Predator-avoidance responses in freshwater decapod-gastropod interactions mediated by chemical stimuli

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Abstract. Previous studies on single species of snails reached conflicting conclusions regarding the importance of chemical cues in predator-avoidance behavior. We performed laboratory experiments to determine if chemically mediated, predator-avoidance behavior, such as crawling out of the water by freshwater gastropods, occurred among prey of different species from several geographic sources: Oklahoma, Oregon, and Wisconsin. We compared responses of eight gastropod populations when they were exposed to predation by three species of crayfish. We observed no crawl-out from two prosobranch species. Individuals from four of six populations of pulmonates responded to crayfish predators; physid and lymnaeid populations consistently responded whereas some planorbid populations did not respond.

We also examined individual variation in response to predators and the proximate costs and benefits to prey associated with crawling out of the water. Trade-offs between risks of immediate, direct mortality from aquatic, amphibious, or terrestrial predation relative to delayed, indirect mortality associated with desiccation, are influenced by shell size, thickness, and morphology, as well as physiological adaptations among various pulmonate populations. If water depth is sufficient to provide spatial refuge from crayfish, smaller snails can reduce their losses to predation by moving to the surface of the water or by crawling out. In previous studies, *Physella virgata* and *Planorbella trivolvis* frequently used predator-avoidance behavior when young, but as shell size and strength increased with age, the larger individuals spent less time crawling out of the water. In this study none of the planorbids (*Helisoma anceps* or *Gyraulus parvus*) crawled out, even when young. These differences are apparently due to differences in selection pressures caused by differences in use of various microhabitats where risk of predation varies over time.

Key words: predation, crayfish, snails, chemical cues, anti-predator behavior.

The specificity of chemical cues as well as potential costs, trade-offs, or limitations associated with these response behaviors are central issues that must be addressed if we are to recognize the full importance of chemical cues in predator–prey interactions. For example, do prey species respond only to naturally co-existing predators because of long-term coevolution or do observed responses represent a generalized communication system? Do prey species not respond to some predators because they cannot recognize some cues or are there morphological, physiological, or ecological reasons for the lack of response? The results reported here address these issues and provide the basis for a more complete understanding of freshwater benthic invertebrate communities. We present some new data on the importance of water-borne chemicals that provide further generalization regarding chemical-cue specificity in freshwater decapod–gastropod interactions and some related costs and/or limitations of avoiding predators. Specifically, we ask if: i) pulmonate gastropod species from several regions show similar responses to a general suite of chemicals that function as alarm signals; ii) proximate responses result in trade-offs, in terms of both other mortality factors and life-time fitness costs.

Chemoreception is important among freshwater gastropods in their search for mates and

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food and in their avoidance of predators (e.g., Etges and Frick 1966, Snyder and Snyder 1971). Snyder (1967) reported that several freshwater pulmonate snails responded to intraspecific extracts or to water coming from tanks housing crayfish and other predators by burrowing into the substrate or by crawling above the waterline (i.e., a crawl-out response). For example, *Biomphalaria glabrata* (=*Australorbis glabrata*), a relatively thin-shelled, widely distributed, tropical freshwater planorbid snail (cited in Snyder 1967) was reported to respond to chemical cues from predators. However, in later experiments, Sodeman and Dowda (1974) observed no crawl-out response in *Biomphalaria glabrata*. Sodeman and Dowda crushed conspecifics in small experimental pools, but no actively feeding predators were present in their experiments. The inability to observe avoidance responses in Sodeman and Dowda's studies may have resulted because active predation and its associated predator-specific chemical cues were not present.

