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RESPONSES OF PREY FROM HABITATS WITH DIFFERENT PREDATOR REGIMES: LOCAL ADAPTATION AND HERITABILITY

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Abstract. We aimed to assess whether prey organisms with limited large-scale dispersal abilities are locally adapted to prevailing predator regimes by studying how chemical cues from predatory fish affected the behavior of *Gammarus pulex* (Amphipoda) from ponds with and without fish. We also examined, in the laboratory, the F1 generation from each pond by incubating them with or without cues from predatory fish. The potential benefits of a behavioral avoidance response were also assessed in an experiment in which *G. pulex* from the different ponds and incubations were exposed to fish predation. *G. pulex* from fish ponds increased their refuge use when exposed to fish cues, whereas populations from fishless ponds reduced their refuge use. The F1 generation responded similarly to their parents. Only the F1 generation from fish pond populations responded with more pronounced antipredatory behavior when raised in fish water. Moreover, both the original and the F1 generation of fish pond *G. pulex* survived longer when exposed to fish predation than those from fishless ponds, independent of whether they were raised in fish water or not (F1). Our results suggest that the behavioral response to predator cues in *G. pulex* is an inherited trait, i.e., a local adaptation to prevailing predator regimes.

Key words: antipredator behavior; fish; *Gammarus pulex*; inherited trait; local adaptation; predation.

INTRODUCTION

Predatory fish (e.g., Diehl 1992, Nyström et al. 2001, Åbjörnsson et al. 2002) and predatory invertebrates (e.g., Cooper et al. 1990, Nyström and Åbjörnsson 2000) have strong negative effects on prey abundance, as shown by several studies in freshwater systems. To escape predators, prey have evolved a variety of adaptations, such as morphological structures, chemical repellents, crypsis, and avoidance behaviors (Sih 1987, Kats et al. 1988, Brönmark and Miner 1992, Åbjörnsson et al. 1997, Hansson 2000). These adaptations are often directed against a specific predator, however, and are not universally effective. Because prey usually live in multiple-predator environments and different predators exhibit different hunting characteristics, adaptations that are efficient in avoiding one predator may not be efficient against another (Wooster and Sih 1995, Sih et al. 1998, Turner et al. 1999).

Since fish, generally, are strong interactors in freshwater systems, habitats with and without fish present fundamentally different predator regimes to prey species. Large invertebrates become dominant predators in habitats without fish, whereas their importance is reduced in habitats with fish, i.e., size-selective predators (Wellborn et al. 1996). Prey species persisting under such dramatically different predation regimes are expected to have different defense adaptations against

predators (McPeck 1990). Hence, there should be weak selection for antipredator behavior against fish in a fishless environment. Nevertheless, some studies have found avoidance responses to fish in prey from fishless streams (Tikkanen et al. 1996, McIntosh and Peckarsky 1999), whereas others have found no such responses (McIntosh and Townsend 1994). Most fishless streams are occasionally invaded by fish, thus creating a variable predation pressure (Tikkanen et al. 1996). Further, in populations allopatric with fish, a key factor in maintaining a flexible avoidance behavior has been suggested to be aerial dispersal between streams with and without fish (Tikkanen et al. 1996). In contrast to the stream work, few studies have considered the performance of species present in ponds and lakes with different predator regimes and with a limited ability to disperse (Storfer and Sih 1998, Storfer 1999, Relyea 2002, Vorndran et al. 2002). In populations with restricted gene flow, maintenance of flexible avoidance responses to different predator regimes demands that there are no costs associated with it (Gomulkiewicz and Kirkpatrick 1992). There may be costs, however, associated with having the ability to detect predators (e.g., Tollrian and Harvell 1999), and further, avoidance behavior may result in lost opportunities, e.g., in foraging or mating (e.g., Skelly 1992). Costly forms of flexible antipredator responses should persist only if they are compensated by benefits (DeWitt et al. 1998), which, in the case of isolated fishless populations, should be negligible. Moreover, the adaptation to a new, different environment may entail a fitness loss in the original environment (reviewed in Futuyama

