

## Functional diversity among predators of a freshwater snail imposes an adaptive trade-off for shell morphology

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### ABSTRACT

We explored how functional diversity among predators of the freshwater snail *Physa* creates an adaptive trade-off for the snail's shell morphology. Physid shells range continuously between elongate and rotund in overall shape. The protection conferred by alternative shell shapes depends on the mode of attack employed by predators. Predators attack *Physa* primarily through shell entry (by crayfish, *Orconectes obscurus*) and shell crushing (by fish, *Lepomis gibbosus*, *Cyprinus carpio*, *Carrasius auratus*). The narrow apertures associated with elongate shells were expected to restrict apertural access by crayfish, as it does in several marine gastropod–decapod interactions. The orbicular body whorls of rotund shells were predicted to disperse better the crushing forces applied by fish. Resistance to one predator then implies susceptibility to the other because shells can be relatively rotund or elongate but not both. Three levels of evidence from this study supported the idea of a trade-off: (1) measurement with laboratory instruments indicated that rotund shells were relatively crush-resistant, whereas elongate shells were more entry-resistant; (2) foraging trials showed that rotund shells required more handling time and were rejected more frequently by fish, whereas snails with elongate shells were more likely to survive with crayfish; and (3) field samples revealed rotund shell morphology in habitats where fish were common. The physical tests, foraging trials and field survey of the present study demonstrate the functional basis for predator-induced plasticity, which has been documented elsewhere for physid shell morphology and serves as a fourth line of support for the existence of an adaptive trade-off. Implications of the trade-off for the behaviour of predators and prey are also discussed.

**Keywords:** adaptive trade-off, crayfish, functional ecology, inducible defences, *Lepomis gibbosus*, multiple predators, *Physa*, shell morphology.

### INTRODUCTION

Predation has been a major force in the evolutionary diversification of gastropod shells (reviewed by Vermeij, 1987, 1993). Most of the evidence for predation-driven radiations has come from comparative or biogeographical studies of marine gastropod taxa. These studies

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have succeeded in revealing many generalities on the adaptive value of shell morphology (e.g. Vermeij, 1976; Palmer, 1979). Studies of shell adaptation have rarely focused on freshwater taxa, intraspecific variation within populations, or multiple types of predators as agents of selection, yet such studies can potentially yield additional insights on the ecology and evolution of gastropod shells.

The study of freshwater shells may elucidate subtle architectural solutions to predation that are not as apparent in marine taxa. For example, a major difference between freshwater and marine habitats is the relatively low availability of calcium in freshwater. Calcium limitation restricts species diversity (Mittelbach *et al.*, 1992), limits growth rate (Palmer, 1981, 1992) and increases vulnerability to predators (Ivlev, 1961). Thus, calcium limitation increases the importance of adaptive architectural innovations that do not require calcium, such as shell shape or microstructure (e.g. West and Cohen, 1996), rather than growth of thicker shells, spines, knobs, and so on (e.g. Trussell, 1996). Freshwater habitats are often ephemeral and, like marine intertidal zones, are prone to dramatic temporal variation and spatial subdivision (Carpenter, 1988). These conditions favour population differentiation, phenotypic plasticity and fast life-cycles, making freshwater gastropods excellent subjects for evolutionary and ecological studies.

Examining intraspecific variation within populations allows researchers to isolate the ecological forces creating the diversity that is so obvious at larger scales (Schluter and McPhail, 1992; Robinson *et al.*, 1996). Studies across taxa or across large geographic areas are indirect by comparison because phylogenetic constraints and unknown ecological differences among sites can confound meaningful trends of evolutionary diversification (Futuyma and Moreno, 1988). Put simply, alternative populations and taxa differ in many ways, and the difference being studied will not always have caused the diversification. Intraspecific diversity is also amenable to breeding experiments that can distinguish genetic and environmental contributions to phenotypic variance (West-Eberhard, 1989; Scheiner, 1993).

Predation studies have typically focused on single predator species (reviewed by Sih *et al.*, 1998), yet molluscs generally face many predators of at least four functional classes (Vermeij, 1979, 1993; detail in next section). Alternative predator types can create adaptive trade-offs just as the presence and absence of a single predator can create (e.g. McPeck, 1995; Eklöv and Persson, 1996). The multiple-predator approach not only reflects nature well, but also provides a richer ecological framework whereby adaptive trade-offs between predators ultimately can be connected to other aspects of ecology, particularly to higher-order community effects (Karieva, 1994). A trade-off within one prey trait may also relate to the functional ecology of other traits, so that we can explore, for example, how morphological and behavioural anti-predator trade-offs work in concert. In some cases, a specific morphology may increase the effectiveness of anti-predator behaviour (Brodie, 1992; McPeck, 1995). Alternatively, morphological defence could decrease the need for anti-predator behaviour or could be used in conjunction with behaviour to specialize defence against a given predator (DeWitt *et al.*, 1999).

In this paper, we define an architectural continuum of shell form (from rotund to elongate morphology) in physid snails. We then postulate and test for an adaptive trade-off between forms (rotundness deters predatory fish; elongateness deters predatory crayfish). Several implications of the trade-off are discussed, including natural selection for phenotypic plasticity (DeWitt, 1996a, 1998) and the interaction between anti-predator morphology and behaviour. We present this work hierarchically. The results of physical tests of our

functional hypotheses prompted foraging studies, which together suggested the need for a field survey of prey morphology.