In our recent laboratory studies (Crowl and Covich 1990, Alexander and Covich 1991a), *Physella virgata* (a temperate-zone, thin-shelled, pulmonate snail) crawled out only in response to actively foraging crayfish. *Physella virgata* did not crawl out when non-feeding crayfish predators were present. Our results suggest that the combination of chemical cues from both concurrently foraging predators and from dead conspecifics activate the crawl-out response in *Physella virgata*. These results minimized the possibility that tactile and/or hydrodynamic cues are involved because actively moving, but non-feeding, crayfish did not elicit crawl-out responses from *Physella virgata*. Thus, we concluded that two types of chemical cues are apparently involved: chemicals emanating from dead, dying, or alarmed conspecifics, as well as chemicals from actively foraging crayfish. Alternatively, crayfish may consume conspecific snail prey and excrete or release a partially digested snail extract that has been modified by crayfish digestive enzymes, so that a single chemical cue is sufficient.

Lack of avoidance responses among local populations of prey may also occur because of genetic differences that have evolved in the absence of shell-breaking predators so that most individuals lack the ability to recognize predators chemically. For example, in our previous studies (Alexander and Covich 1991a) *Physella*

virgata did not crawl out when crayfish (*Procambarus simulans*) from temperate-zone habitats consumed only *Bimophalaria glabrata* (a tropical species). Because *Biomphalaria glabrata* and *Physella virgata* do not generally co-occur with this predator, we suggest that snail prey can only recognize predator-avoidance chemical cues from native, coevolved predators and prey. Thus, local and regional differences may occur in how populations of snails respond to shell-breaking predators. Hence, in this paper we determine if there are geographic differences in specificity of crawl-out responses. We also explore the costs associated with these anti-predation behaviors and determine if constraints on responses among species, populations and/or individuals can be explained by cost/benefit trade-offs, or if other evolutionary factors may be important.

Methods

Specificity of chemical cues

Experiment 1.—To determine if snail recognition of predator-generated chemical cues was generalized or specific, two combinations of snails and crayfish were observed: *Physella virgata* and *Procambarus acutus*, both collected from springs in Oklahoma (Crowl 1989); and a population of *Physella* spp. and the western crayfish (*Pacifastacus leniusculus*) collected from Oregon. Twenty-five snails from a single population were placed in an aquarium with a water depth of 30 cm and no substratum. The number of initial 25 snails at or above the air–water interface were noted after 12 h in the dark. The three treatment combinations were: with co-occurring crayfish; with crayfish from a different geographic region; and without crayfish. Each treatment combination was repeated five times with previously unused snails and crayfish.

Experiment 2.—Additional experiments were conducted to determine if specific differences in crawl-out exist among snails with different shell sizes, thicknesses, and morphologies as well as physiological adaptations. Crawl-out responses were compared using a single species of crayfish predator and six co-occurring species of snail prey from northern Wisconsin. The crayfish predator was *Orconectes rusticus* and the prey consisted of four species of pulmonates (*Physella gyrina, Lymnaea emarginata, Helisoma anceps, Gyraulus parvus*) and two species of pro-

sobranchs (*Amnicola limosa, Campeloma decisa*). Adult male crayfish and snail prey were collected from lakes and ponds near Trout Lake, Vilas County, Wisconsin. Only intermolt, actively feeding crayfish (as determined by an initial overnight predation test on 10 snails of each species) were used in the experiments. Experiments were conducted in aquaria (76 cm long by 36 cm wide by 35 cm high) with sand substratum and water depth of 10 cm. Two hours before the start of the experiment 100 snail prey of a single species and single size class (shell lengths: 2–5 mm; 6–9 mm; 10–13 mm) were placed into aquaria. One crayfish was then added to each aquarium and each experiment was conducted for 12 h overnight in a dark room. This procedure ensured that the snails would have time to disperse within the aquaria before crayfish began to search for them. Each prey-type and size-class treatment was replicated three times. The number of snails at or above the air–water interface was recorded after 12 h overnight in the dark and was used to determine the presence or absence of crawl-out. These procedures for determining frequency of crawl-out were the same as those used in previous experiments by Alexander and Covich (1991a, 1991b).

