



Learning, memory and predator avoidance by freshwater snails: effects of experience on predator recognition and defensive strategy

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Learning may allow animals to fine-tune predator avoidance responses to specific environments, but the degree to which predator avoidance behaviour depends on experience is not known for most taxa. We assessed whether perception of predation risk and choice of defensive strategies by the snail *Physa acuta* is influenced by experience by performing three experiments in which we manipulated exposure to predators and then assayed behavioural responses to predator cues. We first assessed the scope for learned avoidance behaviour by comparing the antipredator response of wild snails (exposed to predators) and captive-reared snails (not exposed to predators). Wild-caught snails showed a stronger response than did captive-reared snails to predators feeding on insect prey, predators feeding on snails and crushed-snail cues. A second experiment in which snails were reared with and without exposure to crayfish predators showed that snails from both rearing treatments responded to fish and crayfish, but the choice of defensive strategy depended on experience. Snails reared without exposure to predators responded to fish cues by moving under cover, whereas snails reared with crayfish responded to fish by moving to the water's surface. The final experiment also manipulated exposure to predators and showed that although snails from a fish-free pond responded to both fish and crayfish, their responses did not depend on experience. Overall, the effects of experience were significant but small relative to the overall effects of predator cues on snail habitat use, showing that the antipredator responses of *P. acuta* are largely innate.

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Predators often induce shifts in prey behaviour (Lima & Dill 1990; Lima 1998a), and a growing number of studies suggest that the development of these antipredator behaviours may depend on the environment that animals experience during ontogeny. For example, work with fish shows that they can learn to recognize predators by associating the odours of predators with the odours of injured prey (Magurran 1989; Mirza & Chivers 2000; Ferrari et al. 2005; Larson & McCormick 2005). Studies of learned predator recognition have focused on vertebrates (e.g. Dill 1974; Griffin et al. 2000; Whitam & Mathis 2000), as their neural complexity and cognitive sophistication make them likely candidates for modification of antipredator behaviours by environmental conditioning. However,

recent studies suggest that the predator avoidance repertoire of invertebrates may also depend on experience (Chivers et al. 1996; Rochette et al. 1998; Hazlett & McLay 2000; Wisenden & Millard 2001).

Learning may conceivably affect several aspects of antipredator behaviour. First, experience may enhance the ability to recognize predators. In aquatic environments, reception of chemical stimuli released by predators and injured prey is the primary sensory mode by which most taxa gather information about the threat of predation (Dodson et al. 1994; Chivers & Smith 1998; Kats & Dill 1998). There are a variety of chemical cues associated with predation, some emanating from the predator (kairomones) and other cues released by injury to prey (alarm cues; Chivers & Smith 1998; Kats & Dill 1998). A number of studies show that naïve prey may fail to recognize predators based on kairomones alone, but may learn to associate kairomones with predation risk when alarm cues are presented in conjunction with kairomones (Chivers et al. 1995; Woody & Mathis 1998; Mirza & Chivers 2000;

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Jachner 2001). Experience may also affect the type of antipredator response used by prey. Prey are often confronted with multiple types of predators, each with unique foraging modes, and prey respond with a range of defensive strategies, each best suited for use against a particular predator (Turner et al. 1999; Relyea 2001). Given incomplete or unreliable information regarding predator identity, the selection of an antipredator strategy should be informed by recent experiences. Work to date, however, has largely focused on acquired cue recognition in vertebrates, and questions regarding the effects of experience on acquired cue recognition and choice of defensive strategy in invertebrates are almost entirely unaddressed.