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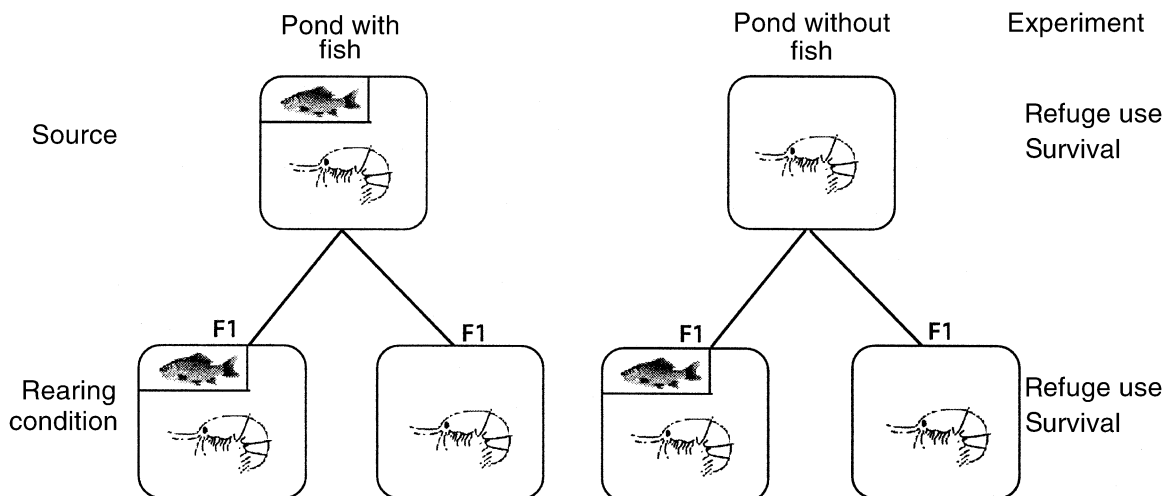


FIG. 1. Flow diagram of the experimental design. Experiments (behavioral response to fish cues and survival time when exposed to fish) were performed on *Gammarus pulex* from ponds in Scania, southern Sweden, with and without the presence of fish and on the F1 generation raised in the laboratory with and without fish.

and Moreno [1988]). Finally, specialists will evolve faster in their preferred habitats and will push aside the generalists, since the intensity of selection in that particular habitat increases with the proportion of the population residing there (Schlichting and Pigliucci 1998). Thus, local adaptation is more likely to occur in prey populations with limited dispersal capability because they experience the same environmental conditions throughout their lifetimes.

Gammarus pulex (Crustacea: Amphipoda) are common in both lentic and lotic freshwater systems. They are present in both fishless and fish habitats and are thus, as a species, exposed to different predator regimes. Because of the restricted ability of *Gammarus* to disperse, their exposure to predator types outside the habitat is limited, and they should therefore be adapted to the local predator regime. Several *Gammarus* species respond to chemical cues released from different predators or from activities associated with predation (Williams and Moore 1985, Wisenden et al. 1999, 2001, Åbjörnsson et al. 2000). These responses may confer a fitness benefit (Wisenden et al. 1999) because they enable the prey to adjust its behavior before the actual encounter with the predator. Thus, *G. pulex* is well suited for the study of local adaptation in predator-avoidance behavior.

The main objective of our study was to determine whether *G. pulex* from populations exposed to different predation regimes (with or without fish) differ in their behavioral response to fish cues and whether the behavior is inherited. Further, we aimed to determine if prior exposure to fish confers survival benefits to *G. pulex* when challenged with predation.

METHODS

We conducted two main experiments in which we studied the behavioral response of *G. pulex* to chemical

cues from fish. In the first, we used *G. pulex* collected from ponds with and without fish (original populations), and in the second, we used the F1 generation raised under fish and fishless conditions in the laboratory (Fig. 1). All experiments were performed at 18–20°C and at a light : dark cycle of 12:12 h.

Experimental animals

G. pulex were collected from five fish ponds and three fishless ponds in Scania in southern Sweden during autumn 2000. All ponds were surveyed for the presence of fish using both net and electrofishing to determine the presence or absence of fish. *Carassius carassius* (crucian carp) was present in the five fish ponds chosen. Each *G. pulex* population (300 individuals/population) was kept in a separate 15-L holding aquarium with aerated tap water and fed a mixture of frozen chironomids and rinsed leaf litter: *Alnus glutinosa* (alder) and *Fagus sylvatica* (beech).

