Nature & Environment
Vol. 19 (1), 2014: 19-27
Website: www.natureandenvironment.com

ISSN (Print) : 2321-810X
ISSN (Online) : 2321-8738

RESEARCH ARTICLE

Reaction Norms and Production Costs of Predator-induced Morphological Defences in a Larval Dragonfly (*Brachythemis cataminata*)

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Received: 1st Dec. 2013, Revised: 22nd Dec. 2013, Accepted: 2nd Jan 2014

ABSTRACT

To understand the evolution and ecology of inducible defence we need to understand the genetics and costs underlying this phenomenon. It has been suggested that the abdominal spines of odonate larvae work as a defensive trait, and that the presence of fish predators induces the production of longer abdominal spines. I performed a laboratory experiment in which I raised 30 families of Brachythemis Contaminata larvae in the presence of absence of fish. environment interaction, suggesting the potential for evolution of plasticity of the traits. No production costs could be found with respect to development time and size at final instar.

Key words: *Reaction Norms, Production Costs, Brachythemis cataminata*

INTRODUCTION

To coexist with predators, prey express traits that reduce the impacts of predation. Morphological adaptations such as protective spines or armour represent one type of defence against predation (Edmunds 1974). The world is heterogeneous, however, and predators are not present in all habitats (Tonn and Magnuson 1982). One way to "deal" with such heterogeneity in predator abundance is to produce the morphological defence only in the presence of predators.

An understanding the genetics of predator-induced defences can best be achieved by studying the reaction norm of the defence trait. . If the reaction norms of different genotypes run parallel, there is potential for evolution of the trait in a single environment but not for plasticity per se. For plasticity to evolve, variation in plasticity among gentoypes is necessary. When the genetics and reaction norms of predator-induced morphological defences are explored, information on the costs of plasticity can also be gained. Most models of the evolution of inducible defences assume some form of cost, because in the absence of any cost, it is predicted that individuals will produce a constitutive defence true cost of plasticity. I will focus only on production costs in this paper. Character-production costs are important to determine because they assess the net value of plasticity, i.e., the costs of producing a character when it is not necessary (De Witt *et al.* 1998).

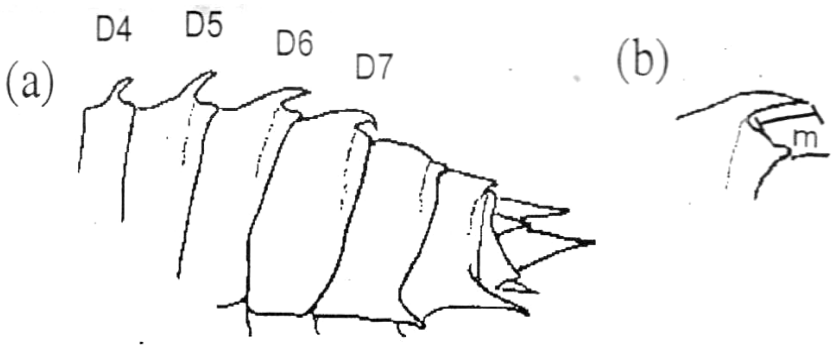
In this study I measure the reaction norms of dorsal spine length and the cost of producing longer spines in larvae of the dragonfly *Brachythemis Contaminata* (Van der Linden). Like many other dragonfly larvae. *Brachythemis Contaminata* larvae posses prominent lateral and dorsal spine on the abdomen (Fig.1a) . These spines have been hypothesized to be a defence against predators (Johansson and Samuelsson 1994) in the same way that the spines of sticklebacks (Reist 1980a) and daphnids (Kolar and Wahl 1998) provide protection from predation by fish. In support of this, Johansson and Samuelsson (1994) showed that handling time was longer when fish preyed of *Brachythemis Contaminata* larvae with long spines than when they preyed on larvae with short spines. Recent data suggest that larvae with long spines have a higher probability of escape from an attack by fish (F. Johnasson, unpublished data). In addition, Johansonn and Samuelsson (1994) found that larvae from lakes with fish had much longer spines than larvae from lakes without fish,

suggesting that fish induce changes in spine morphology in the larvae. Arnqvist and Johansson (1998) verified this by showing that laboratory-reared larvae raised with fish had a different spine shape from those raised in the absence of fish. To date we have no knowledge about the reaction norms of these spine changes and no estimates of production costs.