Here, we investigate the role of experience in shaping predator recognition and choice of defensive strategy by the freshwater snail *Physa acuta* (Draparnaud). *Physa acuta* is adept at detecting and avoiding predators, but it is not known whether these behavioural responses are innate or influenced by experience. Published and unpublished studies show that *P. acuta* show surprising variation in their response to predator cues (e.g. Snyder 1967; Turner et al. 1999), and variation in the extent of prior exposure to predators is one mechanism that could give rise to such variable responses. *Physa acuta* are important grazers of periphyton in lakes and streams, so their behavioural responses have important ecological consequences (Bernot & Turner 2001), and variation in the way in which they perceive and process chemical stimuli may have important consequences for the ecology of littoral communities in general (McCollum et al. 1998; Turner et al. 2000; Bernot & Turner 2001). Thus, we investigated the cognitive ecology of *P. acuta* with the goal of better understanding variation in their responses to predators. The effect of experience on predator recognition and choice of defensive strategies was tested by manipulating exposure to predators and subsequently assaying behavioural responses to predator cues. Our expectation was that recognition of predators would be enhanced by prior exposure to predators and that when confronted with multiple types of predators, the choice of antipredator strategy should depend on the type of predation risk previously experienced.

METHODS

Study System

The freshwater snail *P. acuta* (synonymous with *Physa integra* and *Physa heterostropha*, Dillon et al. 2002) is locally abundant, geographically widespread and found across a broad environmental gradient from small temporary ponds lacking predators to deep permanent lakes with fish, crayfish and other snail predators (Mower & Turner 2004). Different populations of *P. acuta* experience very different levels of predation risk as well as different types of threats from predators, so they are a good candidate species with which to look for environmental induction of behavioural plasticity.

Physa acuta use chemical cues to detect predators (Snyder 1967; Covich et al. 1994), and in response alter

their morphology, life history and behaviour (Crowl & Covich 1990; DeWitt 1998; DeWitt et al. 2000). We used the decapod crayfish *Cambarus bartoni* (Fabricius) and/or the molluscivorous pumpkinseed sunfish *Lepomis gibbosus* (Linnaeus) as predators. Fish and crayfish have different foraging modes, with fish posing a danger to prey on exposed substrates and crayfish posing a danger to prey under cover as well as on exposed substrates (Turner et al. 1999). Snails can distinguish the chemical signatures of fish and crayfish and respond differently. *Physa* move under cover or to the water's surface in the presence of pumpkinseeds, but they avoid cover and move to the water's surface in the presence of crayfish (Turner et al. 1999; Bernot & Turner 2001), which is consistent with the foraging modes of these two predators (Turner 1996). Field studies confirm that *Physa* habitat use depends on the sort of predators present in a lake, and that the presence of fish or crayfish can induce such shifts in a natural setting (Turner et al. 2000; Bernot & Turner 2001; Turner & Montgomery 2003).

General Protocol

We conducted three experiments aimed at evaluating environmental effects on the ontogenetic development of behavioural plasticity in the freshwater pulmonate snail *P. acuta*. Each experiment consisted of two phases. Snails were first acclimated in multiple environments that differed with respect to the sorts of predator cues to which they were exposed (acclimation phase). We then tested for behavioural plasticity by exposing snails to caged predators or water that had been conditioned by predators and monitoring snail habitat use (assay phase).

All behavioural assays were conducted in 130-litre mesocosms placed outdoors at the Pymatuning Laboratory of Ecology in northwestern Pennsylvania, U.S.A. Mesocosms were constructed of polyethylene plastic and measured $1.32 \times 0.78 \times 0.30$ m deep. For each assay, mesocosms were first filled with well water, fertilized with phosphate and nitrate, inoculated with lake water, and covered with 50% shade cloth. Mesocosms were aged for 6–21 days to allow development of periphyton and zooplankton communities before snails were stocked and treatments initiated.

Treatment effects on snail habitat use were evaluated by conducting spot observations twice daily. We counted the number of snails under covered substrata, the number within 2.5 cm of the water's surface, and the number in the open. Covered substrates were constructed of 20×20 -cm ceramic tiles supported on legs 2.5 cm tall and placed in the centre of the mesocosm. Spot counts of snails in each habitat were converted into proportions (number in habitat type/total number in mesocosm). As outlined in more detail below for each experiment, we then calculated the overall mean near-surface and covered habitat use, averaged across the duration of the experiment, and tested for treatment effects on refuge use. Mean habitat use of a mesocosm was the unit of observation for all analyses.