Crucian carp were collected by trap-netting in a pond in University Park, Lund. Thirty crucian carp (size range: 114–138 mm) were kept in aerated tap water in a fish-holding aquarium (volume = 200 L) during the whole experiment and fed frozen chironomids. All experimental animals were allowed to acclimatize to laboratory conditions for at least 3 wk prior to the experiment.

Preparation of treatment water

The fish cue was prepared by placing three crucian carp in each of three aerated 10-L aquaria for 3 d. To ensure that there were no diet cues or alarm substances from *G. pulex* in the water, the fish were not fed during these days, nor three days before. The control water was prepared in the same way except there were no fish in the aquaria. Water from the three aquaria containing the same treatment was mixed and immediately

frozen to -20°C in 20-mL plastic vials. Freezing does not affect the efficiency of the cue, which retains its activity for at least 2 mo (Pettersson et al. 2000). Treatment water was thawed the same day it was used.

Local adaptation experiments

To determine if *G. pulex* behavior is influenced by the local habitat, we conducted an experiment in which, using *G. pulex* from ponds with and without fish, we studied their behavioral response to chemical cues from fish (Experiment 1.1). We also confronted *G. pulex* with fish to find out whether local adaptations, by populations inhabiting fish ponds, result in a survival benefit (Experiment 1.2).

Experiment 1.1: Behavioral responses to predators (original population).—We measured *G. pulex* refuge use in four experimental arenas (plastic containers: diameter = 0.24 m, volume = 1.5 L) with the insides covered with luminous adhesive tape. A piece of synthetic grass-like carpet (10 × 10 cm) was placed in the middle of the arena to serve as a refuge. Water in the experimental arena was taken from tanks containing aerated tap water. Each arena was stocked with one *G. pulex*, which was allowed to acclimatize for 20 min before the start of a trial. We used the largest *G. pulex* individuals because they were assumed to be more vulnerable to predation and, thus, exhibit a lower response threshold than small individuals (Wisenden et al. 2001). One individual from each population was tested with control water and one with fish cue. This procedure was replicated four times for each population for a total of eight individuals from each population. Water from tanks with aerated tap water was pumped into the arenas through plastic tubes and from arenas to the waste at a rate of 20 mL/min throughout each trial. Ten minutes after the start of an experiment, 20 mL of control water or fish cue was added automatically as the pump switched, for 1 min, from continuously added tap water to treatment water. Each trial lasted 20 min. Treatments were interspersed in random order. Plastic tubes and experimental arenas were carefully cleaned with ethanol (95%) and rinsed with tap water between trials. All four experimental arenas were monitored with a video camera, installed above the experimental arenas, linked to a video recorder in order to register movements by *G. pulex* simultaneously in the four arenas. A motion analysis computer program, EthoVision (Noldus Information Technology, Wageningen, The Netherlands) was used to analyze changes in behavior. The position of the *G. pulex* in the experimental arena was registered every second to calculate refuge use (time [in seconds] in refuge).

Analysis of the response variable was performed on the means from each population. If necessary, data were natural log transformed prior to analyses to meet the assumptions of normality and equal variances. In the statistical analysis, the proportion change in refuge use (RU) of *G. pulex* was estimated as the change in

refuge use after treatment addition (the last 10 min) divided by refuge use before the addition (the first 10 min) (RU[after control]/RU[before control] and RU[after fish cue]/RU[before fish cue]) for each population. The change in refuge use was analyzed by a two-way ANOVA for effects of source (fish pond, fishless pond) and treatment (control, fish cue). For the graphical presentation we calculated the net change in response as: (RU[after control]/RU[before control]) – (RU[after fish treatment]/RU[before fish treatment]).

Experiment 1.2: Survival experiment (original populations).—Ten aerated aquaria (volume = 10 L) were divided into one large (3/4 of the total volume) and one small compartment with a plastic wall. The wall had a window (120 × 130 mm) covered with 10 μm nylon screening. A piece of synthetic grass-like carpet (45 × 45 mm) was placed in one corner in the large compartment to serve as a refuge for *G. pulex*. Four hours before starting the experiment, one crucian carp was added to the small compartment. Then one *G. pulex* was placed in the large compartment and allowed to “sample” the aquarium for 2 min before the plastic wall was removed. A stopwatch was used to measure the survival time (in seconds) of *G. pulex*. If *G. pulex* hid in the refuge, the fish was unable to find and eat it. The experiment was stopped after 300 s (5 min) because *G. pulex* could stay in the refuge for hours. Ten *G. pulex* from the same population were tested at the same time, one individual per aquarium. This was repeated for each population. Only large *G. pulex* individuals were used. Each aquarium was carefully cleaned with ethanol and rinsed with dechlorinated tap water between trials to remove possible cues (e.g., alarm substances) from the previously tested population.

