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Fish-induced variation in abdominal spine length of *Leucorrhinia dubia* (Odonata) larvae?

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Abstract The lengths of dorsal and lateral spines on abdominal segments 4, 6 and 9 were measured on last-instar larvae of *Leucorrhinia dubia* (Odonata) from seven natural lentic systems containing fish and nine systems lacking fish. Larvae from systems with fish had significantly longer spines than larvae from systems without fish. In contrast, lake/pond area and pH had no effect on the length of spines. The length of the spines was not correlated with larval size, but there was a high correlation between the length of the three spines measured. Also, abundances of *L. dubia* larvae differed between systems, being significantly lower in systems with fish. Laboratory experiments showed that perch (*Perca fluviatilis*) handled long-spined larvae for significantly longer times than short-spined larvae. The results suggest that fish predators may induce morphological defences in insects.

Key words Morphological defences · Spine length
Predator-prey interactions · Handling time · Odonate larvae

Introduction

Animal prey can reduce their mortality risk from predation by developing and adopting morphological, chemical and behavioural defences (Edmunds 1974; Havel 1987; Lima and Dill 1990). Such defence mechanisms may be either genetically fixed, i.e. they occur whether predators are present or not, or induced, i.e. the responses occur only in the presence of predators. It has been suggested that induced defences involve costs, since otherwise responses should be fixed rather than flexible (Dodson 1989; Harvell 1990). Such costs could be reduced growth (e.g. Harvell 1986), reduced fecundity (e.g. Liveley 1986) or delayed reproduction (e.g. Havel and Dodson 1987). However, there are also studies of flexible responses that demonstrate the absence of costs (Spitze 1992 and references therein).

Induced morphological defences include changes in size and shape and the development of spines. Phenotypes with these induced characters are often better protected against the predators that induce them (Havel 1987). Induced morphological changes have most commonly been reported for a restricted set of animal taxa including protozoans, rotifers, cladocerans, bryozoans and barnacles (Havel 1987; Dodson 1989). From these examples two patterns emerge. First, most taxa with predator-induced morphological defences show asexual reproduction during at least one part of their life cycles. Second, there are few examples of induced morphological defences from species-rich groups such as plants, vertebrates and insects.

Odonate larvae are frequently preyed upon by fish (Crowder and Cooper 1982; Martin et al. 1991; Diehl 1993). One common feature, at least in the majority of the species in the suborder Anisoptera (Odonata), is the presence of conspicuous spines on the abdomen of the larvae. The larvae of one of the most common odonates in northern Sweden, *Leucorrhinia dubia* (Johansson 1993), have several spines on the abdomen. These spines are often used for species identification in larval keys (Askew 1988; Heidemann and Seidenbush 1993). However, at least in northern Sweden these spines are useless for species identification in the genus *Leucorrhinia* since there is great individual variation in the number and length of abdominal spines. Preliminary observations suggest that some of this variation in spine length is correlated with the presence or absence of fish. The purpose of this study was to test the hypothesis that larvae of *L. dubia* from systems with fish had longer abdominal spines than larvae from systems lacking fish. We predicted that larvae from systems with fish should have longer abdominal spines since this would provide better protection against predation. Since it has been suggested that *L. dubia* larvae have weak antipredator behaviour (Henrikson 1988), we also predicted that systems with fish should have lower abundances of *L. dubia* larvae. Final-

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ly, since animals with induced morphological defences such as spines are often better protected against their predators (Havel 1987), we predicted that fish should have longer handling times when consuming larvae with long spines than those with short spines.