Experiment 1: Predator Recognition

We experimentally decomposed the predator cue into components and assessed the role of each component in the induction of antipredator behaviour in captive-reared and wild-caught *P. acuta*. Captive animals were raised without any exposure to predators, whereas their wild-reared counterparts had been exposed continuously to predators. These two environments clearly differ in ways other than exposure to predators, but such a comparison provides a sound starting point in assessing the potential scope of learned responses to predation risk. Captive-reared snails were derived from parental stock collected from two populations, Pymatuning Reservoir and Hartstown Marsh, northwestern Pennsylvania, and were reared in 750-litre mesocosms without any exposure to predators. Populations were established in the autumn, and the experiment was conducted the following July on the adult offspring of the original colonists. Wild-caught adult snails were also collected from Pymatuning Reservoir and Hartstown Marsh (both contain pumpkinseed sunfish and crayfish) one week prior to the behavioural assay.

We compared the response of captive and wild snails to chemical cues associated with unfed predators, crushed conspecifics and predators fed conspecifics. In addition, we fed predators an unrelated prey item with which they have no ecological overlap in order to assay the importance of variation in predator diet. Thus, the behavioural assay consisted of five predator cue treatments: (1) reference pools, (2) crayfish that were unfed, (3) crayfish fed insect prey, (4) crayfish fed snail prey and (5) crushed snails. Reference pools received no cues. Unfed crayfish pools each contained a single crayfish held without food in a cage built from slotted polyvinyl drainpipe (10-cm diameter) covered on the ends with mesh screening. Crayfish–insect pools contained a caged crayfish fed two larval blue bottle flies (*Calliphora* sp., Diptera: Calliphoridae) daily. *Calliphora* larvae are not found in aquatic habitats, so they are distantly related to *P. acuta* in both phylogenetic and ecological terms. Crayfish–snail pools contained a caged crayfish fed one *P. acuta* each day. Finally, crushed-snail cue pools received one snail, mechanically crushed (mortar and pestle), each day. The rate at which bottle flies and snails were fed to crayfish (or crushed by hand) was selected so as to equalize the mass of snail and bottle fly tissue consumed at 40 mg/day (wet mass) and not confound feeding rate with prey type.

Ten snails were stocked into each outdoor mesocosm. Crayfish were fed in the morning, and observations of habitat use were conducted late morning and early afternoon. Because *P. acuta* typically respond to crayfish by crawling to the water's surface (Turner et al. 1999, 2000), we use near-surface habitat use as our index of refuge use. The observation period lasted for 6 days, so 12 observations were collected from each mesocosm.

Effects of rearing environment, source population and predator cue treatments on snail refuge use were analysed with $2 \times 2 \times 5$ factorial ANOVA. There were 100 replicate mesocosms in this experiment, arranged in a randomized block design (rows of 20 served as a block), yielding five replicates per treatment combination. Tukey's test was used to

conduct an all-pairwise comparison between cue treatment means. The effect of rearing environment depended on the cue treatment, so a simple effects test was used to contrast rearing environments within each level of cue treatment.

Experiment 2: Choice of Defensive Strategy

In this experiment, we tested whether snails reared in captivity and acclimated to one species of predator differed from predator-naïve animals in their reaction to familiar and novel predators. Wild-caught snails were also evaluated for reference. Captive-reared animals were derived from adult *P. acuta* collected from Pymatuning Reservoir in the autumn and stocked into eight outdoor mesocosms (10 snails per 750-litre mesocosm), where they overwintered and reproduced. By the following June, each mesocosm contained ca. 300 adult offspring of the original colonists. Four randomly selected mesocosms were then stocked with two crayfish each (*Orconectes virilis*), and four mesocosms served as no-predator controls. Each crayfish was confined to a cage as described above and was fed five snails/day. Feeder snails were *P. acuta* gathered from wild populations in the Pymatuning area. Thus, snails in the predator acclimation tanks were exposed to the chemical and mechanical cues associated with crayfish predation on snails, but there was no direct mortality or selection on the snails. Snails in the predator acclimation treatment were exposed to crayfish for 12 days immediately before the assay of behavioural plasticity. Wild-caught snails were gathered from Pymatuning Reservoir one week before initiation of the behavioural assay and held in mesocosms without exposure to predators.