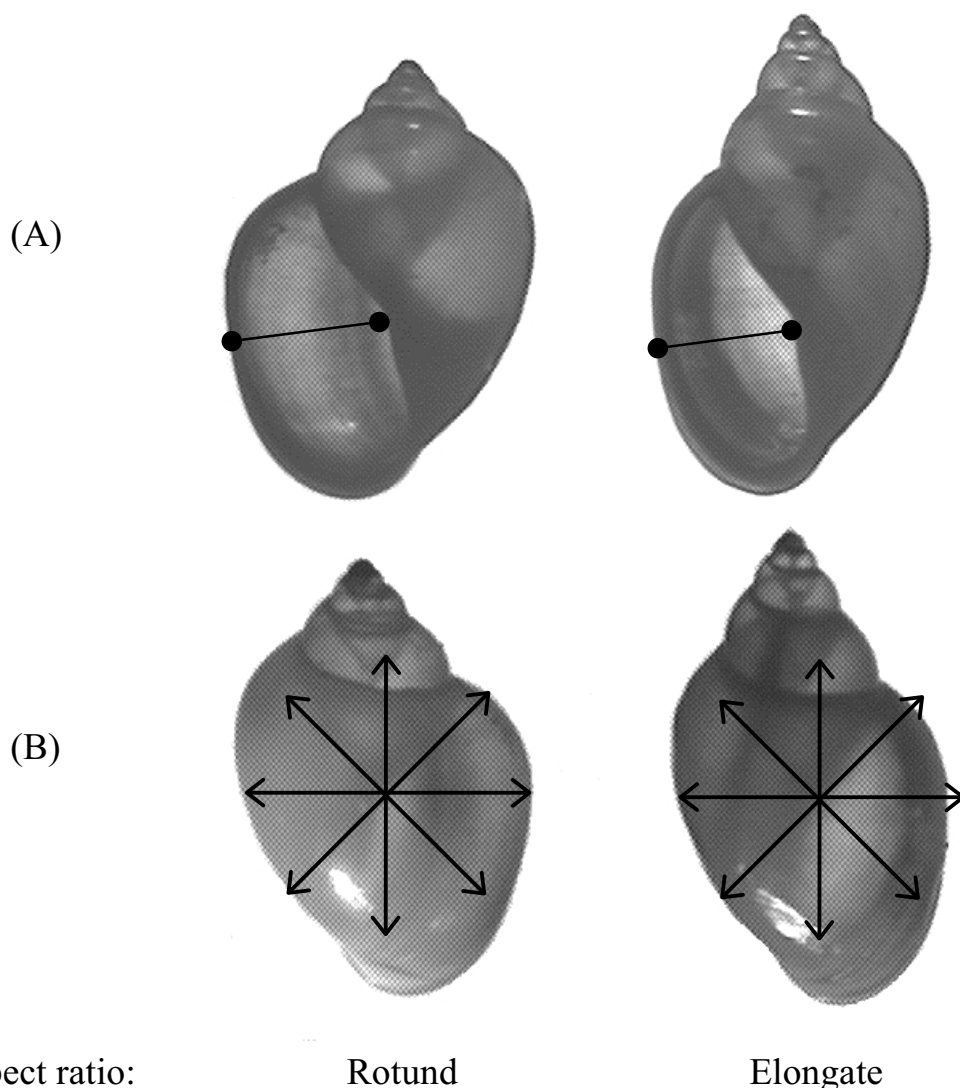
### FUNCTIONAL ECOLOGY OF SHELLS

Gastropods experience four primary modes of predation, although we focus on the first two only: shell entry, shell crushing, shell boring and whole-shell swallowing (Vermeij, 1979, 1993). Shell boring is not frequently observed in freshwater snails and is thought not to be an important cause of death in marine snails, except for small inshore species (Vermeij, 1979). Whole-shell swallowing is likely to be deterred by a large effective shell width or by opercula (Vermeij, 1993). Large effective shell widths, which can be conferred by knobs or exaggerated whorl width, deter gape-limited predators by making shells difficult or impossible to swallow. Opercula can reduce the value of swallowed prey because sealed shells yield little or no energetic return to predators for as long as the operculum remains closed during digestion.

Shell *entry*, as frequently performed by decapods, is deterred by narrow or otherwise occluded apertures (Ebling *et al.*, 1964; Kitching *et al.*, 1966; Zipser and Vermeij, 1978; Vermeij, 1979; Appleton and Palmer, 1988). For example, Appleton and Palmer (1988) showed that apertural teeth are induced in *Nucella* (= *Thais*) *lamellosa* in response to predatory crabs. The apertural teeth help to block entry into the shell. In freshwater snails, a narrow aperture may be the best way to deter shell entry because it is a purely architectural solution that does not require additional calcium, as do apertural teeth (Fig. 1A). Narrow apertures are a potentially important defence in freshwater because snails frequently occur with crayfish. Crayfish primarily attack snails via the aperture (Snyder, 1967; Alexander and Covich, 1991; DeWitt, 1996a). In addition, anecdotal information suggests that relatively large crayfish may sometimes also use shell-crushing or spire-snapping attacks (A.P. Covich, T.J. DeWitt and R.K. Grosberg, unpublished observations). Only shell entry was observed, however, in the present study.

Shell-crushing predators, such as molluscivorous fish, may be deterred by knobs and crenulation, which spread crushing force over an increased surface area or reduce the muscular leverage of the predator (Palmer, 1979; West *et al.*, 1991). Thickened shells may also deter shell-crushing predators (e.g. Trussell, 1996; West and Cohen, 1996). However, these defences involve additional calcium and may be prohibitively costly in freshwater. The calcium issue is heightened for rapidly growing species such as *Physa*, because little time is available to sequester much calcium. *Physa* are thus among the thinnest shelled molluscs (Vermeij and Covich, 1978; Osenberg and Mittelbach, 1989). Where shell material is limiting, an alternative to adding shell material to increase crushing resistance may be to alter what Palmer (1979) refers to as 'overall shell shape'. In this paper, we predict that relatively rotund shells (i.e. orbicular body whorls) spread crushing forces more evenly over a given amount of shell material (Fig. 1B). This morphological solution is potentially independent of calcium availability; the available calcium need only be deployed differently. Thus, altered shell shape may provide adaptive solutions to a given predator technique, so long as costs of alternative shapes are low. DeWitt (1998) tested for but found no indication of production costs (reflected in reduced growth or fecundity) of shell shape variations in *Physa*.

The costs of altering morphology to cope with a given predator technique, if there are any, could be in adaptive trade-offs with other selective pressures, such as the risk of



**Fig. 1.** High and low aspect ratio shells illustrating two functional hypotheses about shell morphology. (A) Ventral view showing shell apertures. Wide apertures (left) leave snails more exposed to entry-based predators than narrow apertures (right). Narrow openings are more difficult to reach into than are wider openings. (B) Dorsal view. Arrows represent vectors of a crushing force applied to the shell. Note that the arrows exceed the shell material in the high aspect ratio shell (right). Relatively rotund shells (left) should be more resistant to shell-crushing predators. The shells pictured correspond to Vermeij's (1979) shell classes B and C (rotund and elongate, respectively) and are from family 237 of DeWitt (1996a, 1998). The snail on the left was raised with pumpkinseed sunfish, whereas its sib on the right was raised with crayfish.

predation by alternative predator techniques. A functional trade-off arises if alternative agents of selection favour different values for a given developmental parameter. Trade-offs in shell architecture result from the geometrical simplicity of shells (Raup, 1966; Raup and

Gould, 1974; Stone, 1996). The constrained phenotype space of shell design thus prevents gastropods from being optimally adapted to all physical phenomena (Gould, 1992). For example, if aperture width alone is increased, a rotund shell results as a consequence. If aperture width is decreased, an elongate shell results (Fig. 1). Aspect ratio, the ratio of shell length to width, can serve as an easily measured, if gross surrogate for the shape of the first whorl and aperture, which are the mechanically important architectural elements of the shell. A trade-off is unavoidable for aspect ratio because a shell cannot be rotund and elongate at once. The subject of this investigation is whether the constraint just outlined results in a functional trade-off with ecological (and perhaps evolutionary) consequences for physid snails.