MATERIALS AND METHODS

Eggs from 30 female *Brachythemis Contaminata* were collected in June 2006 from a small fishless pond in the vicinity Agra. Females were induced to oviposit eggs by the method of Boehms (1971). The 30 egg clutches were brought to the laboratory, where they hatched after about 2 weeks. Upon hatching, eight first-instar individuals from each clutch (family) were used for rearing. Each family group of eight was divided into two groups of four, which were raised in either the presence or the absence of fish until they reached the final instar about 1 year later. Sibs were probably close to being full sibs, since the proportion of eggs fathered by a second male to mate varies between 0.10 and 0.00 for species (including the congeneric) in the family Libellulidae (Simmons and Siva-Jothy 1998). Each larvae was held separately in a small transparent plastic cup (height 8 cm, diameter 7 cm). Four such cups, i.e., one half of each family clutch, were held in a plastic tub (height 13 cm, diameter 33 cm) filled with tap water to a depth of 11 cm. A piece of Styrofoam (20x20 cm) with holes drilled in a circle with the appropriate diameter was used as a floating device for the cups. To allow water circulation between the floating cups and the tubs, 10 small holes (diameter 0.4 nu II) were punched in the lower end of each cup. The plastic tubs were placed in a walk-in climate room with a temperature of 20 $\pm$ 1^{0}C and a light level set to a 14 h light : 10 h dark cycle. To induce longer spines in larvae, one perch *Perca fluviatilis* (initial length range 3-4 cm).

Fig. 1: (a) Abdomen of a *Brachythemis Contaminata* larva, showing the dorsal spines. D4-D7 are the spines measured on abdominal segments 4-7 (b) Closeup of an individual spine; m indicates where spine length was measured



The perch is one of the most common fish predators in Indian lakes (Svardson 1976; Johansson and Persson 1986) and its diet include odonates (Rask 1986). The larvae in the transparent cups thus received visual, chemical and mechanical cues from the perch in the tubes. In summary a 2 x 30 experimental design was used, and each climate room housed one half of each female's clutch accommodated in four plastic cups in 30 plastic tubs. To minimize environmental effects from the rooms, the tubs were shifted between rooms twice a month.

The odonate larvae were fed protozoans during their first month, and thereafter brine shrimp until they were 6 months old. From this age until the final instar (about 11-12 months of age) they were fed a mixture of worms (enchytraeidae) and Daphina pulex. All prey animals were from laboratory cultures. Larvae were fed every second day for the whole rearing period and all larvae received the same food ration. The perch in the fish tubs were fed commercial chironomid larvae twice a week,