The behavioural assay measured the response of snails to a familiar predator (crayfish) and a novel predator (fish), along with a no-predator reference treatment. The assay was conducted in 36 mesocosms, each of which held 10 snails. Habitat use (use of covered habitats, use of near-surface habitats) was assessed twice each day over a period of 7 days. Because snails were acclimated in three environments (cultured without predators, cultured with crayfish and wild caught) and subsequently tested in three predator treatments (fish, crayfish, no predator), and two sorts of refuge use were measured (proportion of population under cover, proportion of population near water's surface), a 3×3 MANOVA was used to analyse treatment effects on refuge use. Multivariate contrasts examining the effect of predator identity (fish versus crayfish) on refuge use at each level of acclimation treatment were also conducted.

Experiment 3: Defensive Strategies of Wild-caught Snails

This experiment was similar in design to experiment 2 except that instead of using captive-reared animals, we tested the effects of short-term exposure to predators on a population of wild-caught *P. acuta*. *Physa acuta* were gathered from a shallow (<20 cm deep) temporary pond near Pymatuning Reservoir ('Thompson's gravel pit'). This pond was isolated from other nearby ponds and typically dried by early summer of each year, and yet

contained a dense population of *P. acuta* (~100 snails/m²). The pond lacked fish predators, but crayfish and other invertebrate predators may have been present. No other species of snails were present in the pond.

Snails were collected and stocked into 36 acclimation tanks on 27 May, with 10 snails placed into each tank. The acclimation phase consisted of two treatments, exposure to crayfish cues and no-predator controls. After 12 days of acclimation treatment, snails were transferred into 36 130-litre mesocosms for a behavioural assay. The behavioural assay consisted of exposure to crayfish cues, exposure to fish cues and no-predator controls. Observations of habitat use (covered and near-surface) were conducted twice daily for 5 days. Treatment effects on habitat use were analysed with 2×3 factorial MANOVA, followed by multivariate contrasts examining the effects of predator identity for each level of acclimation. Univariate tests were also conducted to separately test the effects of acclimation on covered habitat use and near-surface habitat use.

RESULTS

Experiment 1: Predator Recognition

Predator cue treatments had strong effects on snail refuge use (Table 1). Averaged across population and acclimation treatments, *P. acuta* responded most to crayfish feeding on snails and responded least to unfed crayfish and crayfish fed insects, illustrating the very strong effect of predator diet on prey responses (Fig. 1). Rearing environment also had a significant effect on refuge use, but these effects were largely dependent on predator cue treatment (Table 1). Contrasts of cell means testing for effects of rearing environment at each level of predator cue showed that wild-caught snails responded more strongly than captive-reared snails to crayfish fed insects, crayfish fed snails and crushed snail cues (Fig. 1), although the magnitude of the effects of rearing environment was small relative to the overall effects of the predator cues (Table 1). Rearing environment had no effect on snail behaviour in reference treatments and unfed crayfish treatments (Fig. 1). Population effects were generally weak, but the effect of predator cues on refuge use did have

Table 1. Effects of rearing environment, source population and predator cues on *Physa acuta* refuge use

Factor	Effect size	df	F	P
Rearing environment	2.8	1	17.6	<0.001
Source population	0.4	1	2.29	0.134
Predator cues	77.9	4	121.1	<0.001
Block	1.2	4	1.82	0.134
Environment × population	<0.1	1	0.019	0.891
Environment × cues	2.6	4	4.00	0.005
Cues × population	1.8	4	2.73	0.035
Environment × population × cues	1.1	4	1.79	0.140

Significant treatment effects are in bold. For each factor, effect size is defined as $SS_{\text{factor}}/SS_{\text{total}}$, and is an estimate of proportion of the variation in habitat use attributable to that factor (%). Model $R^2 = 0.88$.