Following the premises above, we can predict for *Physa* that: (1) rotund shells will be crush-resistant but entry-susceptible and vice versa for elongate shells, demonstrating a mechanical trade-off; (2) rotund shells will be less susceptible to shell-crushing predators but more susceptible to shell-entering predators, and vice versa for elongate shells, demonstrating that the trade-off operates in predator-prey interactions; (3) rotund shells will be more likely in spatial or temporal patches with shell-crushing predators, demonstrating the ecological impact of an adaptive trade-off; and (4) phenotypic plasticity may evolve, which would suggest the historical significance of an ecologically important trade-off. In this paper we address issues 1–3. A quantitative-genetic study demonstrating phenotypic plasticity (issue 4) is reported elsewhere (DeWitt, 1996a, 1998).

## MATERIALS AND METHODS

### Study organism

*Physa* (= *Physella*) are common freshwater pulmonate snails in most of the world. Over 30 species have been described, based primarily on shell characteristics (Te, 1980; Burch, 1989). The reliance of physid taxonomy on shell morphology has been problematic because of the considerable shell variation within and between populations. Many of the morphospecies are thought to be synonymous (e.g. Wurtz, 1949) and much of the variation has environmental rather than genetic causes (DeWitt, 1998). We note here that the two morphospecies included in this study are *P. gyrina* (from the Massachusetts site described below) and *P. heterostropha* (from New York sites). To avoid confusion, we follow several ecologists (e.g. Osenberg and Mittelbach, 1989; Turner, 1996, 1997) in referring only to the genus for the remainder of this paper. Of particular importance is the fact that the behaviour and ecology of the morphospecies are often similar or identical (e.g. Snyder, 1967; DeWitt, 1996b).

The primary predators of physid snails are crayfish (Snyder, 1967; Crowl and Covich, 1990; Alexander and Covich, 1991; Lodge *et al.*, 1994) and fish such as carp (Ivlev, 1961; Stein *et al.*, 1975) and some sunfish (e.g. Snyder, 1967; Carothers and Allison, 1968; Stein *et al.*, 1984; Mittelbach *et al.*, 1992; Robinson *et al.*, 1993, 1996; Turner, 1996, 1997). Physid snails are also consumed by leeches (Townsend and McCarthy, 1980; Brönmark and Malmqvist, 1986; Wilken and Appleton, 1991), flatworms (Tripet and Perrin, 1994), aquatic insects (Snyder, 1967; Manguin *et al.*, 1986) and turtles (Snyder, 1967).

The high susceptibility of physid snails to an array of predators is often attributed to their thin shell relative to other snails (Vermeij and Covich, 1978). Perhaps that is why most studies of physid ecology have not addressed morphology but have commonly focused on

anti-predator behaviour (e.g. Snyder, 1967; Townsend and McCarthy, 1980; Alexander and Covich, 1991; Tripet and Perrin, 1994; Turner, 1996) and life-history (e.g. Brown, 1985; Crowl and Covich, 1990). The only measure of morphology in most studies has been overall body size, which is generally estimated using shell length or the blotted wet mass of snails. It appears likely, however, that shell size and shape will jointly determine predation risks to individual snails.

### Morphometric measurements

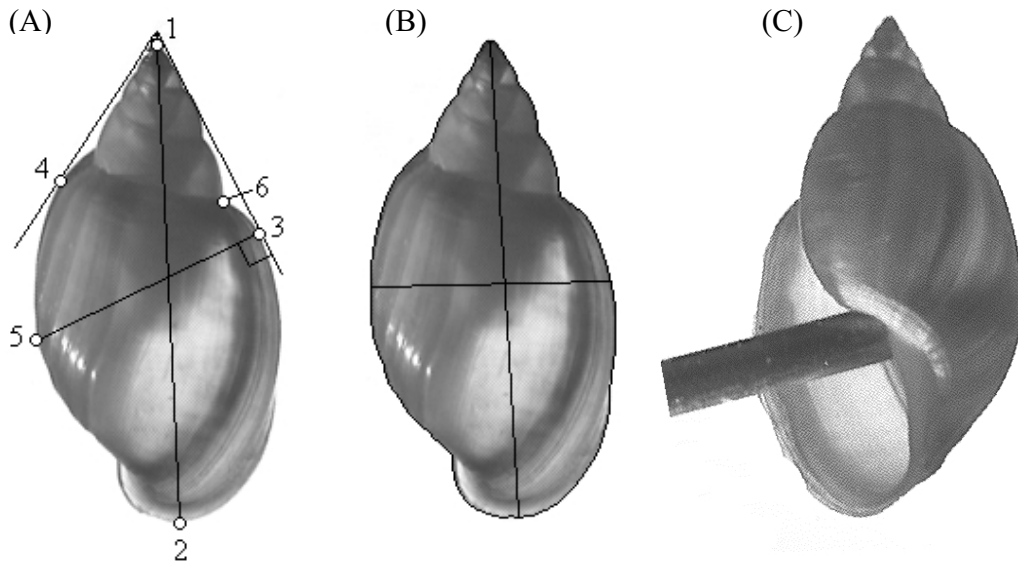
We report related studies conducted over several years. As we used two methods to measure shell morphology, we describe them here, and simply refer to Method 1 or Method 2 as we describe specific studies. To test whether the methods provided similar information, 100 shells were measured both ways. The two size measures (centroid size and area; see below) were correlated by  $r = 0.99$  ( $P < 0.0001$ ) and the aspect ratio measures were correlated by  $r = 0.96$  ( $P < 0.0001$ ). These high correlations imply that the methods are essentially equivalent.

#### *Method 1*

Shells were placed aperture down on the stage of a microscope fitted with a camera, which conveyed images at a resolution of  $640 \times 480$  pixels ( $0.025 \text{ mm} \cdot \text{pixel}^{-1}$ ) to a computer. The aperture-down position was standard among shells because the shells rested on three points of contact: two on the apertural lip and one on the body whorl. Six landmark points were digitized along the outline of the shell using the MorphoSys computer imaging system (Meacham and Duncan, 1989; Fig. 2A). Fifteen morphological trusses (linear distances between pairs of points) were calculated among the six points. The truss structure was used to estimate the centroid size of the snail as  $(\sum \text{truss length}^2 / \# \text{ trusses})^{1/2}$ , which is an unbiased estimator of size (Bookstein, 1991). The shell aspect ratio was calculated as the long axis of the shell (1–2 truss) divided by the 3–5 truss. The 3–5 truss approximates the minimum gape needed for a fish to take the snail into its mouth. Shell size and shape measured by this method were uncorrelated (see the crush-resistance study below).