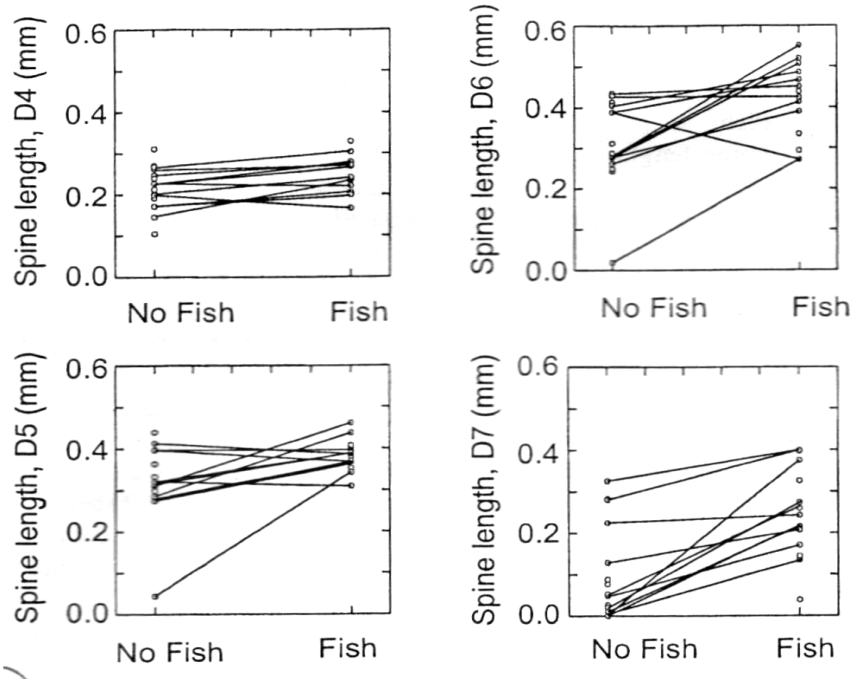
and during the first 6 months they were also fed once a week with two *Brachythemis Contaminata* larvae taken from a fishless bog pond.

When larvae had moulted into their final instar they were preserved in 70% ethanol. Since larval growth is exponential, no overlap between the sizes of final-instar larvae is evident. The time from hatching of the egg to the final instar was used as the development time. The final instar was determined by comparing the head with width measured in this study with the head-width histograms obtained in another study (F. Johansson, unpublished data). Spine length was estimated by digitizing landmark data. Larvae were viewed from the side in a dissection microscope (Leica® MZ8) and the image was projected through a camera lucida onto a digitizing tablet (Summasketch ® III). Data were recorded for the dorsal spine on segments 4-7, hereinafter referred to as spines D4-D7. Two landmarks were used to characterize the length of each spine (Fig. 1b). Head size, which is the most reliable measure of length in dragonfly larvae (Benke 1970), was estimated using two landmarks representing the outer-most points on each eye when the larva was viewed from above. All landmark data were collected with the computer program DS-Digit (Slice 1994).

STATISTICAL ANALYSIS

The 30 original families, 21 produced offspring that survived untilt he final instar, and 14 of these had offspring that survived in both treatments. Analysis of the spines were Fig.2 Reaction norms of dorsal spin length to fish treatment (fish absent or present).

Fig. 2: Reaction norms of dorsal spin length to fish treatment



Since the design is unbalanced with empty cells, analysis was done using type IV sums of squares. The analysis was run in SPSS (SPSS inc. 1998) and data were In-transformed before analysis to equalize variance and improve normality. I also ran the model using restricted maximum likelihood fitting in SAS PROC MIXED module (Littell, *et al.* 1996) as suggested by Shaw (1987). These runs gave similar results to the mixed-model ANOVA in SPSS.

Potential costs of producing longer spines could be related to growth variables such as body size at maturation and time to maturation, which in many cases are important variables contributing to

fitness (Rowe and Ludwig 1991; Roff 1992). Large body size often implies higher reproductive success, and a long time to maturation usually implies a risk of emerging too late in the season. I used size at final instar and time to final istar as characters that are potentially affected by production costs. To eliminate container effects that could be erroneously attributed to family, the mean value for each family was used for estimating production costs. I estimated costs of spine production using principal component analysis (PCA), since size and growth rate of spines might be correlated. Spine lengths were in-transformed to homozenize variance and were thereafter entered into a single matrix. The PCA was run on the correlation structure among the variables. Since 70% of the variance was explained by the first principal component (PC), I used the scores from this component for further analysis with two separate analyses of covariance (ANCOVAs). Fish treatment was entered as factor, spine score (spine length) as covariate, and body size at final instar (head which) and time to final instar as dependent variable. The PCA and ANCOVAS were run in SYSTAT (SPSS Inc. 2000).

