

Inter- and intraspecific trait compensation of defence mechanisms in freshwater snails

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Trait compensation occurs when mechanically independent adaptations are negatively correlated. Here, we report the first study to demonstrate trait compensation in predator-defence adaptations across several species. Freshwater pulmonate snails exposed experimentally to predation chemical cues from fishes and crushed conspecifics showed clear interspecific differences in their behavioural avoidance responses, which were negatively correlated with shell crush resistance. The type of avoidance response varied between species: thin-shelled species (*Lymnaea stagnalis* and *Physa fontinalis*) moved to the water-line or out of the water, while those with thick shells moved under cover or showed a mixed response. There were also intraspecific size-linked differences, with an ontogenetic increase in shell strength accompanied by a decrease in behavioural avoidance. Such trait compensation in response to predation has important implications for interspecific interactions and food-web dynamics.

Keywords: Gastropoda; predator-avoidance behaviour; morphology; predation; chemical cues

1. INTRODUCTION

Predation has selected for adaptations in prey organisms that reduce the mortality from predators, including morphological and chemical defences, and changes in behaviour and life history (Kerfoot & Sih 1987). Changes in behaviour such as reduced activity, shelter seeking or altered habitat use reduce the probability of an encounter between predator and prey, whereas morphological defences reduce the probability of a successful predator attack once a prey has been encountered. The degree of expression of a behavioural response is dependent on a number of factors including the state of the individual (e.g. hunger level, reproductive status) and its vulnerability (e.g. size) (e.g. Stein 1977; Sih 1982; Alexander & Covich 1991; Pettersson & Brönmark 1993). Further, a species may have evolved a suite of 'anti-predator' adaptations. Different types of dependence or compensation relationships exist between these defence adaptations (DeWitt *et al.* 1999), including co-dependence (when traits are mechanically linked), complementation (when traits are mechanically independent but must be combined to be efficient), co-specialization (when traits are independent and used alone or in combination) and compensation (when there are negative correlations between mechanically independent traits). The last relationship, trait compensation among defence adaptations, has recently been shown to occur within species (Berenbaum & Zangerl 1999; DeWitt *et al.* 1999) and between two species of freshwater fish (Abrahams & Healey 1993; Abrahams 1995) but there has been no systematic investigation of this relationship across several species.

Implicit in the concept of trait compensation is that there is a cost associated with having a specific trait. Thus, when defences are costly and the resources available for allocation to defences are limited, defence adaptations that are independent should show trait compensation. For example, prey that have a well-developed morphological

defence adaptation should not need to allocate resources to behavioural defence. Morphological defences may be costly to construct and maintain, whereas behavioural anti-predator responses have been shown to result in reduced growth due to a decrease in the time spent foraging (e.g. Sih 1982; Turner 1997; Lima 1998; Anholt & Werner 1999).

Freshwater snails are model organisms for studying anti-predation adaptations. There are several types of predator that specialize on freshwater snails and influence freshwater snail populations (e.g. Brönmark *et al.* 1992; Brönmark 1994; Lodge *et al.* 1994; Nyström *et al.* 1999). Freshwater snail species vary widely in body size and in the degree of shell development, both of which are morphological traits that relate to predation risk. Shell-crushing predators, such as fishes and crayfishes, for example, have been shown to prefer small and thin-shelled snails (Stein *et al.* 1984; Slootweg 1987; Osenberg & Mittelbach 1989; Alexander & Covich 1991; Nyström *et al.* 1999). Snails also show clear behavioural avoidance responses to predators, such as reduced activity, hiding under cover and crawling out of the water, that are easily measured in the laboratory (e.g. Alexander & Covich 1991; Turner 1997; Levri 1998; McCarthy & Fisher 2000). Often, these behaviours are mediated by chemical cues from the predator. Thus, freshwater snails have evolved a diverse set of anti-predator adaptations, and a recent study demonstrated compensation and co-specialization in defensive traits within a freshwater snail species, *Physa* sp. (DeWitt *et al.* 1999). There has, however, been no investigation of how interspecific variation in shell morphology is reflected in behavioural differences between taxa. In this study, we compared five species of pulmonate freshwater snails to investigate the relationship between investing in morphological defences (shell) and showing a behavioural response to the threat of predation. Both shell construction and a behavioural avoidance response should incur a cost to the individual; hence, we predicted a negative correlation between the expressions of these two traits (i.e. trait

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compensation) across taxa. Further, we investigated whether vulnerability (size) affected the strength of intraspecific behavioural responses.