Statistical analysis was performed on the means from each population. If necessary, data were natural log transformed prior to analyses to meet the assumptions of normality and equal variances. The survival time was then analyzed by one-way ANOVA for effects of source (fish pond, fishless pond).

Heredity experiments

To find out if the response to fish is inherited we conducted behavioral experiments with the F1 generation of *G. pulex* raised in fish and fishless environments.

Rearing conditions.—Twelve amplexus pairs of *G. pulex* from each population were collected from the holding aquaria and placed in aerated aquaria (volume = 2 L), one amplexus pair per aquarium. To avoid cannibalism, we removed the male as soon as the pair separated and the female was carrying eggs. When she had released all her offspring she was also removed from the aquarium. We added water (50 mL twice per day) to half of the experimental aquaria from an aerated 15-L aquarium containing three crucian carp and to the other half from a control aquarium (without fish), thus

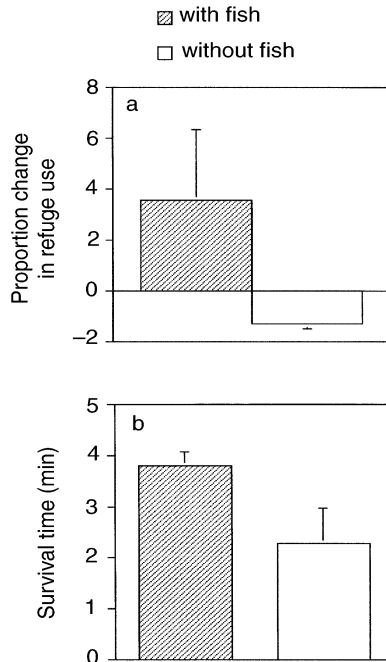


FIG. 2. (a) The net response (refuge use) of *Gammarus pulex* to chemical cues from fish (means \pm 1 SE). The *G. pulex* populations had different sources (ponds with and without the presence of fish). (b) The survival time of *Gammarus pulex* from different sources (ponds with and without the presence of fish) when *G. pulex* was exposed to predation by *Carassius carassius* (means \pm 1 SE).

simulating different predator regimes. The water addition started as soon as an amplexus pair was placed in an aquarium. Crucian carp were fed every second day with 20 *G. pulex*. The formation of amplexus pairs was not synchronized within or between populations. But all offspring were raised for 13–15 wk, for all treatments, before being used in the behavioral experiments.

Experiment 2.1: Behavioral responses to predators (F1 generation).—The behavior of *G. pulex* from the different populations and incubations in response to fish cue was studied and analyzed as in Experiment 1.1. The proportion change in behavior was analyzed by a three-way ANOVA for effects of source (fish pond,

fishless pond), incubation (water, fish), and treatment (control, fish cue).

Experiment 2.2: Survival experiment (F1 generation).—The experiment was performed in the same way as for *G. pulex* from the field (Experiment 1.2). Ten *G. pulex* from the same population and rearing condition were tested at the same time, one individual per aquarium. This was repeated for each population. The four experimental groups were tested in separate runs of the experiment as in Experiment 1.2. The results were analyzed by two-way ANOVAs (source and rearing condition).

RESULTS

Experiment 1.1: Behavioral responses to predators (original population).—The proportion change in *G. pulex* refuge use did not differ between the control and the fish cue treatment (two-way ANOVA, $F_{1,12} = 0.02$, $P = 0.89$). The origin of *G. pulex* (fish pond or fishless pond) did not affect the proportion change in refuge use (two-way ANOVA, $F_{1,12} = 0.30$, $P = 0.59$). But fish pond populations tended to increase their refuge use when exposed to fish cues, whereas populations from fishless ponds decreased their refuge use (two-way ANOVA, treatment \times origin interaction, $F_{1,12} = 3.69$, $P = 0.07$) (Fig. 2a).

Experiment 1.2: Survival experiment (original population).—*G. pulex* populations from fish ponds survived almost twice as long as conspecifics from fishless ponds (one-way ANOVA, $F_{1,6} = 6.31$, $P = 0.04$) (Fig. 2b).