#### *Method 2*

This method was designed to be simpler and less laborious than Method 1. Shells were positioned aperture down as in Method 1, but no landmark points were used. Instead, shell contours (outlines) were captured using MorphoSys, and the following data were calculated: area of contours, length of the long axis of contours, and the length of an axis halfway along, and perpendicular to, the long axis (i.e. shell width; Fig. 2B). The area of the contour served as our estimate of shell size, and the ratio of shell length to width served as our estimate of aspect ratio. As with Method 1, these size and shape variables were uncorrelated (see the entry-resistance study below). The lack of phenotypic correlation between the size and shape variables concurs with the lack of significant genetic correlation between these traits (e.g. for snails raised without predator scent,  $r_G = 0.065$ ,  $n = 31$  family means,  $P > 0.7$ ; T.J. DeWitt, unpublished data).



**Fig. 2.** Measurement techniques for shell traits. (A) Method 1 consisted of digitizing six landmark points along the shell's image. Points 3 and 4 were located where tangents from the shell apex broke away from the shell outline in the lowest whorl. Point 5 was located by extending a line segment at a right angle from point 3 to the opposite side of the shell. (B) Method 2 consisted of capturing the shell outline and using MorphoSys software to find the shell's longest axis and the perpendicular axis at the midpoint of the long axis. (C) Penetrability of shells was assessed by extending the depth probe on a standard pair of callipers into shells in the manner shown.

### Physical tests: Morphological correlates of crush- and entry-resistance

#### *Estimation of crush-resistance*

Snails ( $n = 33$ ) were collected from Fuller Hollow Creek on the campus of Binghamton University in Vestal, New York, approximately 1 km upstream from its entry into the Susquehanna River. Both rivers contained patchily distributed pumpkinseed sunfish (*Lepomis gibbosus*) and crayfish (*Orconectes obscurus*). Snails were humanely sacrificed with 2-phenoxyethanol and measured for shell size and shape using Method 1. After each shell was measured, it was placed aperture down in an apparatus to measure crush-resistance following Osenberg and Mittelbach (1989). This apparatus consisted of a flat-bottomed glass vial (17.15 mm outside diameter) placed within a slightly wider (17.65 mm inside diameter) vial containing the shell. Sand was poured into the interior vial until the shell burst below it, at which time the vial and sand were weighed ( $\pm 0.01$  g) to estimate crush-resistance of the shell.

Shell size was expected to be a strong predictor of crush-resistance (e.g. as in Stein *et al.*, 1984; Osenberg and Mittelbach, 1989), so it was used as a covariate in a multiple regression testing for an effect of shell shape (aspect ratio). Aspect ratio was transformed to its square root to meet conditions of normality (Sokal and Rohlf, 1995). To represent graphically the shape effect independent of size, we first regressed the resistance variable with centroid size, and then plotted residual resistance with aspect ratio.

### *Estimation of entry-resistance*

Snails ( $n = 33$ ) were collected from the Susquehanna River near Binghamton University to see whether shell entry-resistance varied with aspect ratio. The snails were measured using Method 2 to estimate size and shape. Snails were then sacrificed as above and their bodies were removed from the shells using forceps. Penetrability of shells was measured as the distance to which the depth probe on a standard pair of callipers (probe diameter = 1.5 mm) could be inserted into the shell. The entry path was standardized by laying the probe tip in the shell's umbilical region (the probe seated unambiguously in this position) and extending it as far as possible into the shell, parallel with the dorsal whorl sutures (see Fig. 2C). Penetrability was expressed as entry-resistance by changing its sign. Shell-entry measurements were performed three times on each shell and averaged. The repeatability of individual measures was high ( $r_1 = 0.99$ ,  $n = 33$ ,  $P < 0.0001$ ). As with the data for crush-resistance, the entry-resistance data were analysed by multiple regression, but residuals from a univariate regression of entry-resistance and size were plotted with aspect ratio for graphical presentation.

## **Foraging tests: Predation consequences of morphology**

### *Foraging trials with shell-crushing predators (fish)*

Handling times were measured for pumpkinseed sunfish offered snails in laboratory feeding trials. Nineteen limnetic and 18 benthic sunfish were collected from their respective habitats in Paradox Lake (described in Robinson *et al.*, 1993) and transported to Binghamton University for the foraging trials. Fish were housed individually in 38-litre aquaria and fed pelleted fish food. Approximately 1000 snails were collected from the Susquehanna River and were measured by Method 1. On each of 5 days, sunfish were placed in a 38-litre aquarium, allowed to acclimatize for 10 min, and fed five randomly selected snails one at a time (thus, each fish was fed 25 snails over the course of the experiment). We measured the total time from the entry of the snail into the fish's mouth to the distinctly audible breaking of the snail shell, which was followed by expulsion of shell fragments from the fish's mouth and opercular openings.

Handling times were transformed to their natural logarithm and analysed using a mixed-model nested analysis of covariance with the factors snail size, shell aspect ratio (transformed to its square root), trial date, habitat type of fish, snail presentation order and fish identity (nested within habitat). All factors were tested against the overall error variance, except for the fish habitat effect, which was tested using the fish-within-habitat term as error (Keppel, 1991; Sokal and Rohlf, 1995). Based on the results of our crush-resistance tests, we expected that fish would have more difficulty eating rotund snails.

### *Foraging trials with shell-entry predators (crayfish)*

A predation experiment was performed to see whether crayfish (*O. obscurus*) preyed more heavily on snails with rotund morphology. We offered each of four crayfish (carapace length 28–34 mm) 20 individually marked *Physa* snails of known morphology measured by Method 2. Snails of a restricted size range (9–12 mm) from Fuller Hollow Creek were used so that the snails differed primarily in shape, which was our main concern in this experiment. The predation trials were conducted in 10-litre tanks (30 × 15 × 20 cm) with 2 litres



of water (depth = 4 cm) and no substrate. This barren, shallow environment reduced the chances that snails could employ behavioural defences such as crawling to the air–water interface, hiding, or burying in substrate (Snyder, 1967; Alexander and Covich, 1991; Turner, 1996, 1997; DeWitt *et al.*, 1999). Predation was allowed to continue until approximately 50% mortality was evident, which was within 24 h. A fifth crayfish used in the study was larger (45 mm carapace length) and so was kept in a larger tank (38 litres) of the same proportional shape and water depth as in the other trials. The data were analysed using a paired *t*-test contrasting the mean aspect ratios of surviving snails with those of non-surviving snails within replicates (i.e.  $n = 5$  pairs of means). Based on previous studies of gastropod–decapod interactions and results from our shell-entry tests, we expected that surviving snails would have more elongate shells relative to those that were eaten by crayfish.

