

# Dragonfly predators influence biomass and density of pond snails

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**Abstract** Studies in lakes show that fish and crayfish predators play an important role in determining the abundance of freshwater snails. In contrast, there are few studies of snails and their predators in shallow ponds and marshes. Ponds often lack fish and crayfish but have abundant insect populations. Here we present the results of field surveys, laboratory foraging trials, and an outdoor mesocosm experiment, testing the hypothesis that insects are important predators of pulmonate snails. In laboratory foraging trials, conducted with ten species of insects, most insect taxa consumed snails, and larval dragonflies were especially effective predators. The field surveys showed that dragonflies constitute the majority of the insect biomass in fishless ponds. More focused foraging trials evaluated the ability of the dragonflies *Anax junius* and *Pantala hymenaea* to prey upon different sizes and species of pulmonate snails (*Helisoma trivolvis*, *Physa acuta*, and *Stagnicola elodes*). *Anax junius* consumed all three species up to the maximum size tested. *Pantala hymenaea* consumed snails with a shell height of 3 mm and smaller, but did not kill larger snails. *P. acuta* were more vulnerable to predators than were *H. trivolvis* or *S. elodes*. In the mesocosm experiment, conducted with predator treatments of *A. junius*, *P. hymenaea*, and the hemipteran *Belostoma flumineum*, insect predators had a pronounced negative effect on snail biomass and density. *A. junius* and *B. flumineum* reduced biomass and density to a similar degree, and both reduced biomass more than did *P. hymenaea*. Predators did

not have a strong effect on species composition. A model suggested that *A. junius* and *P. hymenaea* have the largest effects on snail biomass in the field. Given that both pulmonate snails and dragonfly nymphs are widespread and abundant in marshes and ponds, snail assemblages in these water bodies are likely regulated in large part by odonate predation.

**Keywords** Food webs · Predation · Gastropoda · Odonata · Snail

## Introduction

Ecologists seek to identify mechanisms that regulate the distribution and abundance of species along environmental gradients. A key gradient in freshwater is the environmental continuum from small, temporary ponds and marshes largely lacking predators to deep, permanent lakes containing fish (Wellborn et al. 1996). Freshwater gastropods are key players in many freshwater food webs, and given suitable abiotic conditions are ubiquitous inhabitants of lentic systems spanning the habitat gradient (Pip 1986; Jokinen 1987; Dillon 2000). Lodge et al. (1987) argue that abiotic conditions ( $\text{Ca}^{2+}$  availability) limit gastropods at a regional scale, but biotic interactions determine snail distribution and abundance at a local scale. A number of experiments, conducted in deep permanent lakes, show that food limitation (Osenberg 1989) and predation by fish and crayfish (Brönmark et al. 1992; Martin et al. 1992; Lodge et al. 1994) can regulate snail abundance and determine the structure of snail assemblages. In contrast, there are few studies of snail population regulation and community structure in shallow ponds and marshes. Such habitats typically lack fish and crayfish but have large insect populations, many of which

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function as top predators in pond food webs (Zaret 1980; McPeck 1990; Wellborn et al. 1996).

Larval dragonflies are particularly abundant in fishless ponds and can play an important role in structuring pond communities (McPeck 1990, 1998; Wissinger and McGrady 1993; Skelly 1996). Although a wide variety of animals are known to prey on freshwater gastropods (reviewed in Lodge et al. 1987; Brown 1991; Dillon 2000), there are no studies examining whether dragonflies prey on snails. Here we present the results of laboratory experiments, mesocosm experiments, and field surveys, testing the hypothesis that dragonflies are important predators of pulmonate snails. Our larger goal is to evaluate the potential importance of predation in structuring the snail assemblages of fishless ponds.