2. METHODS

(a) *Study organisms*

Five species of pulmonate snails with contrasting shell strengths were used in the experiments: *Lymnaea peregra*, *Lymnaea stagnalis*, *Planorbis planorbis*, *Anisus vortex* and *Physa fontinalis*. All of these taxa are widespread and locally abundant in Skåne, southern Sweden (Brönmark 1985). A single collection was made for each species, but each species came from a different site in the region. We assume, therefore, that gross differences between taxa in their behavioural responses and morphological defences reflect interspecific variation and not inter-population variation (Lewis & Magnuson 1999).

(b) *Morphometric measurements*

We used the resistance of snail shells to crushing as a measure of overall susceptibility to predation (Brown 1998; Osenberg & Mittelbach 1989). The relationship between snail shell size (length) and crush resistance was investigated using regression analysis. We measured the maximum shell dimension of at least 40 individuals representing the full size range of field populations during summer for each species. Individuals were then humanely killed in 70% ethanol and their crush resistances estimated using a modified version of the technique described by Osenberg & Mittelbach (1989). Snails were placed in the centre of a ceramic tile, *P. planorbis* and *A. vortex* with their axes at right angles to the tile and *P. fontinalis*, *L. stagnalis* and *L. peregra* aperture down. A glass beaker, supported by a card sleeve, was placed gently on top of the shell and then filled with sand until the shell gave way. The beaker and sand were weighed and the total weight was used to calculate the force, in newtons, applied to the shell.

(c) *General experimental protocol*

Prior to experiments, snails were kept in aerated water in 20 L Plexiglas tanks for 24–48 h and fed on rabbit chow. The experiments were performed in 10 L Plexiglas tanks (width 180 mm, length 300 mm, depth 180 mm). A 'within-habitat' predation refuge was provided by placing a 100 mm × 100 mm ceramic tile on a plastic cylinder (height 10 mm, diameter 40 mm) in the centre of the bottom of each tank. Before trials, 2 L of aerated tap water was added to each tank. Ten snails were then allocated randomly to each arena and allowed to acclimate for 2 h. At the start of each experiment a further 200 ml of control (aerated tap water) or predation-cue water was added. Seven replicate tanks were used for each treatment, and treatments were allocated randomly across tanks. Each species–size combination was examined in a separate experiment; the order of the experiments was haphazard. Predation-cue water was taken from a Plexiglas aquarium containing 10 L of aerated tap water in which four tench, *Tinca tinca* (length 100–120 mm), had been maintained for 12 h. Tench were used as they have been shown to feed extensively on molluscan prey (Brönmark 1994). Fishes were fed on 1 g of coarsely crushed snails of the test species at the start of the 12 h period and again 2 h before the experiment. This preparation ensured that snails were exposed to chemical cues from natural predators and crushed conspecifics, a mixture that has been shown to maximize anti-predator behaviour (Alexander & Covich 1991; McCarthy & Fisher 2000).

At time zero (just after the addition of the control water or cue water) the number of snails taking up avoidance and non-avoidance positions in the tank was noted. Two main types of avoidance were possible: crawl-out, when a snail either crawled out of the water or was positioned at, or within 1 mm of, the water surface; and hiding, where the snail took refuge underneath the ceramic-tile refuge (i.e. it was not visible from directly above the tile). A position anywhere else in the tank, or floating on the water surface, was classified as a non-avoidance response. Observations were then made at 15, 30, 60, 120, 180 and 240 min. Total avoidance was calculated as the sum of snails hiding and crawling out of the water.

(d) *Interspecific variation in behavioural response*

Avoidance behaviour was investigated for individuals of one size class (large) for all five species. A single value was used to represent the responses of snails in each treatment. As we were interested in those individuals showing a sustained response, we averaged the proportions of animals showing avoidance responses (see §2(c)) at 60, 120, 180 and 240 min. These data were converted to proportions, square-root arcsine transformed (Underwood 1997) and used in a factorial analysis of variance (ANOVA) testing for species effects and predation-cue effects. A Cochran's test was first performed to test for homogeneity of variance, and *post hoc* comparisons were made using the Student–Newman–Keuls test at a significance level of $p < 0.05$. This first ANOVA allowed us to confirm whether significant treatment effects were occurring (i.e. whether there was a difference between the predation-cue treatment and the control treatment). We then performed a second ANOVA to investigate the response to predation cues, standardized to account for background (control) habitat use. Here, the mean response from control treatments for each species was subtracted from the individual predation-cue responses, and the resulting values were used in a one-way ANOVA testing for differences between species.