### Field survey: Distribution of prey morphology in natural systems

To test for an association between shell morphology and the abundance of predatory fish, we selected field sites in pairs that differed in the factor of interest (fish abundance) but were similar enough otherwise to form natural contrasts. We focused on the abundance of fish, rather than crayfish, because crayfish occurred commonly in all the lotic environments that were the focus of this study. We predicted that shells from environments in which fish were common would be rotund relative to those from environments with few fish, because of local adaptation, selective predation, phenotypic plasticity of shells, or a combination of these factors. Shells from all field samples were measured by Method 1.

First, snails were collected in July 1991 from two small unnamed creeks, approximately 1 km northwest of Binghamton University (deemed VP1 and VP2), which flowed within 300 m of each other and eventually joined. The physical and biotic character of the adjacent creeks was similar, so the creeks formed a natural pair for comparing shell morphology. The main difference in the creeks for this comparison was that creek VP1 contained many (20–40) large goldfish, *Carrasius auratus*, whereas creek VP2 did not. (The creeks were connected by a 60 m pipe with a 0.3 m diameter, which apparently prevented the migration of goldfish into VP2.)

In addition to the collections made from the VP creeks in 1991, a fortunate natural experiment arose which prompted a collection in July 1992. The goldfish that had been common in VP1 were locally extinct during all of 1992. We predicted more rotund morphology in the sample of snails from VP1 in 1991 (when fish were present), compared to the other two collections (i.e. those lacking fish). A single-factor analysis of variance (ANOVA) with a planned contrast of VP1 in 1991 versus the other two collections was used for data analysis.

Second, snails were collected from two microhabitats in Fuller Hollow Creek on the campus of Binghamton University. Snails were sampled from creek pools that were contiguous with, or disconnected from, the main body of the creek. The disconnected pools did not contain fish, whereas pumpkinseed sunfish were present in the connected pools. Because few snails were typically available in a pool, snails from all pools of a given habitat type were combined ( $n = 19$  and 15, respectively, for contiguous and disconnected pools). We predicted that snails from connected pools would have more rotund shells than those from disconnected pools because of their more direct exposure to fish predators. The morphology of snails comprising these collections was contrasted using a *t*-test.

Third, seasonal collections of *Physa* were made in the Fenway of Boston, Massachusetts in 1991 (site description in DeWitt, 1991). Approximately 100 snails were removed from benthic debris on two occasions in the winter and two occasions in late spring. Pumpkin-seed sunfish and carp, *Cyprinus carpio*, were common in this waterway in the summers of 1990 and 1991, but were uncommon in the 1990–91 winter. Snails collected in late spring had grown and developed with a relative paucity of fish over the previous winter, whereas snails collected in winter were those remaining after a summer of predation and growth in the presence of molluscivorous fish. We predicted that snails collected in the winter would demonstrate the effects of exposure to fish and so would have more rotund shells than snails collected in the spring. Analysis was performed using a nested ANOVA to partition aspect ratio variation into a season effect, with the two collection dates nested within season.

## RESULTS

### Physical tests: Morphological correlates of crush- and entry-resistance

#### *Crush-resistance*

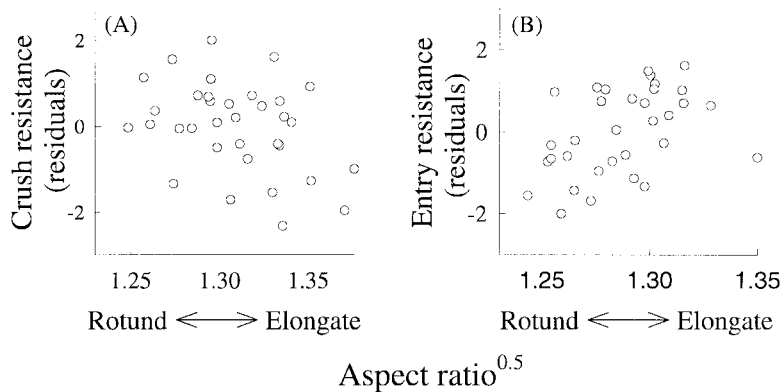
The results of the shell-crushing tests are reported in Table 1. Large or rotund shells were more resistant to crushing than relatively small or elongate shells. Shell size explained most (45%) of the variation in crush-resistance ( $n = 33$ ,  $P < 0.0001$ ). Aspect ratio explained 16% (partial  $R^2$ ) of the residual variation that remained in crushing resistance after factoring out the size effect ( $n = 33$ ,  $P = 0.02$ ). This negative relationship between aspect ratio and residual crush-resistance is plotted in Fig. 3A. Shell size and shape were not correlated for snails in this experiment ( $r = 0.13$ ,  $n = 33$ ,  $P > 0.5$ ).

#### *Entry-resistance*

In this experiment, as in the crush-resistance experiment, both shell size and shape were shown to account statistically for variation in resistance (Table 1). Shell size explained 94% of the variance in shell penetrability; the calliper probe penetrated farther into larger

**Table 1.** Multiple regression for the effects of shell size and shape on the resistance variables

| Variable                | Regression coefficient | Standard error | Standardized coefficient | <i>t</i> | <i>P</i> | $R^2$ | <i>N</i> |
|-------------------------|------------------------|----------------|--------------------------|----------|----------|-------|----------|
| <b>Crush-resistance</b> |                        |                |                          |          |          |       |          |
| Constant                | 5.52                   | 0.99           | 0                        | 5.59     | 0.0001   | 0.54  | 33       |
| Shell size              | 0.48                   | 0.09           | 0.69                     | 5.51     | 0.0001   |       |          |
| Aspect ratio            | -1.31                  | 0.54           | -0.30                    | -2.41    | 0.02     |       |          |
| <b>Entry-resistance</b> |                        |                |                          |          |          |       |          |
| Constant                | 6.40                   | 1.25           | 0                        | 5.12     | 0.0001   | 0.95  | 33       |
| Shell size              | 0.07                   | 0.003          | 0.96                     | 24.37    | 0.0001   |       |          |
| Aspect ratio            | 3.04                   | 1.10           | 0.11                     | 2.77     | 0.009    |       |          |



**Fig. 3.** Correlation of residual resistance and shell shape for (A) crush-resistance and (B) entry-resistance. (A) Rotund shells were more resistant to crushing. After accounting for variation in crush-resistance due to size, shell shape explained 16% of the variation in resistance ( $R^2 = 0.16$ ,  $n = 33$ ,  $P = 0.02$ ). (B) Elongate shells were less vulnerable to entry ( $R^2 = 0.20$ ,  $n = 33$ ,  $P = 0.009$ ).

shells ( $n = 33$ ,  $P < 0.0001$ ). Shell aspect ratio explained 20% of the residual variance left unexplained by shell size; deeper penetrance occurred into rotund shells ( $n = 33$ ,  $P = 0.009$ ). Expressed as entry-resistance, elongate shells were more resistant to entry (Fig. 3B). As in the crush-resistance study, shell size and shape in this experiment were not correlated ( $r = 0.06$ ,  $n = 33$ ,  $P > 0.7$ ).