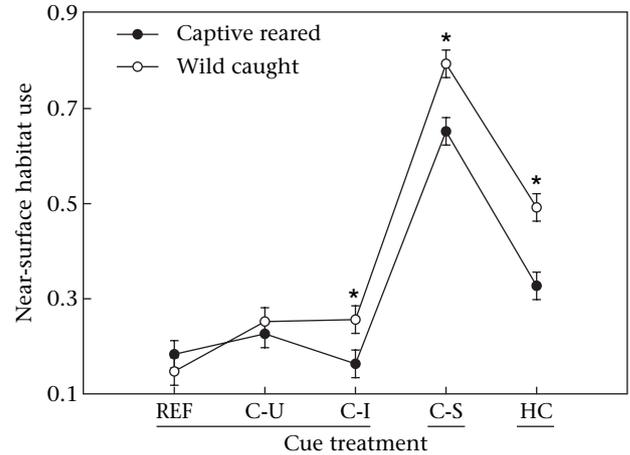


Figure 1. The response of captive-reared and wild-caught snails to five chemical cue treatments. REF = no-predator reference, C-U = unfed crayfish, C-I = crayfish fed larval insects (Diptera), C-S = crayfish fed snails and HC = snails crushed by hand. Bullets represent treatment means and vertical bars represent ± 1 standard error. Horizontal lines join cue treatments not significantly different from each other (Tukey's test: $P < 0.05$), and asterisks denote contrasts in which responses of captive-reared and wild-caught snails were significantly different ($P < 0.05$).

a significant nonadditive component attributable to source population (Table 1). Contrasts of cell means showed that snails from Hartstown Marsh responded more strongly than snails from Pymatuning Reservoir to hand-crushed snail and crayfish feeding on snail cues ($P < 0.05$ for both contrasts).

Experiment 2: Choice of Defensive Strategy

Exposure to fish and crayfish had a strong multivariate effect on snail refuge use (predator effect: Wilk's lambda = 0.085, $F_{4,52} = 31.6$, $P < 0.001$). Averaged across acclimation treatments, exposure to crayfish increased near-surface habitat use relative to reference treatments, whereas exposure to fish increased both near-surface and covered habitat use relative to reference (Fig. 2). However, the reaction of snails to predators was dependent on the nature of acclimation (predator × acclimation interaction: Wilk's lambda = 0.482, $F_{8,52} = 2.86$, $P = 0.01$). Predator-naïve snails responded to fish by moving under cover, but snails previously exposed to crayfish responded to fish by abandoning covered habitats (Fig. 2). Multivariate contrasts confirmed that snails acclimated without predators responded differently to fish and crayfish (Wilk's lambda = 0.448, $F_{2,26} = 16.1$, $P < 0.001$), but snails reared with crayfish responded to fish and crayfish in the same way (Wilk's lambda = 0.933, $F_{2,26} = 0.94$, $P = 0.40$).

Experiment 3: Defensive Strategies of Wild-caught Snails

Snails in this study were collected from a fish-free environment, yet they recognized and responded to both