(e) *Size-based predation avoidance response*

To investigate whether behavioural avoidance of predation was related to relative vulnerability, in this case size, we performed behavioural experiments on additional 'small' individuals of three species, *L. stagnalis*, *L. peregra* and *P. planorbis*. These data were used alongside data for large individuals from the previous experiment in a two-way factorial ANOVA to investigate species and size effects on standardized responses to predation cues (i.e. after subtracting the mean control response from replicate predation-cue values). The avoidance behaviour of an additional size category of *L. stagnalis* (length, mean \pm s.d. = 32.9 ± 1.7 mm) was also measured and used in an intra-specific size-based ANOVA.

(f) *Relationship between morphological and behavioural defence*

The relationship between behavioural responses to predation cues and shell strength was investigated using product-moment correlation between the force needed to crush an individual of average size in each behavioural trial, as predicted from shell-size–crush-resistance regressions, and the avoidance response induced by the addition of predation-cue water (i.e. the difference between the mean responses for predation and control treatments at 60, 120, 180 and 240 min). This analysis was performed on data for 'large' individuals of all species and for all species–size combinations.

Table 1. Morphological parameters of snails.

(Best-fit regression models for the relationship between shell length (mm) and crush resistance (N); more than 40 individuals were used to generate the models and all were significant at $p < 0.05$. The mean (s.d.) size of the individuals used in the experiments is also given.)

	model	r^2	small	large
<i>Lymnaea stagnalis</i>	$y = 0.30e^{0.10x}$	0.91	6.6 (1.2)	10.9 (1.3)
<i>Lymnaea peregra</i>	$y = 0.48e^{0.15x}$	0.65	5.9 (0.6)	11.2 (1.1)
<i>Planorbis planorbis</i>	$y = 0.54x^{1.03}$	0.82	5.5 (0.6)	10.5 (0.5)
<i>Anisus vortex</i>	$y = 0.48e^{0.19x}$	0.59	—	9.1 (0.6)
<i>Physa fontinalis</i>	$y = 0.07e^{0.32x}$	0.44	—	7.9 (0.5)

3. RESULTS

(a) Crush resistance and size

The models of the relationships between shell size and crush resistance showed clear variations between species (table 1 and figure 1). The amount of force required to crush *L. stagnalis*, *L. peregra*, *P. fontinalis* and *A. vortex* increased exponentially with shell size, and the lymneids, in particular, showed very little variation in shell strength when less than 12 mm in size. *P. planorbis* showed a power relationship between shell size and crush resistance (table 1 and figure 1).

(b) Interspecific variation in behavioural response

There were significant effects of species and predation cues on the crawl-out, hiding and total responses of the five species used in interspecific comparisons (table 2). Analyses, after standardizing for background behaviours, showed that there were significant differences in total avoidance behaviour between species, which were confirmed by *post hoc* comparisons (figure 2) and were clearly related to crush resistance: the two least crush-resistant species (*L. stagnalis* and *P. fontinalis*) showed significantly higher avoidance responses than two (*L. peregra* and *P. planorbis*) of the other three species. There were also differences in the type of behaviour shown, with *L. stagnalis* and *P. fontinalis* exhibiting crawl-out and *A. vortex* exhibiting hiding (figure 2).

(c) Size-based avoidance response

There were significant differences in avoidance response between sizes ($F_{1,41} = 4.6$, $p = 0.039$) and species ($F_{2,41} = 6.34$, $p = 0.0044$) (figure 3). Overall, avoidance behaviour decreased with increasing snail size (figure 3), but a significant species–size interaction ($F_{2,41} = 6.8$, $p = 0.0032$) demonstrated that the size-based response was variable across taxa (figure 3). There was also a significant difference in behavioural response between the three size classes of *L. stagnalis* ($F_{2,20} = 14.82$, $p < 0.0002$) (figure 3).

(d) Relationships between morphological and behavioural defence

There was a significant negative correlation between behavioural avoidance and shell strength for large individuals across species ($r = -0.895$, $p = 0.04$) (figure 4a) and for all species–size combinations ($r = -0.626$, $p = 0.039$) (figure 4b).