Materials and methods

Field survey

L. dubia, which has a semivoltine life cycle (Norling 1984), is a common, and often the most dominant, anisopteran species in bog-ponds and similar acidic waters in Sweden (Norling 1984; Henrikson 1988; Johansson 1993). We sampled *L. dubia* larvae in a random order from seven lentic waters with fish and nine lentic waters without fish in August and September 1993. The study ponds and lakes (Table 1) are situated in northern Sweden within a distance of about 100 km south-west to north-west of Umeå. The presence of fish was determined by visual inspection and/or electrofishing and by information from local fishermen. We also measured pH and estimated the area of each water body. To assess the relative abundance of *L. dubia* larvae, we took five qualitative samples in each water body by sweeping a dip net (diameter 26 cm, mesh size 1.0 mm) along the shoreline at a depth of 20–40 cm. Each sweep covered 1.2 m. To estimate abdominal spine lengths of *L. dubia* larvae, we took additional qualitative samples until we had collected at least nine last-instar larvae from each lake/pond. Last-instar larvae of *L. dubia* measure about 17–19 mm in length and about 5.2 mm in head width. Larvae were hand-sorted alive in the field and then preserved in ethanol for later identification, counting and spine measurement in the laboratory. On all last-instar larvae we measured head width, the lengths of the dorsal spines on segments 4 and 6, and the length of the lateral spine on segment 9. These spines are hereafter referred to as spines 4 (D4), 5 (D5) and 9 (L9) respectively. Spine lengths were measured under a dissection microscope at 25× magnification, as shown in Fig. 1.

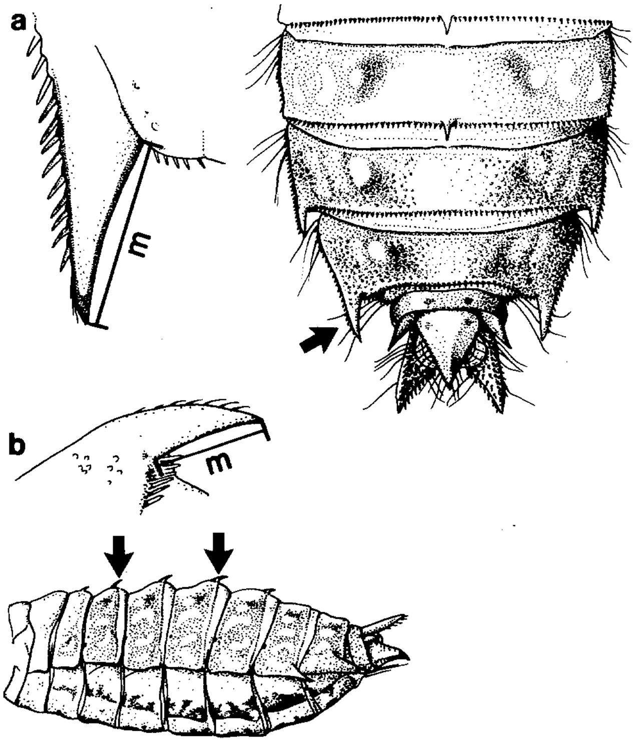

Fig. 1a, b Abdominal segments and spines of a typical *Leucorrhinia dubia* larva from a lake with fish. **a** Dorsal view of a lateral spine on segment 9 (*arrow*); **b** lateral view of the dorsal spines on segments 4 and 6 (*arrows*); *m* indicates where measurements of spine length were made

Laboratory predation experiments

European perch (*Perca fluviatilis*), which is probably the most common and widespread fish species in Sweden (Svärdson and Nilsson 1985), was used as the predator on *L. dubia* larvae in handling time experiments. The experiments were performed in 105-l aquaria (area 100×30 cm, height 35 cm) illuminated by fluorescent lamps on a 14 h light/10 h dark cycle during October 1993. The aquaria were filled with 80 l tap water (18±1°C) and divided with a non-transparent Plexiglas lid into two compartments: a "non-vegetated" compartment and a "vegetated" one. The latter contained four centrally arranged buoyant plastic cords (length 35 cm, diameter 3 mm). The cords were 4 cm apart and attached to a small non-buoyant plexiglass plate. Perch which had been collected from two lakes in the vicinity of Umeå were allowed to acclimatise for 2 weeks prior to the experiments. During this period they were held in the non-vegetated compartment but fed in the vegetated one. For feeding, the lid was lifted and an earthworm was released in the artificial vegetation. In this way the perch were trained to feed in the vegetated compartment.