REPEATABILITY

To assess the reliability of the morphological measure ments, Lesses and Boag's (1987) method of repeatability was used. Three repeated measures of all measurements for each of the individual larvae were taken. Thereafter data were analysed in a one-way ANOVA. Repeatability of the measurements was high for all traits measured: 0.87, 0.94, 0.98, 0.96 and 0.91 for larval length and length of spines D4-D7, respectively.

Table 1 : Results of ANOVAs on Spine Length in the Dragonfly *Brachythemis Contaminata* of the Effects of Environment (Fish Absent or Present) and Genotype (Family).

Character and source	df	Mean square	F	P
D7				
Environment (E)	1	44.29	8.26	**0.014**
Genotype (G)	17	9.14	1.61	0.232
G & E	10	5.42	1.14	0.379
Error	21	4.74		
D6				
Environment (E)	1	2.52	5.60	**0.039**
Genotype (G)	17	0.97	1.79	0.178
G & E	10	0.49	7.73	0.178
Error	21	0.06		
D5				
Environment (E)	1	0.85	2.65	0.13
Genotype (G)	17	0.49	1.27	0.359
G & E	10	0.35	14.94	**<0.001**
Error	21	0.02		
D4				
Environment (E)	1	0.09	3.58	0.083
Genotype (G)	17	0.09	3.49	**0.037**
G & E	10	0.02	3.49	0.037
Error	21	0.02		

Note: D7-D4 are the dorsal spines on abdominal segments 7-4. P values in boldface type are significant.

RESULTS

REACTION NORMS:

Clearly, the presence of fish increased spine length, mean lengths being 96, 31, 19 and 11% greater for spines D7-D4, respectively (Fig. 2, Appendix A). While spines D6 and D7 showed a strong, significant response, spines D4 and D5 showed a much weaker response, with only a tendency

towards significantly longer spines in the presence of fish (Table 1). Except for spine D4, spine lengths did not vary significantly among families (genotypes) (Table 1). For spines D6 and D5 there was a strong treatment x family (genotype (G) x environment (E)) interaction, but no such interaction was found for spines D4 and D7.

Table 2: Summary of ANCOVAs on the Effect of Body Size at Final Instar and Time to Final Instar with Fish Treatment as Factor and Spine Length as Covariate

Source	df	Mean square	F	P
Size at last instar				
Fish	1	0.001	0.28	0.60
Spine length	1	0.009	2.20	0.15
Error	26	0.004		
Time to last instar				
Fish	1	123.54	0.52	0.47
Spine length	1	227.77	0.97	0.33
Error	26	235.23		

Appendix A: Data on Body Size at Final Instar and Time to Final Instar and Length of Abdominal Spins 4-9 (D4-D7) of *Brachythemis cataminata* from the Rearing Experiment