Experiment 2.1: Behavioral responses to predators (F1 generation).—*G. pulex* originating from fish ponds increased their refuge use when exposed to fish cues, whereas populations from fishless ponds spent less time in the refuge (Table 1, Fig. 3a). Moreover, there was a tendency to stronger response by experienced (raised in water containing fish cue) fish pond populations of *G. pulex* compared to naive (raised in water free of fish cue) *G. pulex* (Table 1, Fig. 3a).

Experiment 2.2: Survival experiment (F1 generation).—Fish pond populations used the refuge more frequently than populations from fishless ponds, resulting in longer survival times (two-way ANOVA,

TABLE 1. Three-way ANOVA for effects of origin (fish ponds and fishless ponds in Scania, Southern Sweden), treatment (control, fish cue), and rearing condition (water, fish) and their interactive effects on the proportion change in *Gammarus pulex* refuge use (after/before the addition of treatment water).

Source	df	MS	F	P
Treatment	1	1.12	6.33	0.01
Origin	1	1.41	7.92	0.009
Rearing condition	1	0.64	3.62	0.07
Treatment \times origin	1	4.29	24.15	<0.0001
Treatment \times rearing condition	1	0.1	0.58	0.45
Origin \times rearing condition	1	0.17	0.94	0.34
Treatment \times source \times rearing condition	1	0.000049	0.0003	0.99
Error	24	0.18		

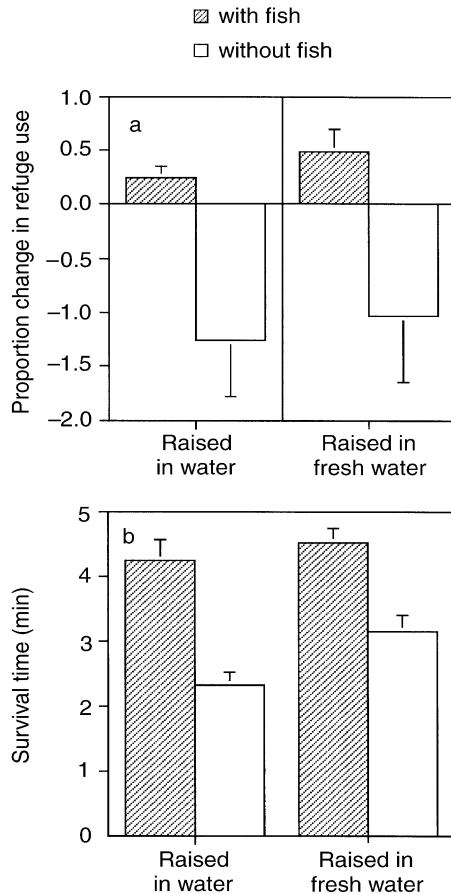


FIG. 3. (a) The net response (refuge use) of the F1 generation of *Gammarus pulex* to chemical cues from fish (means \pm 1 SE). The parents of the F1 generation had different origins (ponds with and without the presence of fish). Of these, each population, independent of source, was divided: half of the individuals were raised in water and the other half in water scented with fish. (b) The survival time of the F1 generation of *Gammarus pulex*, from ponds with and without the presence of fish, respectively, raised with and without fish cue, when exposed to predation by *Carassius carassius* (means \pm 1 SE).

$F_{1,11} = 31.45$, $P = 0.0002$) (Fig. 3b). Rearing conditions did not affect the survival (two-way ANOVA, $F_{1,11} = 3.44$, $P = 0.09$), and there was no significant interaction (two-way ANOVA, source \times rearing condition, $F_{1,11} = 0.77$, $P = 0.39$) (Fig. 3b).

DISCUSSION

Predation is a major mortality risk for prey populations in both terrestrial and aquatic ecosystems (Lima and Dill 1990). Changes in predation rates may impose directional selection on traits that reduce mortality risk, and when migration between populations is restricted this may result in local adaptation to the prevailing predation regime. However, even modest migration between populations may instead favor the evolution of phenotypic plasticity (Sultan and Spencer 2002). In