We measured the handling times of two size classes of perch when feeding on last-instar larvae of *L. dubia* with long and short spines. Larvae for the measurements of handling time were collected from Nydalasjön and Trehörningsmyran (Table 1). Larvae were assigned to long- and short-spined categories according to the length of the easily measured lateral spine. Since there is a good correlation between the lengths of different spines (see below) this did not bias our results. In addition, long-spined larvae used in experiments had a dorsal spine on their sixth abdominal segment whereas short-spined larvae lacked this spine. The mean lateral spine length of short-spined larvae was 0.49 mm ±0.009 SE and 0.50 mm ±0.009 SE for experiments with small and large perch, respectively. The mean spine length of long-spined larvae was 0.70 mm ±0.010 SE and 0.71 mm ±0.008 SE for small and large perch experiments, respectively. Eleven small (mean length 14.9 cm, range 13.0–16.5) and nine large (mean length 18.9 cm, range 17–21.5) perch were used within each larval category. We chose these two size classes because they are often the dominant ones in north Swedish lakes (Alm 1946). An observation of handling time was started with the introduction of one *L. dubia* larva to the centre of the vegetated compartment. After a larval acclimatisation period of 3 min, the lid was lifted and the perch was allowed to prey on the larva. We measured handling time as the time from the capture of a larva until mastication movements had stopped. Each perch was fed with three larvae of the same spine length, and the mean handling time from these three trials was used for further analysis. Individual perch were used in one experiment per larval spine category.

All statistical calculations were performed with the SYSTAT package (Wilkinson 1988). We tried to use parametric statistics, and when the assumptions of normality and homoscedasticity were not met data were transformed. When transformations were unsuccessful we used non-parametric statistics.

Results

Field experiments

The abundance of *L. dubia* larvae was negatively affected by the presence of fish (Table 1). An ANCOVA of larval abundance with presence or absence of fish as factor and pH and area as covariates showed that there was no

Table 1 Acidity (pH), area (ha) and abundance (mean no. of individuals/sample) of *Leucorrhinia dubia* larvae in the lakes and ponds sampled. Two kinds of sampling were performed: one quantitative, for abundance (*abund.*), and one qualitative for measurements of spine lengths (*n*). Also included are mean size (head width in mm), mean lengths (mm) of mid-dorsal spines on abdominal segments 4 (D4) and 6 (D6), and mean length (mm) of lateral spine on abdominal segment 9 (L9) of last-instar *L. dubia* larvae. Values within parentheses are SE; *n* is number of individuals used for measurements of spines

Lake With fish	pH	Area	Abund.	*n*	Size	D4	D6	L9
Nydalasjön	6.8	160.0	1.4 (0.7)	15	5.1 (0.02)	0.24 (0.006)	0.21 (0.026)	0.63 (0.019)
Dalsjön	5.6	16.2	1.4 (0.2)	9	5.1 (0.03)	0.25 (0.014)	0.26 (0.035)	0.65 (0.030)
Fisktjärn	5.0	2.2	0.0	19	5.1 (0.03)	0.24 (0.011)	0.14 (0.024)	0.64 (0.025)
Abborrjärn	7.1	7.6	1.2 (0.5)	9	5.2 (0.02)	0.23 (0.018)	0.12 (0.039)	0.54 (0.022)
Maratjärn	4.8	0.3	6.2 (4.3)	9	5.2 (0.03)	0.25 (0.020)	0.25 (0.052)	0.68 (0.031)
V. Idtjärnen	6.6	0.3	0.6 (0.4)	14	5.1 (0.03)	0.29 (0.013)	0.31 (0.034)	0.73 (0.020)
Skravelsjön	6.0	5.7	0.0	12	5.2 (0.02)	0.29 (0.023)	0.37 (0.028)	0.70 (0.020)
Lake Without fish								
Trehörningsmyran	5.5	0.1	29.2 (5.2)	46	5.2 (0.02)	0.17 (0.007)	0.05 (0.006)	0.56 (0.011)
Finkarsberget	4.8	0.1	11.2 (3.1)	29	5.1 (0.02)	0.21 (0.006)	0.07 (0.010)	0.56 (0.009)
Spelgrunden	4.9	0.1	16.6 (3.8)	26	5.1 (0.02)	0.18 (0.008)	0.04 (0.006)	0.51 (0.014)
Vitskärsudden	5.4	0.1	6.8 (1.6)	23	5.0 (0.02)	0.14 (0.008)	0.02 (0.002)	0.48 (0.009)
S.W Bussjön	4.5	0.2	23.6 (3.1)	47	5.1 (0.02)	0.16 (0.007)	0.03 (0.002)	0.50 (0.010)
Lomtjärn	6.9	0.6	6.2 (1.0)	27	5.1 (0.03)	0.23 (0.009)	0.15 (0.021)	0.67 (0.015)
S. Långtjärn	6.8	0.3	15.2 (7.1)	30	5.2 (0.02)	0.17 (0.008)	0.05 (0.006)	0.58 (0.015)
Klintsjön	5.9	63.0	6.2 (1.1)	27	5.1 (0.02)	0.24 (0.009)	0.08 (0.019)	0.63 (0.016)
Ståbäckstjärnen	6.3	3.3	10.2 (2.6)	13	5.3 (0.04)	0.21 (0.007)	0.06 (0.014)	0.54 (0.019)