Individual	Head Width	Time	D7	D6	D5	D4
N19:1	5.003	330	0.0768	0.2874	0.2874	0.2395
N43:1	5.287	383	0.0544	0.2975	0.3821	0.2531
N14:1	5.144	338	0,0011	0.0200	0.0550	0.1831
N14:3	5.003	350	0.0002	0.0189	0.0324	0.1070
N34:1	5.069	337	0.2985	0.4271	0.3052	0.2193
N34:2	5.078	357	0.3544	0.4434	0.3356	0.1781
N27:1	5.123	328	0.1945	0.4278	0.4119	0.2833
N27:3	5.111	363	0.0358	0.3406	0.4402	0.2790
N27:4	5.042	363	0.0008	0.3900	0.2950	0.2219
N4:1	5.106	335	0.0002	0.2432	0.832	0.1712
N9:1	5.095	375	0.0484	0.2804	0.3104	0.2268
N26:1	5.151	350	0.0002	0.2706	0.3191	0.2135
N26:2	5.165	341	0.0307	0.3143	0.2970	0.1913
N26:3	5.210	335	0.0022	0.3512	0.3826	0.2338
N33:1	5.012	346	0.2678	0.4579	0.3587	0.2278
N33:2	5.245	358	0.2847	0.4401	0.4421	0.3118
N33:3	5.195	352	0.2828	0.4290	0.3836	0.2292
N13:1	5.075	365	0.0282	0.2986	0.2908	0.2296
N13:2	5.001	365	0.0002	0.2760	0.324	0.2520
N13:3	5.101	366	0.0006	0.1512	0.2779	0.2390
N13:4	5.114	361	0.0556	0.3211	0.3927	0.2697
N8:1	5.116	373	0.0265	0.2770	0.2744	0.2021
N12;1	5.111	370	0.0002	0.2805	0.3978	0.1917
N42;1	5.033	349	0.1285	0.3885	0.3958	0.2395
N31:1	5.231	364	0.0004	0.0928	0.1832	0.1800
N31:2	5.245	381	0.2500	0.4616	0.4299	0.2405
N44:1	5.169	321	0.1749	0.4658	0.3713	0.2848
N44;2	5.105	347	0.0004	0.3928	0.3552	0.2497
N36:1	5.187	357	0.2811	0.4053	0.4389	0.3113
N24:1	5,082	378	0.2252	0.4132	0.3142	0.2632
F24:1	5.127	377	0.2426	0.3861	0./4611	0.3042
F12:1	5.092	344	0.3752	0.5514	0.3958	0.1993
F4:1	5.119	339	0.0325	0.4443	0.3014	0.1478

F4:2	5.093	345	0.3994	0.5994	0.4336	0.2626
F34:1	5.040	327	0.3987	0.4513	0.3090	0.2418
F42:1	5.089	325	0.1776	0.4358	0.3344	0.2419
F13:1	5.098	350	0.2714	0.4016	0.3575	0.2406
F13:2	5.051	359	0.2496	0.3739	0.4126	0.2925
F13:3	5.225	351	0.2997	0.4668	0.4385	0.3056
F27:1	5.097	350	0.1415	0.2748	0.3311	0.2529
F27:2	5.225	361	0.1642	0.3728	0.3555	0.2881
F27:3	5.172	362	0.0790	0.3523	0.3787	0.2842
F27:4	5.092	354	0.0999	0.4213	0.3773	0.2320
F35:1	5.144	332	0.3261	0.4248	0.4066	0.2715
F15:1	5.111	346	0.0230	0.1807	0.3952	0.2628
F15:2	5.042	344	0.0540	0.4060	0.3782	0.2137
F14:1	5.123	344	0.2738	0.3164	0.3299	0.2424
F14:2	5.198	366	0.0236	0.2263	0.3543	0.2267
F19:1	5.142	353	0.2594	0.5066	0.4373	0.2689
F8:2	5.163	355	0.3680	0.5260	0.4029	0.1622
F8:3	5.210	355	0.2644	0.4316	0.3759	0.1581
F31:1	5.387	360	0.2379	0.4814	0.4019	0.2782
F6:1	5.256	389	0.2152	0.3416	0.3965	0.3188
F6:2	5.217	368	0.535	0.3272	0.3933	0.3405
F43:1	5.224	354	0.0724	0.2232	0.2620	0.1796
F9:1	5.186	361	0.2607	0.5581	0.3830	0.2867
F9:2	5.289	361	0.0795	0.4816	0.3782	0.2553
F33:1	5.168	347	0.3977	0.4383	0.3890	0.2715

Where N and F denote larvate raised in the presence and absence of fish, respectively. The numbers refer to the family, the number after the colon refers to the individual within the family. For example, N13:2 is individual number 2 from family number 13 raised in the absence of fish.