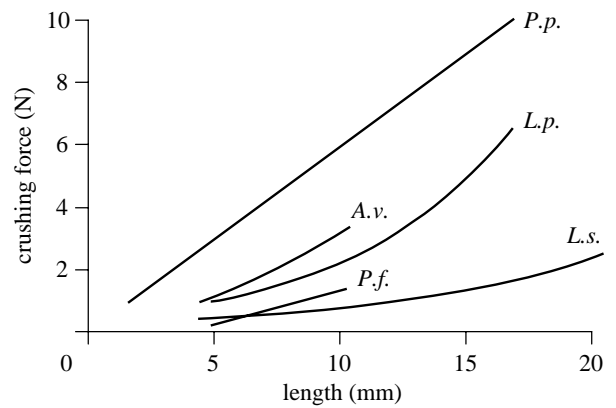


Figure 1. Regression lines for the relationship between snail crush resistance and size for five species of freshwater gastropod: *Lymnaea stagnalis* (*L.s.*), *Lymnaea peregra* (*L.p.*), *Planorbis planorbis* (*P.p.*), *Anisus vortex* (*A.v.*) and *Physa fontinalis* (*P.f.*). Regression equations are given in table 1. Note that, for clarity, only the first part of the curve for *L. stagnalis* is shown.

Table 2. Interspecific comparison of avoidance responses. (a) Results of two-way ANOVA assessing differences in crawl-out, hiding and total avoidance responses between species and between treatments (i.e. control versus predation cues). (b) Results of one-way ANOVAs assessing differences between species for crawl-out, hiding and total avoidance responses standardized for background response.

(a)

source	d.f.	F	p
crawl-out			
species	4, 69	22.4	0.0001
treatment	4, 69	45.1	0.0001
species \times treatment	4, 69	5.1	0.0013
hiding			
species	4, 69	6.3	0.0003
treatment	1, 69	2.7	0.1061
species \times treatment	4, 69	1.3	0.2673
total			
species	4, 69	28.1	0.0001
treatment	1, 69	51.7	0.0001
species \times treatment	4, 69	4.5	0.0028

(b)

source	d.f.	F	p
crawl-out	4, 34	25.2	0.0001
hiding	4, 34	3.9	0.0110
total	4, 34	7.5	0.0003

4. DISCUSSION

To our knowledge, this is the first study to demonstrate trait compensation in predation-avoidance adaptations across several species. Interspecific differences in the morphologies of the five pulmonate gastropods studied were clearly reflected in the wide range of crushing resistances exhibited. Crush resistance was, in turn, negatively

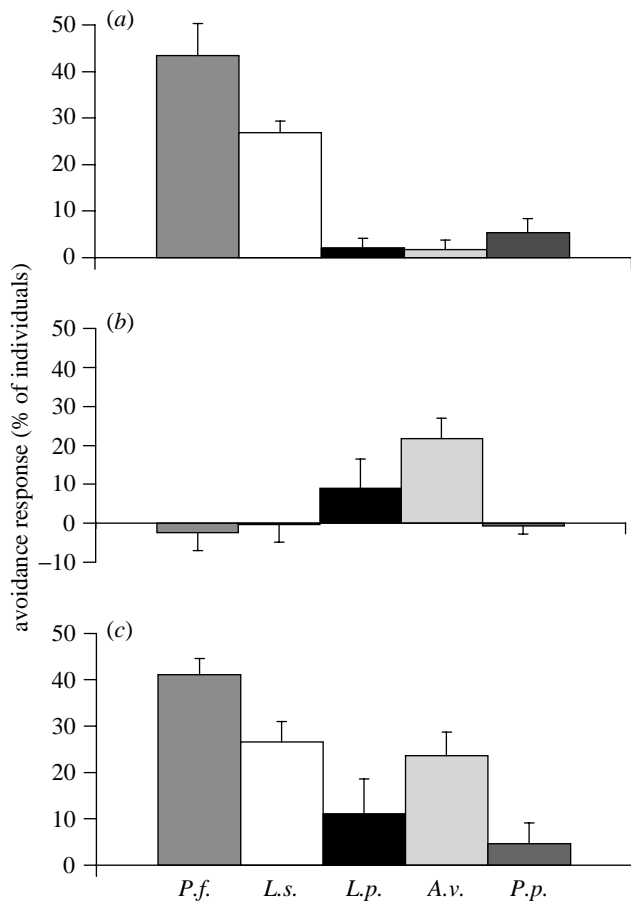


Figure 2. The mean frequencies of avoidance behaviours ((a) crawl-out, (b) hiding and (c) total) of five species of freshwater gastropod (*Lymnaea stagnalis* (*L.s.*), *Lymnaea peregra* (*L.p.*), *Anisus vortex* (*A.v.*), *Planorbis planorbis* (*P.p.*) and *Physa fontinalis* (*P.f.*)) in response to predation chemical cues. Values are the mean proportions of individuals showing the response after accounting for background (control) responses.