Table 2 ANCOVA of the effect of presence or absence of fish, pH and lake/pond area on the lengths of dorsal (*D*) and lateral (*L*) spines on abdominal segments 4, 6 and 9 of *L. dubia* larvae (pH and area were ln-transformed). Significant *P* values shown in bold type

Source	MS	*df*	*F* ratio	*P*
D4				
Fish	0.27	1	13.44	**0.003**
pH	0.01	1	0.38	0.549
Area	0.01	1	0.64	0.438
Error	0.24	12		
D6				
Fish	2.46	1	19.80	**0.001**
pH	0.04	1	0.36	0.566
Area	0.01	1	0.08	0.781
Error	1.49	12		
L9				
Fish	0.64	1	5.82	**0.033**
pH	0.08	1	0.68	0.426
Area	0.00	1	0.00	0.958
Error	1.31	12		

significant interaction effect between the covariates and the factor. When this interaction term was dropped from the model there was no significant effect of pH and area on abundances of *L. dubia* larvae ($P>0.3$ for both pH and area, and SS=10.82, *df*=12 for the error term), but fish presence had a significantly negative effect on the abundance of *L. dubia* larvae ($P<0.001$).

Abdominal spines of *L. dubia* larvae were longer in systems with fish than in systems without fish (Table 1). An ANCOVA of spine length with presence or absence of fish as factor and pH and area as covariates showed that there was no significant interaction effect between the covariates and the factor. When these interaction terms were dropped from the ANCOVA model there were no significant effects of pH or area on spine length, but the lengths of all three spines differed significantly between fish systems (Table 2, Fig. 2).

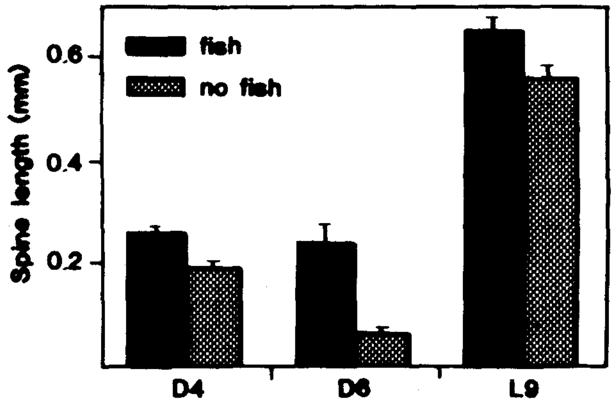

Fig. 2 Mean length (+SE) of dorsal spine on abdominal segment 4 (*D4*) and 6 (*D6*), and lateral spine on segment 9 (*L9*) of *L. dubia* larvae from lakes and ponds with and without fish

Larval head width was not correlated with the lengths of any of the three spines (Bonferroni-adjusted Pearson correlation analysis). This was true for larvae both from systems with fish ($P>0.10$ in all comparisons, *r* range=0.163–0.272, *n*=87) and without fish ($P>0.27$ in all comparisons, *r* range=0.005–0.067, *n*=268). In contrast, there were highly significant correlations between the lengths of all three spines, $P<0.001$ in all comparisons, both in systems with fish (*r* range=0.524–0.603) and without fish (*r* range=0.485–0.552).

