Original article

Foraging and refuge use by a pond snail: Effects of physiological state, predators, and resources

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ABSTRACT

The costs and benefits of anti-predator behavioral responses should be functions of the actual risk of predation, the availability of the prey's resources, and the physiological state of the prey. For example, a food-stressed individual risks starvation when hiding from predators, while a well-fed organism can better afford to hide (and pay the cost of not foraging). Similarly, the benefits of resource acquisition are probably highest for the prey in the poorest state, while there may be diminishing returns for prey nearing satiation. Empirical studies of state-dependent behavior are only beginning, however, and few studies have investigated interactions between all three potentially important factors. Here I present the results of a laboratory experiment where I manipulated the physiological state of pond snails (*Physa gyrina*), the abundance of algal resources, and predation cues (*Belostoma flumineum* waterbugs consuming snails) in a full factorial design to assess their direct effects on snail behavior and indirect effects on algal biomass. On average, snails foraged more when resources were abundant, and when predators were absent. Snails also foraged more when previously exposed to physiological stress. Snails spent more time at the water's surface (a refuging behavior) in the presence of predation cues on average, but predation, resource levels, and prey state had interactive effects on refuge use. There was a consistent positive trait-mediated indirect effect of predators on algal biomass, across all resource levels and prey states.

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1. Introduction

Prey can respond to predation by reducing their activity (Lima and Dill, 1990; Kolar and Rahel, 1993), investing in defensive structures (Hanazato and Yasuno, 1989; Brønmark and Miner, 1992) or chemicals (Coley, 1983; Bryant et al., 1983, 1985), modifying their life-history (Crowl and Covich, 1990; DeWitt, 1998; Chase, 1999; Peckarsky et al., 2001) or restricting their use of habitat (Turner and Mittelbach, 1990; Turner et al., 1999). However, prey often sacrifice some ability to acquire resources by employing anti-predator defenses (Sih, 1980; Gilliam, 1982; Werner and Gilliam, 1984; Lampert, 1987), and the costs of predator avoidance behavior may outweigh the benefits if the actual risk of mortality is low.

More recently ecologists have recognized that the physiological state of prey should influence their response to predators (Kohler and McPeek, 1989; Pettersson and Brønmark, 1993; Werner and Anholt, 1993; Lima, 1998; Luttbeg et al., 2003) because organisms with varying physiological conditions or efficiencies may realize different costs and benefits from the same behavior (Godin and Crossman, 1994; McPeek et al., 2001; Bridges, 2002). For example, an energetically stressed individual risks death from starvation if it is too vigilant in its attempts to avoid predation, while a well-fed organism is better able to afford the costs of hiding or remaining inactive when a predator is near. Similarly, the benefit of resource acquisition is probably highest for the prey in the poorest state, while there may be diminishing returns for prey nearing satiation. Along these lines, energetically stressed fish are found to exhibit "predator inspection" behaviors more often than unstressed fish, presumably because stressed fish need to feed and benefit the most from accurately assessing predation risk (Godin and Crossman, 1994; McLeod and Huntingford, 1994).

While studies of anti-predator responses of prey continue to accrue (reviewed in Lima and Dill, 1990; Lima, 1998), few studies have addressed the potential interactions between all three of the main factors that should influence prey decision making: predation risk, resource availability, and physiological state of the prey (Godin and Sproul, 1988; Kohler and McPeek, 1989). Here I report the results of an

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experimental manipulation of all three factors, meant to test three predictions: 1) Increased predation risk should cause prey to spend more time in a refuge and less time foraging. 2) Prey will choose riskier behavior (e.g., foraging) when resources are more abundant. 3) Prey in a poor physiological state (i.e. recently starved) will take more risk than those in a good state. There also may be interactions between these factors, which necessitates their study in concert. For instance, prey in a poor state may be willing to take more risk in general, but if resources are very low there is less benefit from risk-taking, and thus prey may continue to remain inactive or in refuge.

When predators influence the traits of prey species they can have indirect effects on the prey's resource, or trait-mediated indirect interactions (Schmitz et al., 1997; Peacor and Werner, 1997, 2001; Bernot and Turner, 2001; Werner and Peacor, 2003). For example, if a predator induces its prey to hide (a trait change), the resources of that prey may increase in abundance, without any decrease in abundance of the prey. Peacor and Werner (2001) demonstrated that trait-mediated indirect interactions of this kind can exceed the strength of density-mediated indirect interactions under some conditions, and suggest that in some systems trait changes among prey may be responsible for a large part of the community-wide structuring influence of predators. Concordantly, Preisser et al. (2005) concluded from a meta-analysis that predator effects on prey demographics due to intimidation were at least as strong as those due to mortality. Here, I also report the consequences of behavioral (i.e. trait) changes among the consumers (elicited from resource, predation, and prey-state treatments) on the abundance of the basal resource. I expected the basal resource to remain abundant under conditions that would induce strong prey responses (see predictions above).