COSTS:

In the absence and presence of fish cues, development time of the larvae was 353 $\pm$ 4.2 days (Mean $\pm$ SE; N = 15) and 350 $\pm$ 3.9 days (N=14), respectively, and body size of larvae was 5.09 $\pm$ 0.02 and 5.13 $\pm$ 0.02 mm, respectively. The PCA showed that the first two PC axes mm explained 70 and 16% of the variation in spine length and all four spine lengths were correlated with PCI (loading for spines 7, 6, 5 and 4 was 0.78, 0.94, 0.91 and 0.71, respectively).

The subsequent ANCOVAs showed that neither size (head width) nor development time (time to final instar) was affected by spine length or fish treatment (Table 2). Hence, no evidence of production cost with respect to these two variables could be found. Mortality did not differ between fish and no-fish environments (Mann – Whitney U test, P = 0.80, U = 138) and 30 and 29 individuals survived in the no-fish and fish treatment, respectively.

DISCUSSION

This study is the first on predator-induced reaction norms in an aquatic insect and one of the very few on an animal with obligate sexual reproduction. The results show that the presence of fish does induce the production of longer spines and that families differ in their plasticity. These results support those of Arnqvist and Johansson (1998), who found that the presence of fish induced changes in the shape of the spines in *Brachythemis Contaminata.* That study, however, did not allow a comparison of different genotypes. Lengths of spine D4, the innermost spine measured, showed a genotypic effect but no interaction effect. This suggests that directional selection on spine length in a fish-tree environmental should produce a correlated response in an environment with fish. However, the other spines measured showed no detectable genotypic effect, suggesting the absence of such directional selection. The reaction norms of spines D5 and D6 did cross, suggesting the potential for evolution of plasticity in spine length. Hence, a population in either a fish or a fishless habitat would probably evolve towards being more plastic in spine length. Examining spine length

in *Brachythemis Contaminata* from areas that vary in the time that they have had fish or been fish-free could provide evidence of whether and how fast such evolution is proceeding.

Studies on predator-induced defenses have shown that there is considerable genetic variation in the response of life-history characters to predator cues (e.g., Spitze 1992). This study shows that even characters directly associated with defense, like spines, can show considerable variation in their response. For example, spine D4 showed a significant genotypic response but no G & E effect, and spines D5 and D6 showed a G & E effect but no genotypic response. The underlying genetic causes and possible adaptation of this is an open question requiring further research. For example, is there an adaptive value of no plasticity in the innermost spine (D4) compared with plasticity in the outermost spines (D6 and D7)?

Sibs were not reared in several containers within treatments, therefore it could be argued that some container effects could be attributed erroneously to family. In interpreting the results, two points should be noted. First, only spine D4 showed a family effect. Of all the spines measured, this spine showed the least increase in length in the presence of fish, i.e., a weak response, regardless of whether it was a family or container effect. Second, spines D5 and D6, which showed greater increases in length and the strongest G & E interaction, did not show any family effects.

This study failed to show any cost of spine production for the two traits measured (body size and development time). Similar results, i.e., absence or weak evidence of production costs, have been obtained in other studies (De Witt 1998; DeWitt *et al.* 1998; Scheiner and Berrigan 1998). The absence of any distinct costs in these studies could be interpreted in two main ways. First, cost could have been very low and therefore hard to detect. Second, other kind of costs, such as environmental costs, might be more important and should be looked for (Spitze 1992; Tollrian and Harvell 1999b). In the case of odonate larvae, spines might increase predation success for other predators. Evidence from sticklebacks, which show intra-and inter-specific variation in spine characteristics, suggests that large invertebrate predators such as water beetle larvae have higher predation succession long-spined individuals (Reimchen 1980; Reist 1980b). In contrast, the spines of sticklebacks provide good protection against fish predation (Hoogland *et al.* 1957; Reist 1980a). Hence, in the case of sticklebacks, long spines seem to represent a cost in terms of higher predation from invertebrates but to be beneficial in terms of protection from vertebrate predators. Investigating this in odonate larvae in which longer spines have been induced could provide valuable insight into the costs and benefits of induced defences. Lakes with and without fish differ in invertebrate composition, with fishless lakes having a much higher abundance of large predatory invertebrates (e.g., Eriksson, *et al.* 1980: Mallory, *et al.* 1994). If fish and invertebrate predators differ in their success in preying on animals with different morphological defences, we would expect selection pressure to differ between fish and fishless lakes. Adult female *Brachythemis Contaminata* disperse widely from their native lake during maturation and before egg deposition (Pajunen 1962), therefore plasticity in their morphological defences could be beneficial if predator species differ in their predation success on larvae with different spine morphologies.