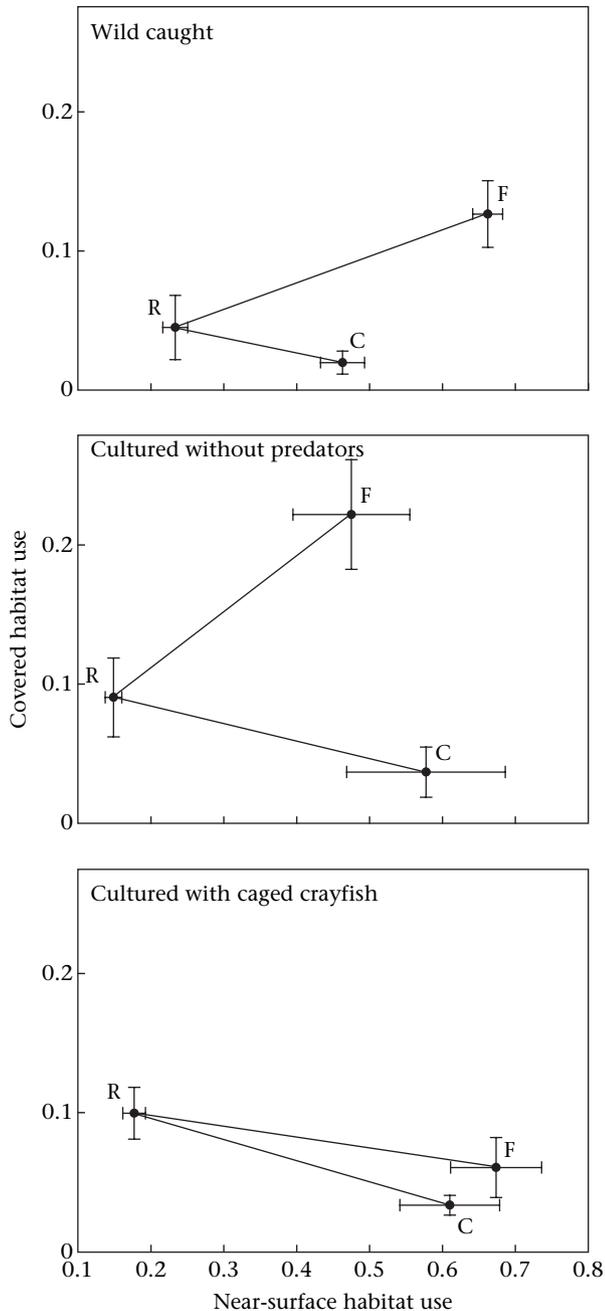


Figure 2. The effect of experience on the multivariate response of *Physa acuta* to crayfish and fish. Bullets represent treatment means and bars represent ± 1 standard error. R = reference treatment (no cues), F = fish cue treatment and C = crayfish cue treatment. Crossed bars show standard errors for both variables.

fish and crayfish chemical cues (Fig. 3). There were strong multivariate effects of predator cues (fish and crayfish) on snail refuge use (Wilk's lambda = 0.033, $F_{4,58} = 65.4$, $P < 0.001$). As in experiment 2, fish induced more use of covered habitat relative to reference treatments, whereas crayfish induced less use of covered habitats (Fig. 3). Multivariate contrasts of refuge use in fish and crayfish predator treatments confirmed that fish and crayfish induced different sorts of habitat shifts for both acclimation treatments (Fig. 3; snails reared without predators: Wilk's

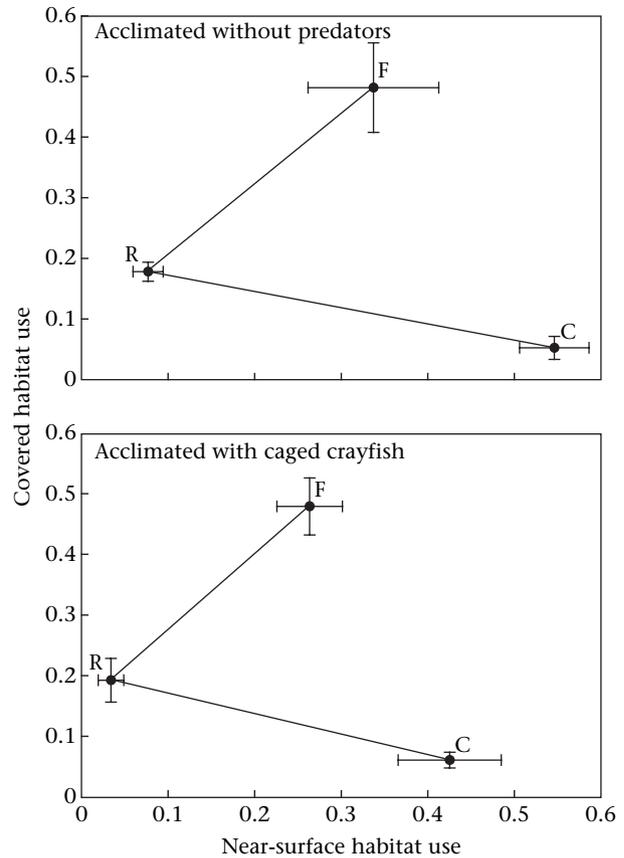


Figure 3. The effect of short-term exposure to crayfish on predator avoidance response of wild-caught snails. Bullets represent treatment means and bars represent ± 1 standard error. R = reference treatment (no cues), F = fish cues and C = crayfish cues. Crossed bars show standard errors for both variables.