recent years, a number of studies have shown that prey exposed to spatially or temporally variable predation pressure have evolved inducible predator defenses and thus show a high degree of phenotypic plasticity in these traits (Tollrian and Harvell 1999). Further, among-population asymmetries in plasticity may occur if there is a risk associated with an improper reaction to an unpredictable cue of a selection pressure (Etter 1988, Trussell 1997). For example, intertidal snails show plasticity in foot size in response to wave action but transplant experiments showed that snails from protected areas responded to higher wave action by producing a larger foot whereas snails from wave-exposed areas developed the same foot size irrespective of wave exposure (Etter 1988, Trussell 1997). Intertidal snails also show population differences in the degree of plasticity of a defense adaptation, shell thickness growth, in response to predators (Trussell 2000). Thus, to understand variation between populations in a trait we need to carefully evaluate if it is a result of local adaptation or phenotypic plasticity in response to environmental heterogeneity, such as differences in predation regime, and this is best done by reciprocal transplants or common garden experiments over several generations (e.g., Reznick and Travis 1996). Adaptive traits that reduce predation mortality can be morphological (spines or cryptic coloration) and behavioral (direct responses to predation threat) (Tollrian and Harvell 1999). An even more sophisticated adaptation is the ability to sense the presence of a predator by chemical exudates and thereby avoid direct interactions. Although few such chemical cues have been identified (Brönmark and Hansson 2000), the phenomenon has been repeatedly demonstrated both in aquatic animals (Brönmark and Pettersson 1994) and plants (Hansson 1996). The response to predator chemical cues may be fixed; that is, all individuals within a certain prey species respond irrespective of whether they have been previously exposed to a predator or not. It may also be that a relevant response to a predator must be induced, suggesting that a predator-naïve individual will not respond or will show a weaker response to a predator than an experienced individual. Here we have tested whether predator avoidance behavior in *G. pulex* differs between populations with and without fish, i.e., if there is local adaptation to prevailing predator regimes and, further, if the trait is inherited.

The different responses to crucian carp by *G. pulex* from ponds with and without fish predators in our study indicate that they have adapted to different predator regimes and thus employ different antipredator strategies. Other studies have shown both presence and absence of between-population responses to fish cues (e.g., Tikkanen et al. 1996, Storfer and Sih 1998, Laurila 2000, Relyea 2002). Fish search for prey over a broad spatial area (Healey 1984), and prey have little chance of outswimming an approaching fish (Wellborn et al. 1996). Hence, decreased activity and shelter-seek-

ing are commonly reported antipredator responses to fish (reviewed in Lima and Dill [1990] and Wooster and Sih [1995]). These behaviors reduce encounter rates with predators and thus decrease predation rates (Skelly 1994). In our study, *G. pulex* from fish ponds responded with increased refuge use, indicating an adaptation to the local fish predator regime. That *G. pulex* from fish ponds survived longer than individuals from fishless ponds further suggests an adaptive value in detecting a fish predator by chemical cues and changing behavior accordingly.

In contrast, *G. pulex* from fishless ponds increased their activity in response to chemical cues from predators. Decreased refuge use by *G. pulex* from fishless ponds may be a response to avoid invertebrate predators. Large invertebrates are the dominant predators in habitats without fish (Wellborn et al. 1996). Vegetation stands in ponds and lakes usually have a much richer invertebrate community than unvegetated sites (Hargeby et al. 1994, Diehl and Kornijów 1997). These stands offer food for invertebrate prey (Kornijów et al. 1995, Scheffer 1998) and consequently also for invertebrate predators (Scheffer et al. 1984). Thus, invertebrate prey may suffer from invertebrate predation more in the vegetation than outside. As a short-term response to immediate danger (a pulse of predator odor above its local background level), prey may leave dense structures (vegetation) to escape their predator. Furthermore, in contrast to fish, predatory invertebrates might be avoided by swimming away from them, resulting in increased activity of the prey (McPeck 1990).

The breeding experiment clearly showed that the differences between populations in antipredator response are inherited. *Gammarus* that were raised in the laboratory (F1 experiment) responded along the same general pattern as their parents that had been collected directly from the ponds. Offspring from fish pond populations increased their refuge use in response to predator cues, whereas offspring from fishless pond parents showed decreased refuge use. There was a slight effect of rearing condition (fish cue or control water) (Table 1), but this was only due to a minor increase in refuge use by fish populations raised in fish cue water. There was no directional change in behavior due to incubation, and most importantly, in response to conditioning. *G. pulex* from fishless ponds did not change their behavior; a change would have been expected, upon change of predation regime, if the behavior was a flexible response. It has been suggested that developmental switches, i.e., presence/absence of an environmental cue during a critical period of development, may be the mechanism behind phenotypic plasticity (e.g., Stearns 1989). However, the presence of predator cue during the complete development of the offspring, even since the amplexus of the parents, suggests that absence of cues is not the mechanism behind the similarity in response of offspring and parents, independent of incubation regime. Another alternative explanation for