correlated with avoidance behaviour: the thin-shelled gastropods *P. fontinalis* and *L. stagnalis* showed the strongest behavioural responses to chemical predation cues; *P. planorbis*, with a high resistance to shell crushing, showed a very weak behavioural response; and species with intermediate shell strengths exhibited intermediate behavioural responses. We also found evidence that ontogenetic increases in shell strength were accompanied by reductions in avoidance behaviour.

Negative correlations, or trade-offs, between different traits have been more typically described between life-history traits, such as size and number of gametes, age at first reproduction and life expectancy (see Stearns 1992). Evidence for trade-offs between different defensive traits is scarcer, but some examples exist. In wild parsnip there is a negative correlation between the production of two chemical defence substances, probably due to competition for a limited supply of precursors (Berenbaum & Zangerl 1999). DeWitt *et al.* (2000) also found a trade-off in shell morphology in a freshwater physid snail: individuals had either a rotund shell, for protection against shell-crushing predators such as fishes, or an elongated shell with a narrower aperture, for resistance to attacks from shell-invading predators such as crayfishes. They also demonstrated size-related trait compensation, with smaller,

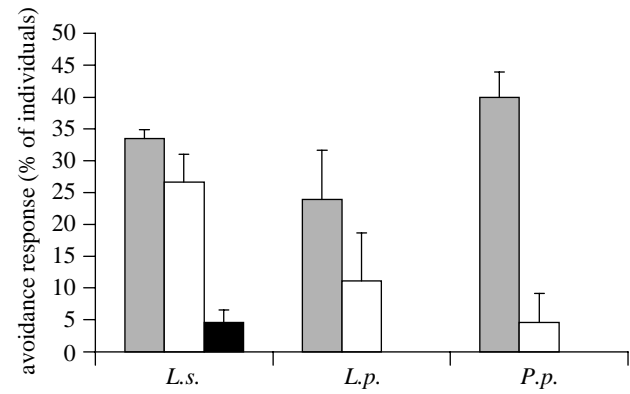


Figure 3. The mean total avoidance behaviours of two size classes (grey bar: ca. 5 mm; and open bar: ca. 10 mm) of three species of freshwater gastropod: *Lymnaea stagnalis* (*L.s.*); *Lymnaea peregra* (*L.p.*) and *Planorbis planorbis* (*P.p.*). Values are the mean proportions of individuals showing an avoidance response after accounting for background (control) responses. An additional size class for *L. stagnalis* (black bar: ca. 35 mm) showed a significantly lower response than the other two size classes for this species (see § 3(c)).

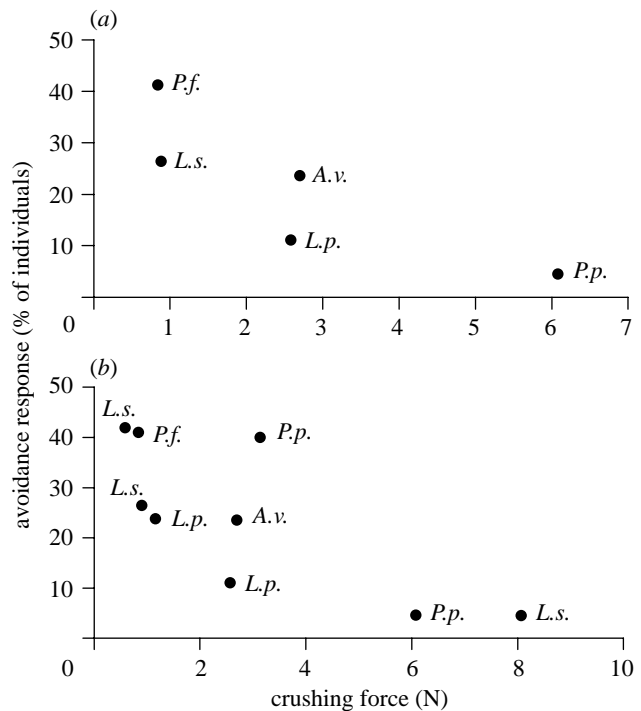


Figure 4. The relationship between crush resistance and avoidance response for different sizes of five species of freshwater pulmonate gastropod (*Lymnaea stagnalis* (*L.s.*), *Lymnaea peregra* (*L.p.*), *Anisus vortex* (*A.v.*), *Planorbis planorbis* (*P.p.*) and *Physa fontinalis* (*P.f.*)): (a) same-sized (large) individuals; and (b) all species-size combinations.