Though I have no direct estimates of fitness for the two induced morphs, the two traits used as fitness substitutes are likely to be important for reproductive success in odonates. In odonates, body size of final-instar larvae is positively correlated with size at emergence (Falck and Johansson 2000), and a recent meta-analysis suggests that large size is associated with high lifetime reproductive success in odonaes (Sokolovska, *et al.* 2000). A shorter development time should result in earlier emergence, and Thompson (1997) reviewed evidence that indicated an advantage to odonates of emerging early.

The larvae in this study all came from the same population and one could ask whether populations vary genetically in their reaction norms of defences, as has been shown for daphnid populations (Spitze 1992; Spitze and Sadler 1996). Since adult *Brachythemis Contaminata* disperse during their maturation period, and marked individuals are seldom recaptured at emergence sites (Pajunen 1962), it seems unlikely that great differences exist between populations. Harvell (1998) found no

consistent differences in reaction norms of induced defences in a marine bryozoans with high dispersal ability.

REFERENCES

1. Arnqvist G. and Johansoson F. (1998): Ontogenetic reaction norms of a predation-induced defensive morphology in dragonfly larvae. Ecology, 79: 1847-1858.
2. Benke A.C. (1970): A method for comparing individual growth rates of aquatic insects with special reference to the Odonata Ecology, 51: 328-331.
3. DeWitt T.J. (1998): Cost and limits of phenotypic plasticity: tests with predator-induced morphology and life history in a fresh-water snail: J. Evol. Boil., 11:465-480.
4. DeWitt T.J., Sih A. and Wilson D.S. (1998): Costs and limits of phenotypic plasticity. Trends Ecol. Evol. 13: 77-81.
5. Dodson S. (1989): Predator induced reaction norms: cyclic changes in shape and size can be protective. Bioscience, 39: 447-452.
6. Edmunds M. (1974): Defence in animals. Longman, New York.
7. Eriksson M.O.G., Henrikson L., Nilsson B.-I, Nyman G., Oscarson H.C., Stenson A.E. and Larsson K. (1980): Predator prey relations important for the biotic changes in acidified lakes. Ambio, 9:248-249.
8. Harvell C.D. (1990): The ecology and evolution of inducible defences. Rev. Biol., 65: 323-340.
9. Harvell C.D. (1998): Genetic variation and polypmorphism in the inducible spines of a marine bryozone, N. 1957. The spines of sticklebacks (*Gastrosteus and Pygosteus)* as means of defence against predators *(Perca and Esox*). Behaviour, 10: 205-237.
10. Johnsson F. and Samuelsson L. (1994): Fish-induced abdominal spine length of *Brachythemis Contaminata* (Odonata) larvae? Oecologia, 100: 74-79.
11. Johnsson L. and Persson L. (1986): The fish community of temperate, entrophic lakes. In Carbon dynamics of eutrophic, temperate lakes: the structure and function of the pelagic environment . Edited by B. Reimann and M. Sondergaard. Elsevier, Amsterdam pp. 237-266.
12. Kolar C.S. and Wahl D.H. (1998): Daphnid morphology deters fish predators. Oecologia, 116:556-564.
13. Lessels C.M. and Boag P.T. (1987): Unrepeatable repeatabilities: a common mistake. Auk, 104: 116-121.
14. Littell R.C., Milliken G.A., Stroup W.W. and Wolfinger R.D. (1996): SAS system for mixed models. SAS Institute Inc., Cary, N.C.
