures for lakes without fish ($n = 9$) is 13.9 and 7.2. *L. albifrons* might be adapted to coexisting with fish and therefore has long spines and a relatively low activity, that is, it shows cospecialization, which provides protection against fish predation. In contrast, *L. dubia* and *L. rubicunda* co-occur with fish only occasionally, and *L. dubia* presumably saves the cost of the morphological defense by being more active. In conclusion, our results suggest that *L. albifrons* enhances overall defense, whereas *L. dubia* tries to save the cost of using the morphological defense, and *L. rubicunda* shows low

activity because it displays no morphological defense. In addition, *L. rubicunda* showed no response in activity to the presence of fish, which further strengthens our interpretation that the species with the least morphological defense showed the strongest fixed anti-predator behavior. However, more experiments are needed to confirm that the low activity of *L. rubicunda* is an antipredator behavior.

We would like to stress that although there were differences in the behavior of *L. dubia* between lakes, the relationships between species regarding activity does not depend on lake origin. For example, it could be argued that larvae from lake Täftebölesjön are less active and therefore if *L. rubicunda* larvae from lake Mjösjön had been studied instead, then this species would have been more active than was *L. albifrons*. However, the relationship between *L. dubia* and the sympatric species would still be the same, given that lake origin does not affect relative activity of the species.

It could be argued that trait compensation would be the expected relationship in the *Leucorrhinia* system, because this relationship is the most commonly observed in other studies, and several explanations could be put forward to why we did not find trait compensation. First, larvae may differ in some other antipredator behavior that we did not measure. Although this might be the case, activity has been shown to be very important for predation risk (Skelly, 1994), and hence, any adjustment in activity should influence predation risk. Second, the activity differences observed among species could reflect the time left until emergence. When larvae are close to emergence, they reduce activity, and early emerging species should therefore show less activity. However, the order of emergence in our three species did not reflect the behavior pattern observed. Activity decreases in the following order: *L. dubia*, *L. albifrons*, and *L. rubicunda*. The order of emergence is *L. rubicunda*, *L. dubia*, and *L. albifrons* (Valle, 1938). Third, larvae might differ in habitat choice, which in turn might make them differentially vulnerable to predation. For example, *L. rubicunda* might use a much more risky microhabitat and therefore not behave very actively or not show a flexible response to the presence of the predator. All larvae were sampled within the same macrohabitat, that is, at a depth of 0.1–0.5 m along the shoreline, but unfortunately, we have no data on microhabitat use in the larvae of these species. Hence, we conclude that trait compensation, as a single explanation for our result, seems unlikely in system we have studied.

The spines of the *Leucorrhinia* larvae point backward, and therefore, their protection potentially works best when a larva is attacked from behind. Our results suggest that the direction of an attack is important. When a larva was attacked from the front, species did not differ in escape probability, but when attacked from behind, the long-spined species had a higher escape probability. Similarly, when the long-spined *L. albifrons* was devoured, it was always when it was attacked from the front, whereas this was not the case for the other two species. Similar results with respect to attack direction and rejection of attacked prey have been found in stonefly larvae, which possess stiff abdominal cerci (Otto and Sjöström, 1983). Furthermore, the size of larvae differed between our *Leucorrhinia* species. We expected fish to have more difficulties handling larger larvae and, hence, the survival probability of larger larvae would be higher (Christensen, 1996). We did not, however, find support for this pattern, which further strengthens our suggestion that spine size is important for survival probability in these larvae. Although all larvae in our experiments were eventually devoured, rejected larvae in a natural environment would have a higher probability of escaping, because many larvae did survive their first attack. The structural complexity in the littoral zones where

dragonfly larvae live should increase the chances of escaping a second attack after being rejected.

Spines might also be adaptations to factors other than predation. It has been suggested that spines provide an advantage when larvae are moving among the vegetation (Aguilar, 1989), act as a backstop that reduces recoil during protraction of the labium (Nestler, 1980), or help to avoid sinking into the substrate (Corbet, 1957). Another benefit could be that spines help stabilize larvae during jet propulsion in the water column. More work regarding alternative use of these spines is certainly needed.

Trait compensation is the commonly observed response between traits used to avoid predation (Abrahams, 1995; DeWitt et al., 1999; Rundle and Brönmark, 2001). We are only aware of one other study in which cospecialization has been showed. That study showed that snails that were morphologically protected showed a stronger antipredator behavior than less protected snails (DeWitt et al., 1999). We suggest that cospecialization is more common than suggested from the literature and that more examples will be found if they are looked for. We should be able to find species or genotypes with strong morphological defense in systems with a high predation risk. In such systems we should also expect to find animals with a high antipredator behavior. Hence, in such systems animals (relative to others) might benefit from having superior morphological defense in addition to having a strong antipredator behavior.