Costs of crawl-out

Experiment 3.—This experiment was designed to measure costs of crawl-out behavior (such as desiccation) relative to seeking an alternative spatial refuge at the water's surface or direct risk of mortality when exposed to crayfish predation. *Physella virgata* were the prey and *Procambarus acutus* were the predators. Both co-occurring species were collected in Oklahoma. The methods were similar to those in Experiment 1 (25 snails and 1 crayfish in each aquarium with 5 replicates per treatment). The treatment consisted of a mesh barrier (opening of approximately 5 mm) placed across the tank at different heights. Treatment levels included: no screen barrier (crawl-out allowed); a barrier ~10 cm above the tank bottom (restricted snail movement within immediate reach of the predator); a barrier ~20 cm above the tank bottom (restricted snail movement just within reach of the predator at 1.5 times the length of crayfish); and a barrier at the air–water interface at 30 cm (restricted snail movement within water but well

beyond the reach of the predator). Video recorders (cameras with low-light sensitivity and located outside aquaria) were used to monitor mortality due to direct crayfish predation and desiccation (for snails that crawled completely out of the water and remained out for an extended period). A low-intensity red light was positioned 20 cm above the aquaria to mimic nocturnal conditions when crayfish foraging is most active. Observations on predation and crawl-out were made continuously for 4 h between 2300 and 0300 h. A one-way ANOVA was used to compare mortality not due to crayfish predation (non-consumptive mortality) for snails limited to: the lower 10 cm of the tank; the lower 20 cm; below the water level (30 cm); and no upper limit.

Results

Specificity of chemical cues

Experiment 1.—Both species of snails (*Physella virgata* and *Physella* sp.) crawled out of the water significantly more times in the presence of their co-occurring crayfish predators than when no crayfish were present ($F = 57.92, p < 0.0001; F = 86.26, p < 0.0001$, respectively). For both species, at least 60% of the individuals were observed out of the water when predators were present (Table 1). A two-way ANOVA was used to test whether or not snails responded differently to the crayfish that do not naturally co-occur with them, with snail species and crayfish species as the two treatment variables. The interaction ($F = 0.18, p = 0.677$), snail species effect ($F = 0.44, p = 0.5154$), and crayfish species effect ($F = 0.18, p = 0.4777$) were not significant, suggesting that both species of snails responded equally to both crayfish predators. For the two-way ANOVA, the no-crayfish treatment was omitted because of extreme heterogeneity of variance. Because one-way comparisons confirmed that each snail species showed significant crawl-out behavior when compared with non-predator controls, an analysis without a control is warranted.

Experiment 2.—The two prosobranch species (*Amnicola limosa* and *Campeloma decisa*) showed no crawl-out response (Table 2). *Campeloma decisa* buried their entire shells in the sand substratum. None of pulmonate planorbid snails (*Helisoma anceps* or *Gyraulus parvus*) demonstrat-

TABLE 1. Mean number (out of 25) snails showing crawl-out in Experiment 1 in response to co-existing crayfish predators, crayfish from different geographic regions, and controls (no crayfish). $n = 5$.

Snail origin	Crayfish origin	Number out (percentage)
Oklahoma	Oklahoma	16.6 (66.4)
Oklahoma	Oregon	16.2 (64.8)
Oklahoma	None	2.2 (8.8)
Oregon	Oklahoma	18.0 (72.0)
Oregon	Oregon	15.9 (63.6)
Oregon	None	2.0 (8.0)

ed any crawl-out response. The other two pulmonate species (*Physella gyrina* and *Lymnaea emarginata*) responded with a high frequency of crawl-out behavior in the presence of crayfish predation by *Orconectes rusticus* (Table 2). The highest crawl-out response was by *Physella* with 55% of the snails in the 6–9 mm shell-length class crawling out.

Costs of crawl-out

Experiment 3.—A significant effect was observed ($F = 7.77$, $p < 0.0020$) for non-consumptive mortality. A Ryan-Einot-Gabriel-Welsch Q (REGWQ) post-hoc comparison (Day and Quinn 1989) revealed that all of the variance was explained by mortality incurred by snails that were able to crawl completely out of the water (Table 3). Snails confined to the water did not show significantly different non-consumptive mortality rates. When mortality due to crayfish predation was compared, we again observed a significant treatment effect ($F = 16.83$, $p < 0.0001$). Post-hoc multiple comparisons tests suggested that mortality due to direct crayfish predation was highest for snails limited to the lower 10 cm and lowest for snails limited to the lower 30 cm or not limited at all (Table 3). Hence, if water depth is sufficient to provide spatial refuge from crayfish, snails can reduce predation mortality as effectively by crawling up to the surface of the water as when they completely leave the water.