the found patterns (that does not include genetic differentiation) is that offspring behaviors, in some way, are learned from the mother during development. Nevertheless, although we cannot rule out this mechanism with the present experimental design, we think that it is less likely that the F1 offspring behaviors were learned in the brooding pouch because the mothers never experienced fish odor while these offspring were being reared. Instead, we suggest that the behavioral response to predator cues in *G. pulex* is an inherited trait.

Regarding between-population differences in behavioral responses to predation, their inheritance implies that this is an example of local adaptation by a prey to prevailing predator regimes. The behavioral traits of each population have been selected for under different predator regimes. And these traits should be closer to their respective optimum because selection, in the absence of gene flow, should drive populations to local adaptive peaks (Slatkin 1987). This concept is supported by our observation that when *G. pulex* originating from fish ponds were exposed to predation, their survival increased (compared to those from fishless ponds). If we assume that ability to respond to fish cues is the ancestral character state, as has been suggested for damselflies (Stoks et al. 2003), then this adaptive behavior must have been lost after local extinction of fish. The loss of such adaptive behaviors in the absence of the selection force driving them requires that there is a cost associated with them (e.g., Gomulkiewicz and Kirkpatrick 1992). In amphibians it has been shown that predator-induced avoidance behaviors result in reduced growth and development due to a decrease in foraging activity (Skelly 1992). In *Gammarus* it has been shown that presence of predator cues results in a reduction of short-term foraging activity (Åbjörnsson et al. 2000). Avoidance behavior may also affect other fitness variables, mating activity, and investment in offspring. Further, there should also be costs for providing and maintaining a sensory system that enables the prey to detect and respond to predator cues (Moran 1992, DeWitt et al. 1998, Tollrian and Harvell 1999).

Differences in avoidance behavior induced by predator presence have also been demonstrated for other species with populations that experience spatial or temporal heterogeneity in predation pressure (Storfer and Sih 1998, Storfer 1999, Relyea 2002, Vorndran et al. 2002). Nevertheless, a number of factors may constrain and prevent local adaptations to predators. Gene flow has been reported as a factor constraining adaptive evolution (Storfer and Sih 1998, Storfer 1999) with an ineffective antipredator behavior as a consequence. Storfer and Sih (1998) found that gene flow from fishless populations prevented adaptive evolution in populations exposed to fish predation. And Laurila (2000) suggested that, for *Rana temporaria* tadpoles, gene flow may be one of the factors behind a lack of between-population differences in antipredator response.

Further, in fishless streams occasionally invaded by fish and in which prey organisms have aerial dispersal phases (and thus a higher degree of gene flow), behavioral traits are flexible and adaptations to local predation regimes are rare (Tikkanen et al. 1996). With respect to organisms with more limited dispersal ability, such as *G. pulex*, adaptation to local predator regimes is to be expected. Accordingly, on alteration of predator regimes, *G. pulex* from fishless ponds showed no flexibility in behavioral response. Variability in predation pressure may also constrain the evolution of antipredator defenses; even short-term presence of predators may prevent local adaptations. The ponds in our study have existed for more than 100 years but we have no long-term records of fish populations in these ponds. However, 25 years' experience with ponds in the area suggests that changes in fish presence/absence, i.e., local extinction or immigration, is rare (C. Brönmark, *personal observation*). But adaptive responses to changing predation pressures may evolve quickly if the selection pressure is strong, as has been shown for, e.g., amphibians (Kiesecker and Blaustein 1997) and fish (Reznick et al. 1997). Thus, we suggest that for *G. pulex*, which can have three generations per year (they grow from birth to sexual maturity in ~3–4 mo [Goedmakers 1981, Sutcliffe et al. 1981]), the predation regime in these ponds has been sufficiently stable, and in addition, gene flow is sufficiently low to promote local adaptation in behavioral responses to predator cues. Such local adaptation may prove highly adaptive, as illustrated by the almost 50% higher survival for animals with experience of fish, compared to those without.

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