lambda = 0.325, $F_{2,29} = 30.1$, $P < 0.001$; snails reared with crayfish: Wilk's lambda = 0.319, $F_{2,29} = 30.9$, $P < 0.001$). There were marginally significant effects of acclimation treatment on refuge use (Wilk's lambda = 0.814, $F_{2,29} = 3.31$, $P = 0.05$; Fig. 3). Univariate analyses showed that snails that had been exposed to crayfish used near-surface habitats less than did snails acclimated without crayfish (ANOVA: $F_{1,30} = 4.40$, $P = 0.04$), but acclimation had no effect on covered habitat use (ANOVA: $F_{1,30} = 0.04$, $P = 0.84$; Fig. 3). There were no significant nonadditive effects of test environment and acclimation environment on refuge use (Wilk's lambda = 0.953, $F_{4,58} = 0.35$, $P = 0.84$), confirming that the predator-specific defences were similar for snails acclimated with and without crayfish.

DISCUSSION

A full understanding of antipredator behaviours requires a knowledge of whether the responses are innate or learned, but for most taxa the answer to this question is not known. We found some evidence that the perception of danger by *P. acuta* depends on experience. Most notably, the choice of defensive strategy by *P. acuta* was contingent on rearing environment. Snails reared in the absence of

predators responded to fish cues by moving under cover and they responded to crayfish by moving to the water's surface. In contrast, snails that had been previously conditioned by exposure to crayfish cues responded to fish cues with the response typically associated with crayfish cues: they moved to the water's surface (Fig. 2). This effect of acclimation environment on defensive strategy can be viewed as one sort of memory: when presented with a test cue different from the acclimation cues, snails responded in a manner appropriate to the acclimation cue. The cost of this error may be small, because moving to the water's surface confers some protection against fish predators since molluscivorous fish tend to avoid very shallow water (Turner et al. 2000). Indeed, latent responses like these have an adaptive interpretation: if at any one point in time the prey cannot reliably identify the predator but predator identity is consistent through time, then animals will maximize survivorship if they use past experiences to inform interpretation of current cues.

Experiment 1 was designed to establish the potential scope for learned antipredator behaviour by testing animals reared in strongly contrasting environments. We found that wild-caught snails showed a stronger response to several cues than did captive-reared animals, including predators fed insect prey. Factors other than experience (e.g. energy reserves, parasitism) may differ between wild-caught and captive-reared snails, and experimental manipulations of experience are necessary in order to rigorously test the learned recognition hypothesis. In the present study, the effect of rearing environment (captive-reared versus wild-caught snails) was small relative to the influence of predator diet. Predator cues, by themselves, explained 78% of the variation in snail habitat use. In contrast, the additive effects of rearing environment explained just 2.8% of variation in habitat use, and nonadditive effects of rearing environment explained another 3.7% in habitat use (Table 1). Clearly, although the effects of rearing environment were statistically significant, they were not particularly important.

The effects of predator diet on prey behaviour shown in experiment 1 are broadly consistent with the results of other studies showing that unfed predators or predators feeding on prey unrelated to the target species generally elicit weak behavioural responses from prey, but predators feeding on conspecifics induce strong responses (review in Schoeppner & Relyea 2005). The lack of a response of many prey taxa to predator kairomones is surprising, especially in light of the large literature demonstrating the capacity of both vertebrates and invertebrates for associative learning (Dukas 2004). It is possible that prey in these cases may be unable to detect predator kairomones. However, given the impressive ability of aquatic animals to detect and use chemical information, it is also possible that prey are assessing risk based on predator diet and are adaptively balancing the costs and benefits of predator avoidance. Further study is necessary to determine whether the lack of a response to predator kairomones represents a perceptual constraint or an adaptive response.