Discussion

Specificity of chemical cues

The results of experiments 1 and 2 showed that four of six populations of pulmonates used

in our studies crawled out in response to chemical cues from predators, regardless of predator origin (Tables 1, 2). That this crawl-out behavior is widespread among populations of fast-growing, thin-shelled physids and lymnaeids fits our expectations derived from our previous review of their habitat distributions and life histories (Vermeij and Covich 1978, Crowl and Covich 1990, Alexander and Covich 1991a, 1991b). Although these data are in no way exhaustive, it appears that the ability to respond to chemical cues is a general phenomenon for those physid and lymnaeid snails which have been studied. Response does not depend on prior experience with the predator, either at the species or population level.

Unexpectedly, populations of two planorbid species (*Helisoma anceps* and *Gyraulus parvus*) from Wisconsin lacked a crawl-out response. Other planorbid species (e.g., *Biomphalaria glabrata*) in previous studies (Snyder 1967, Alexander 1987, Alexander and Covich 1991a, 1991b) did crawl out in response to decapod predation. As discussed below, planorbids show more distinct differences in the presence or absence of crawl-out, perhaps because of differences in physiological adaptations such as oxygen-storing hemoglobin.

Costs of crawl-out

Pulmonate snails typically move up and down in the shallow littoral zone while seeking food and mates along the substratum and frequently return to obtain oxygen at the air–water interface (Townsend 1975, Corr et al. 1984). As described above, we have observed pulmonate snails actively moving in and out of the water

TABLE 2. Mean number (out of 100), sizes, and species of snails that crawled out in Experiment 2 in response to the crayfish predator *Orconectes rusticus*. $n = 3$.

Snail species	Mean number (SE) out of water		
	2–5 mm	6–9 mm	10–13 mm
Amnicola	0	0	0
Campeloma	0	0	0
Gyraulus	0	0	0
Helisoma	0	0	0
Lymnaea	10 (3.2)	30 (5.3)	4 (1.1)
Physella	35 (6.7)	55 (6.8)	16 (3.3)

and eventually returning to the water (usually within hours) after predation has ceased. However, conspicuous numbers of these snails adhere to the aquarium glass for hours or days after active predation has ceased. Some of these individuals presumably were aestivating but others appeared not to recover when placed in water. This apparent mortality is typically due to snails cementing themselves to substrata above the water and then failing to return to the water before above-water environmental conditions become stressful (e.g., during very warm temperatures and/or very low humidity). The results of the experiment designed to quantify direct mortality due to crawl-out confirm the notion that significant mortality can arise due to cementing and extended aestivation (Table 3). Although the mortality rate was low (3.2/25 snails), it nevertheless represents a loss not incurred by simply crawling up to the water surface or merely dispersing to lower encounter rates with predators (Table 2).

A second potential cost of aestivating or being temporarily out of the water is an increased risk of terrestrial predation (e.g., by birds) and exposure to predators such as belostomatids (Crowl and Alexander 1989, Kesler and Munns 1989) at the air–water interface, and leeches (Michelson 1957, Townsend and McCarthy 1980, Brönmark and Malmqvist 1986, Brown and Strouse 1988). Sciomyzid (Diptera) larvae may be a major source of mortality for aestivating *Lymnaea* (Jokinen 1978), and ducks and other bird species may be responsible for some snail mortality (Collias and Collias 1963, Dirschl 1969, Morris and Boag 1982).