15. Mallory M.L., Blancher P.J., Weatherhead P.J. and McNicol D.K. (1994): Presence or absence of fish as a cue to macroinvertebrate adubdance in boreal wetlands. Hydrobiologia, 279/280; 345-351. Pajunen, V.I. 1962. Studies on the population ecology of *Brachythemis Contaminata* V.D. Lind. (Odon, Libellulidae).Ann. zool. Soc. Zool. Bot. Fenn. 'Vanamo', 24: 1-79.
16. 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.
17. Reimchen T.E. (1980): Spine deficiency and polymorphism in a population ofGasterosteus aculeutus; an adaptation to predators. Can. J. Zool., 58: 1232-1244.
18. Reist J.D. (1980a): Selective predation upon pelvic phenotypes of brook sticklebacks, Culea inconstans, by northern pike Esox lucius. Can. J. Zool., 58: 1245-1252.
19. Reist J.D. (1980b): Predation upon pulvic phenotypes of brook stickle-back, Culaea inconstans, by selected inverterbates. Can J. Zool., 58: 1253-1258.
20. Roff D.A. (1992): The evolution of life histories. Chapman and Hall, New York. Rowe, L., andLudwig. D. 1991 Size and timing of metamorphosis in complex life cycles: time constraints and variation. Ecology, 72: 413-427.
21. Scheiner S.M. and Berrigan D. (1998): the genetics of plasticity. VIII. The cost of plasticity in *Daphania pulex:* Evolution, 52: 368-378.
22. Shaw R.G. (1987): Maximum-likelihood approaches applied to quantitative genetics of natural populations. Evolution, 41: 812-826.
23. Simmons L.W. and Siva-Jothy M.T. (1998): Sperm competition in insects: mechanisms and the potential for selection. In sperm competition and sexual selection. Edited by T.R. Birkhead and A.P. Moller. Acadeic Press, San Diego. pp. 341-434.
24. Slice D.E. (1994): DS-DIGIT: basic digitizing software. Department of Ecology and Evolution, State Univerity of New York. Stony Brook.
25. Sokolovska N., Rowe L. and Johansson F. (2000): Fitness and body size in mature odonates. Ecol. Entomol. 25: 239-248.
26. Spitze K. (1992): Pedator-mediated plasticity of prev life history and morphology: *Chaoborus americanus* predation on Daphnia pulex. Am. Nat., 139: 229-247.
27. Spitze K. and Sadler T.D. (1996): Evolution of generalist genotype; multivariate analysis of the adaptiveness of phenotypic plasticity. Am. Nat., 148 (Suppl.): 108-123.
28. SPSS Inc. (1998): SPSS base 8.0, user's guide. SPSS Inc. Chicago. SPSS Inc. 2000. SYSTAT, version 10.0 SPSS Inc., Chicago.

29. Svardson G. (1976): Interspecific population dominance in fish communities. Rep. Inst. Freshw. Res. Drottninghom No. 56 pp. 144-171.
30. Thompson D.J. (1997): Lifetime reproductive success, weather and fitness in dragonflies. Odonatologica, 26: 89-94.
31. Tonn W.M. and Magnuson J.J. (1982): Patterns in the species composition and richness of fish assemblages in norther Wisconsin lakes. Ecology, 63: 1149-1166.
32. Van Tienderen P.H. (1991): Evolution of generalists and specialists in spatially heterogeneous environments. Evolution, 45: 1317-1331.
33. Via S. (1994): The evolution of phenotypic plasticity: what do we really know? In ecological genetics, Edited by L.A. Real. Princeton University Press, Princton, N.J., pp.35-57.
34. Worltereck R. (1909): Weitere experimmentelle Unter suchungen uber Artveranderung, speziell iiber das Wesen quantitative Artunterscheide bei Daphniden. Verh. Dtsch. Zool. Ges. 19: 110-172.