Taken together, the crush- and entry-resistance data for shell shape form a fitness set that describes two abilities (i.e. resistances to alternative predation techniques) that are inversely related (Fig. 3). The trade-off demonstrated here followed our predictions and motivated the foraging trials with predators employing the two techniques. Thus, in the following tests with predators, we used specific (i.e. one-tailed) hypothesis tests to fit the hierarchical structure of our investigation and nature of the prior information (Keppel, 1991; Sokal and Rohlf, 1995).

### Foraging tests: Predation consequences of shell morphology

#### *Shell-crushing predators (fish)*

Pumpkinseed sunfish spent more time handling snails with rotund shell morphology ( $F_{1,881} = 8.47$ ,  $P = 0.002$ ; Fig. 4A). Handling time also was greater for larger snails, for trials earlier in the testing period, and for some individual fish (Table 2). Fish size has been shown to influence handling time in studies in which pumpkinseed sunfish were fed snails, with larger fish taking less time to consume snails (Osenberg and Mittelbach, 1989). Fish identity, rather than size *per se*, was used as our independent variable because it accounted for all differences between fish, including size, and hence explained more variance (i.e. the statistical model using fish as a categorical variable had an  $R^2 = 0.46$ , whereas using fish length yielded  $R^2 = 0.26$ ). The model using fish size (standard length) indicated that the fish effect from our primary model was due largely to fish size ( $F_{1,915} = 102.3$ ,  $P < 0.0001$ ),

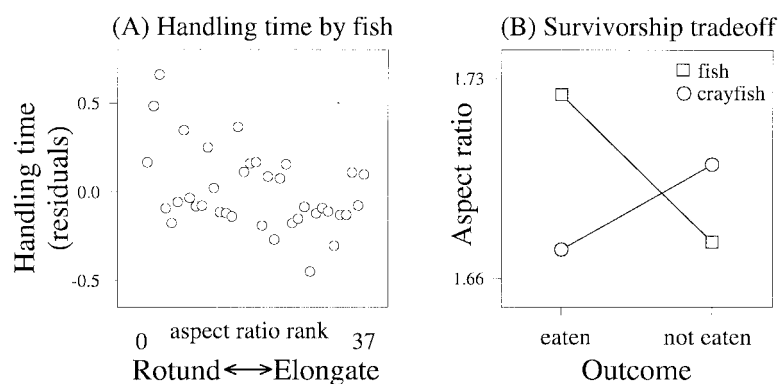
concurring with the results of previous studies. There was no indication that fish size interacted with shell size or shape to determine handling time (i.e. for both interaction terms,  $F_{1,913} < 3.75$ ,  $P > 0.05$ ).

Fourteen snails were rejected by pumpkinseed sunfish and had to be replaced. Shell size did not differ between the 14 rejected and 925 consumed snails ( $F_{1,937} = 1.80$ ,  $P = 0.2$ ). However, rejected snails were more rotund than snails consumed by fish ( $F_{1,937} = 2.92$ , one-tailed  $P = 0.04$ ; Fig. 4B). Surviving snails had a mean ( $\pm$  standard error) aspect ratio of  $1.67 \pm 0.017$ , whereas snails that were eaten had a ratio of  $1.72 \pm 0.004$ . Thus, a more rotund shell morphology both increased handling times and rejection rates in accordance with expectations from the shell-crushing tests.

#### *Shell-entering predators (crayfish)*

Observations of predation confirmed that the crayfish attempted to extract snails from the shell aperture and would chip at the aperture on occasion to facilitate shell entry. We also observed some snails escaping predation by extruding egg jelly onto the mouthparts of crayfish (see also DeWitt, 1996a). When employed, the behaviour commonly resulted in snails being dropped. It also appeared to increase strongly the handling time of snails employing the behaviour that were ultimately consumed. In this study, we did not attempt to quantify any aspect of this apparently defensive behaviour.

Crayfish were offered snails of similar sizes that differed in shape. To ensure that no size effect was evident within the restricted size range of snails used (9–12 mm in shell length), we performed a paired  $t$ -test comparing the size of surviving snails to that of snails consumed. The two groups did not differ in size (paired  $t_4 = 0.28$ ,  $P = 0.8$ ). The shape effect on survivorship matched expectations from the mechanical shell-entry tests. Snails that



**Fig. 4.** Results of foraging trials with predators. (A) Handling time of variously shaped snails by pumpkinseed sunfish. For clarity, the 925 snails were ranked by aspect ratio (shell length/width) and the mean handling time for successive groups of 25 snails were plotted (i.e.  $925/25 = 37$  points). (B) Survivorship of snails exposed to predators. In the foraging study with fish, surviving snails had rotund shells relative to the shells of snails that were consumed. The opposite pattern occurred in trials with crayfish: snails with elongate shells survived better than those with rotund shells. Results from the two experiments are plotted on the same graph to illustrate the trade-off. Crossing of the lines indicates that increasing resistance to one predator confers susceptibility to the other.

**Table 2.** Nested ANCOVA for shell handling time by pumpkinseed sunfish

| Source             | d.f. | MS-III | <i>F</i>          | <i>P</i>           |
|--------------------|------|--------|-------------------|--------------------|
| Shell size         | 1    | 35.774 | 262.93            | 0.0001             |
| Shell aspect ratio | 1    | 1.152  | 8.47              | 0.002 <sup>a</sup> |
| Test date          | 4    | 0.332  | 2.44              | 0.05               |
| Habitat of fish    | 1    | 2.893  | 1.62 <sup>b</sup> | 0.2                |
| Snail order        | 1    | 0.049  | 0.36              | 0.5                |
| Fish{Habitat}      | 35   | 1.786  | 13.13             | 0.0001             |
| Error              | 881  | 0.136  |                   |                    |

Note:  $R^2 = 0.46$ ,  $P < 0.0001$ . <sup>a</sup> One-tailed test. <sup>b</sup> The denominator (error term) for this variance ratio was the Fish {Habitat} mean square (Keppel, 1991).

survived exposure to crayfish had elongate shell morphology relative to those eaten by crayfish (paired  $t_4 = 2.46$ , one-tailed  $P = 0.035$ ). Survivors had a mean aspect ratio of 1.70, whereas consumed snails had a ratio of 1.67 (standard error of the difference = 0.01). Figure 4B shows the mean aspect ratios for surviving and consumed snails from this study (using crayfish), together with those from the study using fish. The fact that the lines cross implies that defence against one predator is inversely related to defence against the other. That is, no single morphology maximizes or minimizes protection across predators.