Experiment 3 demonstrated that the effects of experience on choice of defensive strategy appear to be contingent on some unknown factor because the follow-up

experiment found that the response of wild snails gathered from a different population was largely independent of acclimation environment. Snails exposed to crayfish for two weeks responded to fish and crayfish in the same way as predator-naïve snails. The contrasting results of experiments 2 and 3 could be accounted for if there are only certain phases of ontogeny during which exposure to predators will alter subsequent responses, and the adult snails used in experiment 3 had already passed through this developmental window. There was a modest additive effect of acclimation environment in experiment 3, with use of near-surface habitats lower for snails reared with crayfish. Differential mortality during the acclimation phase may partly account for this result. Thirty-three per cent of the snails reared with crayfish died during the acclimation phase, but 24% of the snails in the no-predator treatment suffered mortality during acclimation. Most mortality in both treatments was due to desiccation when snails crawled out of the water. If individuals differ in their propensity to crawl out of the water (e.g. DeWitt et al. 2000), then when raised with crayfish, the 'crawl-out' specialists will suffer higher mortality during the acclimation phase, and the population on average will show less of a propensity to crawl out of the water in subsequent behavioural assays.

Experiment 3 also demonstrated that snails collected from a temporary pond without fish predators retain the ability to recognize and respond to fish cues. Bernot & Whittinghill (2003) showed that a *P. acuta* population living in the absence of fish failed to respond to fish cues, and studies of other taxa have also shown that in the absence of continued selection, prey can lose antipredator behaviours (e.g. Flecker 1992; Storfer & Sih 1998). The shallow pond containing this population was human-constructed and may have been colonized recently, which would limit the opportunity for selection to operate. Alternatively, the presence of other predators (crayfish) may select for the retention of the full suite of avoidance behaviours (Blumstein & Daniel 2002). Additional tests on populations in isolated habitats that have been predator-free for a long period will show whether selection favours the loss of plasticity in the absence of predators, as has been shown for some mammalian taxa (e.g. Blumstein & Daniel 2002, 2003). Our results, however, support the notion that predator avoidance in *P. acuta* is largely innate, and may further suggest that the cost of plasticity per se in *P. acuta* is relatively small.

The degree to which inducible antipredator behaviour depends on experience has important consequences for interpretation of ongoing studies of predator avoidance behaviour and behaviourally mediated indirect effects (Luttbeg & Schmitz 2000). Current work is somewhat divided, with some studies using captive-reared animals that have no prior exposure to predators (e.g. most amphibian work), and other studies using wild-caught animals or animals that have otherwise been exposed to predators (particularly investigations of fish and aquatic insects). The choice of wild-caught versus captive-reared animals seems driven by availability of study animals rather than biological considerations. The generality of these studies depends on the extent to which learning is

important, but few studies have compared the response of captive-reared and wild-caught animals to predators (but see Gallie et al. 2001). A comprehensive understanding of the role of experience in the development of antipredator behaviour is also key to predicting the effects of novel invasive predators on indigenous prey assemblages as well as the successful reintroduction of captive-reared animals to the wild (Griffin et al. 2000). Few studies, however, have examined the role of experience in the development of antipredator behaviour, and work to date has largely focused on acquired cue recognition in vertebrates.

In summary, our results suggest that the answer to the question 'Does the predator avoidance behaviour of *P. acuta* depend on experience?' is 'a little, sometimes'. The choice of defensive strategy by snails is in some cases malleable, but the strong responses to variation in predator diet were largely independent of prior exposure to predators. Further work is needed to determine what environmental factors may favour learned responses versus innate responses, and to explore the various constraints on learning. Studies with *P. acuta* also need to explore the effects of longer-term exposure to predators. In any case, the magnitude of the behavioural modifications induced by experience shown here was small relative to the large effects of predator cues, and are probably of minor importance for most ecological processes. The large interest in antipredator behaviour is driven, in part, by the realization that antipredator behaviours may have important consequences for the organization of communities and ecosystems (Lima 1998b; Luttbeg & Schmitz 2000; Werner & Peacor 2003). A knowledge of how learning and memory modify behavioural responses to predators is key to making the link between individual-level processes and higher-level organization in ecological systems.

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