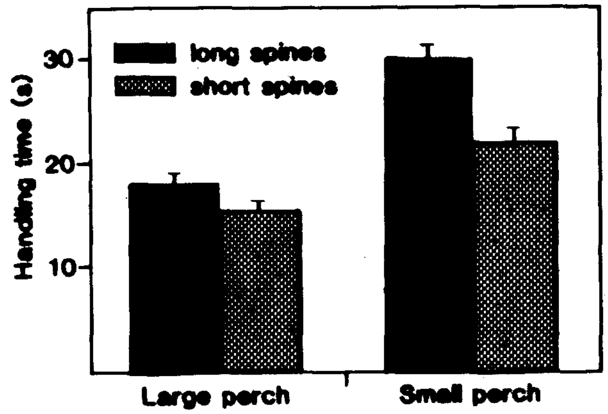

Fig. 3 Mean handling time (+SE) of small and large perch preying on *L. dubia* larvae with long and short spines

Laboratory experiments

All handling-time trials except one resulted in the ingestion of the *L. dubia* larvae by the perch. However, perch occasionally spat out a larva after a successful attack. This was observed three times in small perch, but never in large perch. The trials showed that perch had more difficulties when handling long-spined larvae than short-spined larvae (Fig. 3). A repeated-measure ANOVA with spines as repeated measures showed that perch had a significantly longer handling time on long-spined larvae (P=0.031, $F_{1,18}$=3.81). On the other hand, there was no significant effect of perch size on handling time (P=0.067, F_1=5.51, repeated-measure ANOVA. However, the low significance level of the effect of perch size and of the interaction term between spine size and perch (P=0.064, $F_{1,18}$=3.88) indicates that small perch had more difficulties than large perch in handling long-spined larvae (Fig. 3).

Discussion

This study shows that *L. dubia* larvae from north Swedish systems with fish had longer abdominal spines than larvae from systems without fish. On the basis of our data, we dismiss the hypothesis that abiotic factors such as pH and lake/pond area were significant. Furthermore, since we found no correlation between the length of spines and larval size, we reject the hypothesis that factors which affect larval size, such as resource productivity, might be important. Instead, we will discuss three main biotic hypotheses that might produce the observed differences in spine length: an ecological one, selective predation by fish on short-spined larvae; and two evolutionary ones, genetically fixed local adaptation of *L. dubia* to fish predation, and inducible morphological defences of *L. dubia* larvae in response to fish predators.

Fish are known to be selective predators (Werner and Hall 1974; Zaret 1980; Osenberg and Mittelbach 1989). Such selective predation can be either an active choice or the passive result of differential prey vulnerability (Sih 1987; Peckarsky and Penton 1989; Sih and Moore 1990). Prey vulnerability, in turn, depends on behavioural and morphological traits of the prey. In our system, we would expect prey selection to be a passive result of prey vulnerability, since long-spined larvae were more difficult to handle than short-spined larvae. A longer handling time implies an additional handling cost, and according to optimal foraging theory (e.g. Stephens and Krebs 1986), prey with longer handling times should not be preferred, all else being equal. Thus, our handling-time data indicate that short-spined larvae should be preferred by fish. If fish predation is a significant source of mortality for larval *L. dubia*, this could produce a shift towards long-spined larvae in populations of *L. dubia* in systems with fish.

The difference in spine length between the two types of systems could be a result of local adaptation of *L. dubia* to the presence of fish. If so, genetically determined long-spined larvae are expected to have a higher survival rate, which after some generations should result in populations dominated by long-spined larvae. However, *L. dubia* adults, like most other anisopterans, move randomly over wide areas during their prereproductive period and marked individuals are seldom recaptured at their emergence site (Pajunen 1962). Thus a genetically fixed local adaptation in spine length to fish seems unlikely.

Finally, the longer spine length observed in systems with fish could be an example of a predator-induced response. This hypothesis is supported by the frequency distributions of spine lengths. If predators had induced the observed response in spine length we would expect the frequencies of the spine lengths from systems with and without fish to show two distinct distributions with different means but similar variances (Fig. 4a). If on the other hand selective predation by fish had caused the observed difference, the frequency distribution of spine lengths should have greater variance in systems without fish (Fig. 4b). This is because both short- and long-spined larvae would be found in this system, whereas short-spined larvae should be less frequent in systems with fish. Our data do not show this last kind of distribution; instead they appear more like two distinct peaks (e.g. data for spine 9 plotted in Fig. 4a). Thus, our results favour the predator induction hypothesis. However, additional experiments are needed to provide more support for this hypothesis.