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REFERENCES

- Abrahams MV, 1995. The interaction between antipredator behaviour and antipredator morphology: experiments with fathhead minnows and brook sticklebacks. *Can J Zool* 73:2209–2215.
- Aguilar SDS, 1989. What is the function of the dorsal hooks and lateral spines in larval dragonflies (Anisoptera)? *Notul Odonatol* 3:43–44.
- Askew RR, 1988. *The dragonflies of Europe*. Colchester: Harley Books.
- Benke AC, 1970. A method for comparing individual growth rates of aquatic insects with special reference to the Odonata. *Ecology* 51:328–331.
- Benke AC, Benke SS, 1975. Comparative dynamics and life histories of coexisting dragonfly populations. *Ecology* 56:302–317.
- Butler MJ, 1989. Community responses to variable predation: field studies with sunfish and freshwater macroinvertebrates. *Ecol Monogr* 59:311–328.
- Christensen B, 1996. Predator foraging capabilities and prey antipredator behaviours: pre- versus postcapture constraints on size dependent predator-prey interactions. *Oikos* 76:368–380.
- Corbet PS, 1957. Larvae of east African Odonata. 6–8. *Entomologist* 90:28–34.
- Corbet PS, 1999. *Dragonflies: behavior and ecology of Odonata*. Ithaca, New York: Cornell University Press.
- Crawley MJ, 1993. *GLIM for ecologists*. Oxford: Blackwell Science.
- DeWitt TJ, Robinson BW, Wilson DS, 2000. Functional diversity among predators of a freshwater snail imposes an adaptive trade-off for shell morphology. *Evol Ecol Res* 2:129–148.
- DeWitt TJ, Sih A, Hucko JA, 1999. Trait compensation and cospecialisation in a freshwater snail: size, shape and antipredator behaviour. *Anim Behav* 58:397–407.
- Dodson S, 1988. The ecological role of chemical stimuli for the zooplankton: predator avoidance behavior in *Daphnia*. *Limnol Oceanogr* 33:1431–1439.
- Edmunds M, 1974. *Defence in animals*. Harlow: Longman.

- Henrikson B-I, 1988. The absence of antipredator behaviour in the larvae of *Leucorrhinia dubia* (Odonata) and the consequences for their distribution. *Oikos* 51:179–183.
- Henrikson B-I, 1993. *Sphagnum* mosses as a microhabitat for invertebrates in acidified lakes and the colour adaptation and substrate preference in *Leucorrhinia dubia* (Odonata, Anisoptera). *Ecography* 16:143–153.
- Johansson F, 1993. Intraguild predation and cannibalism in odonate larvae: effects of behaviour and zooplankton availability. *Oikos* 66: 80–87.
- Johansson F, 2000. The slow-fast life style characteristics in a suite of six species of odonate larvae. *Freshwater Biol* 43:149–159.
- Johansson F, Samuelsson L, 1994. Fish-induced abdominal spine length of *Leucorrhinia dubia* (Odonata) larvae? *Oecologia* 100:74–79.
- Lima SL, 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspective. *Adv Stud Behav* 27:215–290.
- Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640.
- Lively CM, 1986. Competition, comparative life histories, and maintenance of shell dimorphism in a barnacle. *Ecology* 67:858–864.
- Lüning J, 1995. How do predator-induced changes affect prey vulnerability? larvae of *Chaoborus flavicans* (Diptera: Chaoboridae) feeding on *Daphnia pulex* (Crustacea: Cladocera). *Freshwater Biol* 34:523–530.
- Macan TT, 1975. Structure of the community in the vegetation of a moorland fishpond. *Verh Int Verein Limnol* 19:2298–2304.
- McLean EB, Godin J-GJ, 1989. Distance to cover and fleeing from predators in fish with different amounts of defensive armour. *Oikos* 55:281–290.
- McPeck MA, 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecol Monogr* 68:1–23.
- Nestler JM, 1980. Niche relationships of the Anisoptera nymphs of lake Isaqueena (PhD dissertation). Clemson, South Carolina: Clemson University.
- Nilsson B-I, 1981. Susceptibility of some Odonata larvae to fish predation. *Verh Int Verein Limnol* 21:1612–1615.
- Otto C, Sjöström P, 1983. Cerci as antipredator attributes in stonefly nymphs. *Oikos* 41:200–204.
- Pettersson LB, Brönmark C, 1997. Density dependent costs of an induced morphological defence in crucian carp. *Ecology* 78: 1805–1815.
- Pettersson LB, Nilsson PA, Brönmark C, 2000. Predator recognition and defence strategies in crucian carp, *Carassius carassius*. *Oikos* 88: 200–212.
- Pierce CL, 1988. Predator avoidance, microhabitat shift, and risk sensitive foraging in larval dragonflies. *Oecologia* 77:81–90.
- Rask M, 1986. The diet and feeding activity of perch, *Perca fluviatilis* L., in a small lake in southern Finland. *Ann Zool Fenn* 23:49–56.
- Rundle SD, Brönmark C, 2001. Inter- and intraspecific trait compensation of defence mechanisms in freshwater snails. *Proc R Soc Lond B* 268:1463–1468.
- Sih A, 1987. Predators and prey life style. In: *Predation: direct and indirect impacts on aquatic communities* (Kerfoot WC, Sih A, eds). Hanover, New Hampshire: University Press of New England; 203–224.
- Skelly DK, 1994. Activity level and the susceptibility of anuran larvae to predation. *Anim Behav* 47:465–468.
- Suhling F, Lepkojus S, 2001. Differences in growth and behaviour influence asymmetric predation among early-instar dragonfly larvae. *Can J Zool* 79:854–860.
- Tollrian R, Harvell CD, 1999. *The ecology and evolution of inducible defence*. Princeton, New Jersey: Princeton University Press.
- Valle KJ, 1938. Zur Ökologie der finnischen Odonaten. *Ann Univ Turku* 6:1–76.
- Wellborn GA, Skelly DK, Werner EE, 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Ann Rev Ecol Syst* 27:337–363.
- Westman A, Johansson F, Nilsson A, 2000. The phylogeny of the genus *Leucorrhinia* and the evolution of larval spines (Anisoptera: Libellulidae). *Odonatologica* 29:129–136.