Another potential cost is decreased snail foraging during the crawl-out period. *Physella* cannot always find food while above the waterline if algal growth is lacking. While submerged, many freshwater snails (including *Physella*) can graze more or less constantly, so that any time above the waterline may be lost opportunities for grazing. All freshwater pulmonates lay their eggs in water, and any time above the waterline would also decrease the time available for reproduction. However, crawling above the waterline and avoiding crayfish and other aquatic predators may allow the snail to survive for a few more days and increase the opportunities for foraging, mating, and reproduction (Alexander and Covich 1991a). The reduction in food intake may be offset by a decrease in metabolic demand. No data exist on terrestrial versus

TABLE 3. Mortality associated with crawl-out behavior in Experiment 3 limited to the bottom 10 cm, lower 20 cm, below the water surface (30 cm) and unlimited (0). Letter codes in parentheses represent REGWQ post-hoc results. Within a mortality category, row values with different letters differ significantly ($p < 0.05$). Numbers are out of 25. $n = 5$.

Depth (cm)	Non-crayfish mortality	Crayfish mortality
10	0.6 (A)	12.0 (A)
20	0.4 (A)	7.0 (B)
30	0.6 (A)	2.0 (C)
0	3.2 (B)	1.0 (C)

aquatic respiration rates in freshwater pulmonate snails. Comparable supporting data do exist for the marine intertidal gastropods, particularly the littorine prosobranchs, some subtidal prosobranchs, and pulmonates (McMahon and Russell-Hunter 1981, McMahon 1988, 1990). Anaerobic metabolic rates and tolerances of various freshwater snails demonstrate that planorbid and prosobranch snails are more resistant to anaerobic conditions, surviving longer in anaerobic conditions than physids and lymnaeids (von Brand et al. 1950).

Other physiological costs may also be important in determining if local populations of snail prey crawl out to avoid predators. For example, one physiological cost to freshwater snails is that of eliminating ammonia, the primary metabolic waste product of freshwater snails (McMahon 1983, Brown 1991). While in the air, the production of ammonia requires more water for elimination than urea or uric acid, and this could exacerbate desiccation or possibly be toxic while the snails are above the waterline. Energetic costs of predator avoidance are often related to relative sizes and mobility of prey and predators. Comparative studies on a variety of freshwater animals have shown that closely related or co-occurring species may respond differently to a predator. Generally, smaller prey show stronger anti-predator responses than do larger, less vulnerable prey (e.g., Stein 1977, Schmitt 1982, Stein et al. 1984, Sih 1986, Werner and Hall 1988). In these studies, prey appear to assess the trade-offs between predation risk and continued foraging. Highly vulnerable age/size classes or species forage in different habitats, or at different times, than invulnerable prey (Vermeij and Covich 1978, Covich 1981, Vaughn and Fisher 1988, Alexander and Covich 1991b).

An additional factor besides the relative vulnerability to predation for gastropods is the weight associated with shell thickness and morphology. As snails increase in size, shell weight increases as a cubic function and costs of locomotion increase (Calow 1974). Hence, shell strength, vulnerability to predation, and the energy required to avoid predators are all correlated. In previous experiments, *Physella virgata* and *Planorbella trivolvis* used predator avoidance behavior when young. As shell strength increased with size (and age), these larger individuals spent less time crawling out of the water (Alexander and Covich 1991b). Results reported in this study (Table 2) demonstrate similar patterns for *Physella gyrina* and for *Lymnaea emarginata*. However, our earlier results for *Planorbella trivolvis* (which lives in relatively shallow ponds, streams and wetlands) do not match those for *Helisoma anceps,* a planorbid species that lives in large lakes. Small size classes of *Planorbella trivolvis* showed significant crawl-out response (Alexander and Covich 1991b) whereas small *Helisoma anceps* showed no detectable crawl-out (Table 3). Reasons for differences in response of these two similar planorbid species warrants further study.