2. Methods

I used a simple three trophic-level system consisting of an insect predator *Belostoma flumineum* (Hemiptera), the common freshwater pond snail *Physa gyrina*, and periphytic algae, to test the predictions described above. The behavioral and morphological responses of freshwater snails to predation risk are well described (Osenberg, 1988; Turner, 1996; Turner et al., 1999; McCarthy and Fisher, 2000; Bernot and Turner, 2001), which makes them a particularly good taxon for this study. *Physa* are known to assess predation risk chemically (Turner, 1996), and can distinguish between predator types; *Physa* climb out of the water when crayfish are present and seek covered shelter when fish are present (Alexander and Covich, 1991; Turner et al., 1999; Bernot and Turner, 2001). Less is known about the behavioral responses of snails to *Belostoma*, which are voracious snail predators and may consume up to six snails per day in laboratory settings (Wojdak, 2004; Crowl and Alexander, 1990). *Belostoma* is a good model predator for this study because it is not omnivorous like crayfish (which would make a simple food chain into a web and make results more difficult to interpret) and does not require large volume enclosures like fish.

I experimentally manipulated prey state, resource level, and predation risk in a $2 \times 2 \times 2$ design, replicated seven times. Two separate trials were run, with three replicates of each treatment in the first trial (23–25 Sep 2002) and four replicates of each treatment in the second run (26–28 Sep). There was no effect of trial number on any response variable, and so it is hereafter ignored. Treatments were randomly assigned to experimental units within a trial. One replicate of each of the "good" state-low resource-predator present and "poor" state-low resource-predator present treatments were lost due to accident.

Each experimental unit (18 L plastic bucket) contained 6 L of low nutrient well water and a suspended predator enclosure. The predator enclosure was a clear plastic tube (10 cm diameter) with fine mesh (250 μm) on each end that allowed movement of water, but prevented snails or predators from passing through. Organisms were collected from ponds in the Lux Arbor Reserve (Kellogg Biological Station, MI, USA) where snails and *Belostoma* naturally co-occur. Snails were either fed spinach to satiation or starved for six days, creating snails in "good" state and "poor" state, respectively. The duration of starvation was chosen arbitrarily because I had no *a priori* knowledge of what period would create biologically significant changes in nutritional state. However, because *Physa* forage almost constantly and herbivores in general are thought to require a high food volume, six days was thought to be a strong manipulation. Six *Physa* were placed into each bucket and were allowed to acclimate for 12 h. At the beginning of each trial I placed three additional *Physa* into each predator enclosure, and one *Belostoma* into half of the enclosures. *Physa* in cages with the predators were typically killed very quickly, so it is likely that an immediate and strong predation signal was released in each "predator" experimental unit. Three resource tiles (23 cm² each) were placed into each experimental unit. "High" resource treatments received tiles that had been incubated with a diverse inoculum of local algae species in a high nutrient, high light environment for three weeks (mean algal biomass [SE] = 2.08 [0.22] mg/cm² ash-free dry mass – AFDM). The low resource treatments received similar tiles after some periphyton was removed by shaking them gently underwater (resulting mean algal biomass [SE] = 0.54 [0.18] mg/cm² AFDM). Ash-free dry mass (AFDM) of the algae on tiles was determined as the difference in mass of a dried sample (60 °C for 24 h) and that sample after combustion (550 °C for 1 h). Experimental units were maintained indoors in a controlled temperature and light environment ($\sim$24 °C, 24 h light from 55 W full spectrum bulbs).

Snail habitat use was recorded at ten preplanned but irregular intervals (0.25, 0.5, 1, 1.5, 2.5, 4.5, 19, 26, 43, and 48 h). In previous laboratory experiments, *Physa* have been observed crawling near the surface and above the waterline in response to *Belostoma* (Wojdak, 2004). Snails within 2.5 cm of the surface or above the water were considered to be attempting to evade predators by "crawling out" (*sensu* Turner, 1996). Crawling out clearly protects snails from benthic predators like crayfish, but it is less certain that this behavior represents an effective refuge from an amphibious insect like *Belostoma*. Whether this behavior is adaptive or not, it still seems to be the response elicited. Snails on resource tiles were considered to be foraging. Surface habitat and resource patches represented 8% and 7% of the total habitat area available for snails, respectively, so an average of >0.48 snails on surface habitat or >0.42 snails on resource patches would be an over-representation relative to the null expectation of random spatial distribution of prey. At the end of the second trial one resource tile from each experimental unit was selected at random ($n = 4$ per treatment) and the ash-free dry mass of the algae remaining on the tile was determined as above.

Ideally the snail behavior data could be analyzed first with doubly-multivariate ANOVA (or repeated-measures MANOVA; because refuge use and foraging effort are correlated), then if warranted, each response variable could be analyzed separately with repeated measure ANOVA. Several problems made satisfying the assumptions of MANOVA very tenuous: the loss of experimental units and thus an unbalanced design, the small number of replicates used to compute each marginal cell mean, and a very strong correlation between dependent variables (multicollinearity). Instead, the dependent variables were analyzed separately (using Type-III sums of squares to accommodate the unbalanced design), and I employ caution in interpreting the results from these clearly correlated response variables ($\alpha = 0.05/2 = 0.025$).