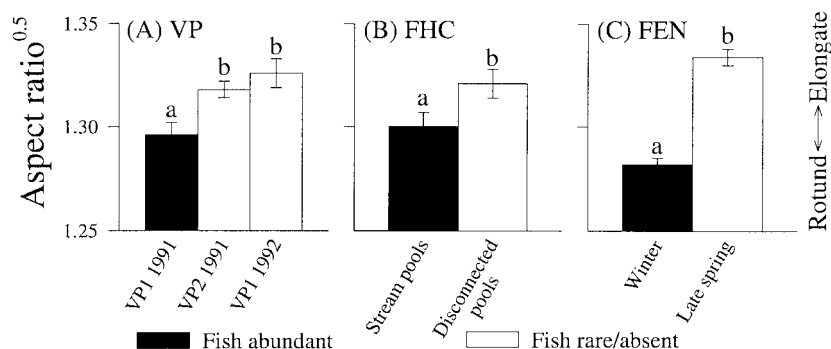
### Field survey: Distribution of prey morphology in natural systems

Snails from habitats in which fish were common had rotund shells relative to snails from habitats with few or no fish (Fig. 5A–C). In the VP system of creeks, snail shell morphology was most rotund in the creek with fish in 1991 (VP1). Relatively elongate morphology was noted among snails taken from that same creek in 1992 (when fish were absent) and for snails taken in 1991 from an adjacent creek which lacked fish (VP2). This difference was revealed by a planned contrast between the VP1 collection from 1991 versus the other two collections ( $F_{1,142} = 14.4$ ,  $P < 0.001$ ). A *post-hoc* (Fisher's LSD) test offered no evidence that snails from the two fishless VP collections differed in shell morphology ( $P > 0.3$ ).

The comparison of shell morphology in the connected and disconnected creek pools of Fuller Hollow Creek revealed that shells from connected pools (i.e. those with predatory fish) were more rotund than shells from disconnected pools which lacked fish ( $t_{32} = 2.04$ ,  $P < 0.05$ ; Fig. 5B).

The test for seasonal variation in shells from the Fenway indicated more rotund morphology among snails collected in winter compared with snails collected in the spring ( $F_{1,191} = 101.9$ ,  $P < 0.0001$ ; Table 3). That is, snails grown during a summer and fall sympatric with fishes were more rotund (Fig. 5C). There was no significant effect of sampling date on shell morphology (Table 3), so the data were pooled by season for presentation in Fig. 5C.

The magnitude of morphological difference was similar for each contrast: approximately 5–6% wider shells for a given length when fish were present. For reference, this difference was less than that observed in a rearing study in which physid snails were raised with fish or crayfish (snails raised with fish were 9% wider for a given length; DeWitt, 1996a, 1998).



**Fig. 5.** Aspect ratio contrasts of physid shells collected from locations or times that differed in fish abundance. Samples of snails that had grown and developed in the presence of fish are indicated by solid bars; open bars indicate that few or no fish were present during the growth and development of snails. Aspect ratio contrasts are shown for: (A) the paired VP creek system; (B) the contiguous and disconnected pools in Fuller Hollow Creek; (C) seasonal variation in the Fenway. Bars with different letters indicate collections with statistically significant differences in mean shell morphology ( $P < 0.05$ ).

**Table 3.** Nested ANOVA for variation in shell aspect ratio between seasons that differed in fish abundance

| Source       | d.f. | MS-III | F     | P      |
|--------------|------|--------|-------|--------|
| Season       | 1    | 0.1354 | 101.9 | 0.0001 |
| Date{Season} | 2    | 0.0032 | 2.43  | 0.09   |
| Error        | 191  | 0.0013 |       |        |

Note:  $R^2 = 0.36$ ,  $P < 0.0001$ .

## DISCUSSION

The predicted functional trade-off, that rotund shells are resistant to crushing but susceptible to entry, was supported by data from a variety of independent sources. Our physical tests demonstrated that relatively rotund shells resisted greater crushing force, whereas elongate shells were less penetrable by a calliper probe (Fig. 3). The overall shell metric used, aspect ratio, seemed to capture the mechanical elements of both resistance variables. When a gastropod expands whorl width slowly relative to overall shell growth, a more elongate shell results than when width is expanded more rapidly, which results in a more rotund shell (Fig. 1). If multiple developmental parameters are altered at once, then more complex patterns of variation in overall shell morphology are possible (Raup and Gould, 1974; Stone, 1996), but such variation was not evident for these snails.

Although the results of our physical tests address mechanical hypotheses, they do not by themselves inform us about ecological or evolutionary impacts. One reason why is that predators could be undeterred by small morphological differences among prey. It is also possible that prey or predators make compensatory adjustments in the field (Futuyma and Moreno, 1988; DeWitt *et al.*, 1999). Mechanical tests do not inform us, for example, about interactions of morphological and behavioural traits that can jointly determine prey

vulnerability. If vulnerabilities can be balanced in part by compensatory mechanisms, or if predators are not deterred by small differences among prey, there may be little overall effect of predators on prey populations in nature. As a partial solution to such problems, we combined physical tests, laboratory predation trials and field surveys to address both the mechanical and ecological consequences of the trade-off.

The predation experiments with crayfish indicated that both prey morphology and escape behaviour determined susceptibility of snails to predators. Crayfish differentially consumed snails with relatively rotund shells (Fig. 4B). This result concurs with those of other gastropod–decapod studies showing that narrow apertures reduce shell entry (Ebling *et al.*, 1964; Kitching *et al.*, 1966; Zipser and Vermeij, 1978; Vermeij, 1979; Appleton and Palmer, 1988). Although predator-avoidance behaviours were prohibited in our experimental apparatus (water was intentionally kept shallow and free of structures for hiding), snails were sometimes able to escape once they had been captured. Escape from crayfish was enacted by egg-jelly (and egg) deposition on the feeding parts of the crayfish (DeWitt, 1996a). Affected crayfish dropped snails to scrape off the jelly from fouled mouthparts using their walking legs. Snails, once dropped, immediately and rapidly crawled away. Morphological defence may facilitate escape behaviours because increased handling time imposed by narrow apertures increases the time available for snails to release egg jelly. Thus, morphological defence may both reduce a snail's intrinsic value as prey and increase the time available for snails to invoke behavioural defences.

Fish experienced difficulty eating snails with rotund shells. Relatively few snails were rejected in our study (14 of 939 trials), but rejected snails were rotund relative to those that were consumed (Fig. 4B). The low rejection rate of *Physa* was probably due in part to our use of relatively large fish (83–153 mm SL). Large fish are not usually gape-limited and can exert powerful crushing forces, so they can eat most physid snails (Osenberg and Mittelbach, 1989). The low rejection rate may also have resulted from our method of presenting single prey items in succession. Foraging animals are often indiscriminant when prey are encountered this way (Elner and Hughes, 1978; Kaiser *et al.*, 1993). With the chance of absolute discrimination minimized, predators can be observed eating prey that they normally would not bother with, thereby facilitating analyses of handling times.