Overview

Differences in predator-avoidance behavior among physid, lymnaeid, and planorbid families and among size classes of various species may partially be due to relatively fixed differences in shell morphology. Alternatively, these differences may be a consequence of selection pressures caused by distinct physiological adaptations characteristic of each of the three families of pulmonates. These distinct adaptations allow each group to use different microhabitats. *Physella* and *Lymnaea* are found in the near-shore littoral zones with abundant macrophytes and woody debris. *Planorbella* and *Helisoma* with their well-developed neomorphic gill and hemoglobin, a more efficient respiratory pigment characteristic of planorbids, are much more "aquatic" than the more "amphibious" *Physella* and *Lymnaea*, which typically retain an air-filled lung for gas exchange (Hutchinson 1993). These pulmonates make periodic excursions to the water surface to renew their oxygen stores. Because of these needs for atmospheric oxygen, physids and lymnaeids are more limited to shallow freshwater habitats or habitats with sufficient

vertical structure (e.g., emergent vegetation and woody debris) than are planorbids. Physids apparently have been selected for a strong crawl-out response and a relatively thin, energetically less expensive shell than many other pulmonate and all other prosobranch snails. Planorbids, with less access for crawl-out sites in deeper, less oxygen-rich water, apparently have been selected for a stronger shell and a lower dependence on crawl-out, at least as large adults (McMahon 1983, Alexander and Covich 1991b).

Data are needed on water loss and aerial respiration in aquatic pulmonates. Because pulmonates have moved from marine to land to freshwater, the freshwater species may be readapting to shallow, aquatic habitats (Russell-Hunter 1964, 1978, McMahon 1983, Brown 1991, Hutchinson 1993). The degree to which each pulmonate family has readapted to aquatic habitats appears to constrain their use of the terrestrial environment as a refuge. In general, the planorbids, physids, and lymnaeids appear to represent a continuum in the physiological adaptations from an advanced neomorphic gill and hemoglobin in planorbids to a rudimentary gill and hemocyanin in physids to no accessory gills or respiratory pigments in lymnaeids. This range of adaptations (Russell-Hunter 1964, 1978, Ghiretti and Ghiretti-Magaldi 1975, Hutchinson 1993) greatly influences each family's capacity to avoid predators by crawling out of the water.

Some freshwater pulmonates have been shown to aestivate on dry land at certain times of the year (Jokinen 1978, Brown 1991), by secreting a mucus covering (the epiphragm) over the aperture. This adaptation suggests that at least some species can stay out of water for extended periods of time. Their life history is geared to minimize desiccation (Russell-Hunter 1964) and they are primarily restricted to nocturnal activities in high-humidity habitats. Because freshwater decapods often actively forage at night, the physiological stress for aquatic pulmonates that have crawled above the water's surface may be less than the heat stress they would suffer if they crawled out of water during the day.

In general, the physiological costs, the costs of decreased opportunities for foraging, and the potential increase in terrestrial predation are minimal for a single crawl-out event, even for larger individuals. During times of heavy predation, however, repeated crawl-out over suc-

cessive days may result in substantial costs in terms of lost foraging time, physiological stress, and lost opportunities for reproduction. The benefits of crawling out are that the snails may live longer, allowing them time to produce a few more egg clutches (Alexander and Covich 1991a).

Future studies are needed to determine how individual prey balance long-term costs and benefits under differing environmental conditions when confronting different types of predators. Variability in rates and intensity of chemically mediated predator-avoidance response may be due to the condition of individual prey. As Townsend (1975) reported, the pattern and frequency of vertical pulmonate snail movements can be influenced by lack of food. Green et al. (1992) also note that crawl-out occurs in response to crowding and low dissolved oxygen among pulmonates. Our low values for crawl-out in controls (no crayfish predation in Table 1) may reflect some of this non-predatory effect. Variability in cover, water temperature, bacterial breakdown of alarm substances, diffusion of compounds, and water currents may also influence the intensity and consistency of chemically mediated prey responses to active predators (Dodson et al. 1994). Prey in a low-quality microhabitat (in terms of availability of food and vertical structure) may also be subject to high risk of predation. Much more work is also needed on genetic variation within and between local snail populations as related to crawl-out and other modes of predator-avoidance behavior.

Acknowledgements

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