more vulnerable physids being more prone to exhibiting avoidance behaviours. A similar compensation was found for two fish species, the brook stickleback (*Culea inconstans*), with well-developed protective morphology (armour and spines), and the fathead minnow (*Pimephales promelas*), without protective morphology (Abrahams 1995). The armoured stickleback showed less behavioural modification (avoidance of risky areas and reactive distance) in response to a predator than did the unprotected minnow.

We also found trait compensation within species, similar to that found by DeWitt *et al.* (1999). Our results clearly demonstrated that the degree of intraspecific behavioural avoidance decreased with increasing size and was roughly proportional to the concomitant increase in shell strength. The difference in behavioural response between small and large snails was most pronounced for *L. stagnalis* and *P. planorbis*, in which the largest individuals showed no significant avoidance behaviour. Vulnerability to predation in freshwater snails is associated with their size and shell thickness, with smaller and thinner-shelled individuals being preferred by molluscivorous predators (Stein *et al.* 1984; Sloomweg 1987; Osenberg & Mittelbach 1989; Alexander & Covich 1991; Nyström *et al.* 1999). Thus, as a snail grows and/or increases its shell thickness, it becomes less vulnerable to predators and may be expected to reduce its behavioural response to a predation threat (see Alexander & Covich 1991; Levri 1998; DeWitt *et al.* 1999).

Negative correlations between traits should occur as a result of allocation of resources to the traits, i.e. there should be a cost associated with having the traits. Construction of a thick shell is a costly process, especially in calcium-poor waters, and resources allocated to shell construction are no longer available for growth or reproduction (Palmer 1981, 1992). A number of studies have also shown that there are costs associated with avoidance behaviours (for a review see Lima 1998). Lost opportunity to forage when inactive or in refuge has been shown to reduce the growth rate of snails exposed to chemical predation cues (Turner 1997; DeWitt 1998). In our study, some species crawled out of the water in response to a predator threat and, in addition to lost-opportunity costs, this may increase the risk of desiccation and of predation by terrestrial predators (Alexander & Covich 1991). Moving back and forth between a foraging site and a refuge should also incur a cost, including energy for mucus production (Calow 1974).

Several studies in freshwater systems have shown that molluscivorous predators may have strong indirect effects on periphytic algae through a reduced grazing pressure by snails (e.g. Brönmark *et al.* 1992; Brönmark 1994; Lodge *et al.* 1994; Nyström *et al.* 1999). These cascading effects on the primary producer are mediated by a direct lethal effect, i.e. through the reduction in density of herbivores caused by the predation of the molluscivore. However, recent studies have shown that predator-induced changes in traits of a prey species may have strong indirect effects on other components of the food web, so-called trait-mediated indirect interactions. For example, predator-induced changes in activity or habitat choice in an intermediate consumer may affect the density of the basal trophic level and/or the strength of competitive interactions with other intermediate consumers (e.g. Turner & Mittelbach 1990; Peacor & Werner 1997; Relyea 2000; Turner *et al.* 2000). In freshwater snails, Turner (1997) found that increases in the perceived predation threat, mediated by water-borne chemical cues, resulted in increased refuge use, a reduction in foraging activity and a concomitant increase in the basal resource, periphytic algae. From our data, we predict that the strong behavioural avoidance response to the threat of predation shown by thin-shelled species such as

P. fontinalis and *L. stagnalis* should result in a similar effect on their food resource. Further, in situations where thin-shelled species coexist with thick-shelled species, predator-induced changes in resource use may also affect the relative strength and even the direction of competitive interactions between the snails, as has been shown for larval anurans (Relyea 2000). Thus, the investment in and trade-offs between different defence adaptations may have complex repercussions for food webs.

This work was facilitated by grants from The Royal Society and the Swedish Institute (to S.D.R.) and from the Swedish Board for Agriculture and Forestry Research (to C.B.) for which we are grateful. We also thank Emilia and Oscar Brönmark, Elena, Isabel and Nia Rundle, Anna and David Roberts and Ashley Rowden who helped us collect snails, and Peter Cotton and Ross Coleman who gave advice on an early version of this paper and statistical analyses, respectively.

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