Fish spent more time handling snails with relatively rotund shells (Fig. 4A). Increased handling time reduces the value of prey because time spent handling prey reduces the predator's energetic payoff per unit time ( $E/T$ ; Stephens and Krebs, 1986). As noted above, the handling time issue has implications for prey behaviour – it increases the time available for prey to enact escape behaviours. However, handling time also has implications for the behaviour of predators in addition to the simple  $E/T$  calculation typical in foraging studies. Prolonged handling of prey may facilitate the escape of future prey. The act of predation releases alarm pheromones that stimulate avoidance behaviours in nearby prey. Thus longer handling times for current prey will be correlated with longer search times for subsequent prey. Freshwater snails, like aquatic organisms in general, have a variety of predator-avoidance behaviours that are mediated by sensing predation on conspecifics (e.g. Snyder, 1967; Alexander and Covich, 1991; Turner, 1996, 1997; DeWitt *et al.*, 1999).

If handling time of current prey and search time for subsequent prey are positively correlated, predators should adjust their preference-ranks of prey items accordingly. Quickly consumable prey should become more valuable when alarm pheromones exist that can alert future prey. Kagel *et al.* (1986) discussed preference for quickly consumable prey

(rather than strict  $E/T$  maximization) because predation is less subject to interruption. Both mechanisms also suggest that predators could also benefit by employing energetically expensive predation tactics as long as they increase the speed of predation. Further detailed study of the snail–fish–crayfish dynamic should provide more insight into the connections between behaviour and morphology in both predators and prey.

Although our laboratory predation trials demonstrated that the functional trade-off can have adaptive consequences under certain (laboratory) conditions, they inform us very little about whether the trade-off commonly influences the distribution and abundance of prey phenotypes in nature. For instance, predators may be of minor importance compared to the other ecological demands on prey morphology. In our comparisons of field sites, we found that rotund shells were associated with temporal and spatial variation in the abundance of fish (Fig. 5). Thus the functional trade-off seems to be among the ecological factors determining the distribution of physid shell types in nature. A survey of environments with varied crayfish abundance would also be interesting, provided that suitable environmental contrasts could be located that differed primarily in crayfish abundance.

Associations between predator abundance and specific prey phenotypes can stem from local adaptation, selective predation or phenotypic plasticity of prey. The small scales over which we observed shell differences – spatially over a few metres and temporally over a few months – argue against local adaptation of trait means as a primary answer in this system. Selective predation probably accounts for some of this variation given the results of our foraging trials. However, phenotypic plasticity of shell shape is known for physid snails and thus provides another probable component of the variation. DeWitt (1996a, 1998) raised sibships from 29 snail families in environments with fish or crayfish. Strong plasticity was observed in which snails raised with fish were 9% wider for a given length compared to those raised with crayfish (see Fig. 1). The direction of induced morphological change is adaptive given the results of the present work. This suggests that the trade-off has been historically important in the evolution of physid snails.

The trade-off documented here stems from functional diversity among *Physa*'s predators. Differences between fish and crayfish in their predation techniques seem to influence both the evolution (e.g. selection for phenotypic plasticity) and present-day distributions of prey phenotypes. However, it is not clear how the predators would influence prey numbers. Multiple predators can create either risk-enhancing or risk-reducing effects on prey (reviewed by Sih *et al.*, 1998). That is, the simultaneous presence of multiple predator types can result in either a greater or lesser impact on prey than the expected additive effects due to individual predator types. Usually, conflicting prey defences are expected to create risk enhancement. In the present context, adaptive morphology with respect to one predator makes a snail more vulnerable to the other predator. Thus, we might expect that the presence of both predators would confine snails to an 'enemy-free space' and impact snails more than the presence of either predator alone. Future work should test explicitly for risk-enhancing effects on snail demography due to the joint presence of fish and crayfish. However, such studies must account for other prey traits related to defence that might be correlated with the morphological defence. For example, snails that are defended morphologically against a given predator could compensate for their morphological vulnerabilities to alternative predators with increased anti-predator behaviour (DeWitt *et al.*, 1999). Thus, another obvious avenue for continued research on multiple-predator trade-offs is to examine multiple traits simultaneously (DeWitt, 1996a; Sih *et al.*, 1998).

Recent theory suggests that trait correlations are important in determining the nature



and magnitude of natural selection on individual traits (Lande and Arnold, 1983; Price and Langen, 1992). If a trait conferring positive fitness effects is correlated with a trait conferring negative effects, it may be hard to determine the ecological consequences of one trait studied without reference to (or control over) other traits. Shell morphology in *Physa* is known to be phenotypically correlated with predator-avoidance behaviours (DeWitt *et al.*, 1999) and genetically correlated with life-history traits that influence predation (DeWitt, 1996a, 1998). In the present study, snails could not behaviourally avoid predators. This restriction allowed us to isolate morphological effects on predation. However, the existence of trait correlations implies that continued study of intraspecific diversity in shell form will provide valuable insight into the evolution of multiple traits across multiple selective regimes. Uniting these themes (multiple traits and multiple selective factors) is necessary to advance our understanding of the ecological and evolutionary mechanisms producing the diversity observed in natural systems.

Classically, evolutionary studies of shell form have used biogeographical, palaeontological and cross-taxon comparative approaches to infer the selective (ecological) pressures producing the diversity seen in present-day communities (e.g. Kitching *et al.*, 1966; Vermeij, 1976, 1977, 1979; Palmer, 1979; Seeley, 1986). Marine gastropods have been the predominant focus of such studies because of their extraordinary interspecific diversity, which presumably stems from a long history of evolution with their predators. With the exception of some large ancient lakes (West *et al.*, 1991; Michel, 1994; West and Cohen, 1996), freshwater systems show a relative paucity of evolutionary innovation in shell morphology (Vermeij, 1987, 1993). As unremarkable as species-level diversity may be in freshwater, however, within-species variation should be copious due to the stochastic and isolating nature of freshwater environments. Determining the ecological consequences of such intraspecific variation is essential for understanding the selection pressures moulding populations and species (Schluter and McPhail, 1992; Robinson and Wilson, 1994; Robinson *et al.*, 1996). Ecological studies within taxa complement the more macro-evolutionary approach by isolating specific mechanisms driving the radiations that are so obvious at larger scales of study. Understanding functional trade-offs should be critical in such studies because organisms perhaps always face multiple (often conflicting) agents of selection at once.

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