Although most odonate larvae are susceptible to predation by fish, there are great differences between species (Morin 1984; McPeek 1990). Some species, such as *L. dubia,* are extremely vulnerable to fish predation (Henrikson 1988). Henrikson (1988) showed that *L. dubia* larvae did not coexist with fish in southern Sweden, and her laboratory studies showed that fish discovered and caught *L. dubia* larvae more easily than other odonate larvae. However, in a later study Henrikson (1992) states that *L. dubia* larvae are able to coexist with fish under certain circumstances: low fish abundance and large areas of *Sphagnum* mosses. We found support for Henrikson's observation in that abundances of *L. dubia*

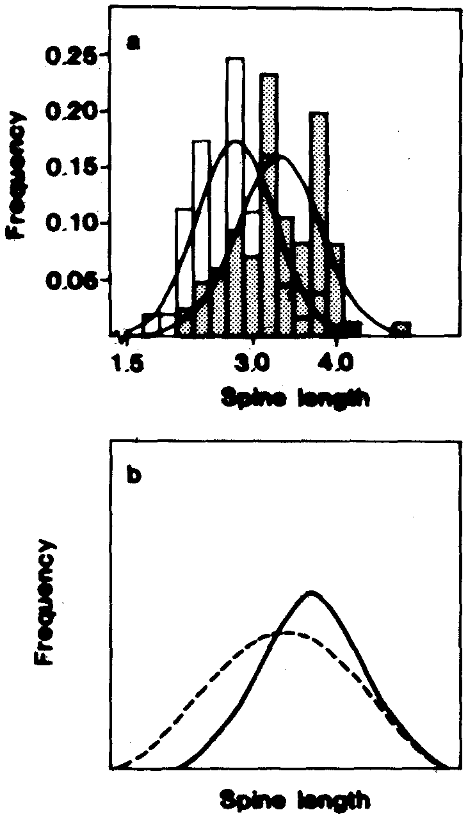

Fig. 4 **a** Frequency distribution of lengths of lateral spine 9 found in this study. *Shaded bars* are systems with fish (n=87) and *unshaded* without fish (n=268). The fitted *curve* is a normal distribution. **b** Hypothetical distributions of spine lengths as a result of prey selection. The *solid line* is a system with fish and the *dashed* line is a system without fish

larvae were much lower in systems with fish than in systems lacking fish. Nevertheless, in contrast to Henrikson, we found that coexistence of fish and *L. dubia* larvae is not uncommon. We can only speculate about this difference. Henrikson's study was performed in southern Sweden while ours was conducted in northern Sweden. It might be that *L. dubia* is more common in northern Sweden, which would allow it to colonise systems with fish more frequently. It might also be that larvae in northern Sweden have longer spines which might reduce predation rate.

If the length of the abdominal spines in *L. dubia* is an induced morphological defence against predators, the production of spines should involve costs as well as benefits. Since we did not detect any correlation between spine length and larval size, the potential costs of longer spines do not seem to be associated with smaller body size. However, long spines may involve other costs such as increased developmental time. If spines involve a cost there should also be an advantage. One of the advantages of long spines could be the longer handling times by predators observed in our experiments. As stated above, prey with longer handling times should not be preferred. This could provide long-spined larvae with a selective advantage over short-spined larvae.

Our results suggest that fish may induce long abdominal spines in *L. dubia* larvae. To our knowledge this would be the second example of induced morphological responses in an insect species and one of the few in an organism with obligate sexual reproduction and a life cycle of several years (see also Brönmark and Miner 1992). However, in both the other insect example (Hershey and Dodson 1987) and this example the final evidence is still lacking. We also showed that long spines may work as a protection against predation in aquatic insect. Reviews on defences in aquatic insects have ignored this kind of defence (Peckarsky 1982; 1984). We suggest that such spines may be very effective against predators regardless of whether they are fixed or induced. Finally, since pronounced spines are very common among odonate larvae as well as many other aquatic insect larvae we agree with Dodson (1989) that many more examples of predator-induced morphological changes may be found if they are looked for.

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