Our study focuses on three species of pulmonate snails; *Physa acuta*, *Stagnicola elodes*, and *Helisoma trivolvis*. *P. acuta* and *H. trivolvis* are both widespread and abundant in the ponds of northwest Pennsylvania (Mower and Turner 2004). *S. elodes* has a narrow habitat distribution, being restricted to shallow ponds with forest cover, but within such ponds they are also quite abundant (Mower and Turner 2004). All three snail species commonly co-occur with the insect predators screened in this study. Of the three species, *S. elodes* is the largest and has a relatively thick shell, whereas *P. acuta* is the smallest and has a relatively thin shell (Mower and Turner 2004; A. Turner, unpublished data). Because these three snail species differ in body size, degree of shell development, and anti-predator behavior (Mower and Turner 2004), we expected that their vulnerability to dragonflies would also differ.

We first screened ten species of carnivorous insects in order to determine which might be the most important predators of pulmonate snails. Based on these results, and informed by the results of a field survey, we then chose for further study three species that likely are the most important snail predators: *Pantala hymenaea*, a libellulid dragonfly, *Anax junius*, an aeshnid dragonfly, and the hemipteran *Belostoma flumineum*. *A. junius* and *B. flumineum* are abundant in permanent, fishless ponds (Dunkle 1989; Kesler and Munns 1989; McPeck 1990; Chase 1999). *P. hymenaea* are largely restricted to and abundant in ephemeral ponds, but we view them as broadly representative of the many species of libellulid dragonflies that are especially abundant in fishless ponds.

## Materials and methods

### Insect screening

In order to determine which insects may pose the highest degree of risk to pulmonate snails, we first screened ten

species of carnivorous aquatic insects in order to determine if they were capable of feeding on snails. We chose to screen insects that were relatively large and commonly encountered in the ponds of northwest Pennsylvania, USA. Insect species screened were the dragonflies *Anax junius*, *Pantala hymenaea*, *Pachydiplax longipennis*, *Tramea lacerata*, and *Erythemis simplicicollis*, the damselfly *Lestes vigilax*, the water bugs *Belostoma flumineum*, *Ranatra nigra* and *Pelecoris fermoratus*, and the larvae of the beetle *Dytiscus verticalis*. Prey in the screening study were *Physa acuta* between 3.0 and 6.0 mm shell height. Due to their small size and thin shell, this size class and species is among the most vulnerable of the snails commonly found in ponds. Trials were conducted indoors in polypropylene shoeboxes (20 × 35 × 14 cm deep) filled to a depth of 4 cm (2.8 l) with aged well water. We chose to use a relatively small foraging arena so as to maximize predator-prey encounter rates and minimize the role of any behavioral avoidance by snails. Fifteen snails and one insect predator were stocked into each container and we recorded snail survivorship after 48 h, along with the method of kill (shell crushed or body extracted from shell). Four replicate trials were conducted for each predator taxa. In addition, for each set of four predator trials we ran a no-predator control trial in order to assure that there was no background mortality in the absence of predators. The environment was controlled with a temperature of 22°C and 14:10 h day:night lighting.

### Field survey

The impact of a particular species of insect predator on snail assemblages will depend both on the feeding rates of individual predators and on the abundance of the predator. We surveyed the biomass of predatory insects in 12 ponds in order to provide an assessment of the relative abundances of different sorts of insect predators. Sampled ponds were located in Crawford County, Pennsylvania, USA. All 12 ponds were more or less permanent but lacked well-developed fish communities, though a couple contained scattered fathead minnows (*Pimephales promelas*). Insects were sampled with a stove-pipe-type sampler, 25 cm diameter, which has been shown to perform well in sampling vegetated habitats (Turner and Trexler 1997). Eight replicate samples were taken from randomly selected locations in each pond, and samples were pooled for further analyses. While in the field we identified insects to the level of family and measured their wet mass. We used biomass as an index of abundance, and not number, because when comparing across size classes or taxa, the biomass of a predator species is a better predictor of its feeding rate (Peters 1983; Yodzis and Ennis 1992). Each pond was sampled twice during the summer, in late May and again in late July, so as to provide a seasonally

integrated view of insect abundance. Thus, the relative biomass of each insect family, calculated for each of the 24 sampling events and then averaged across the two sample dates and across the 12 ponds, was used as an index of their potential impact on snail populations.

### Foraging trials

Because dragonflies capture prey by seizing it between the lobes of their prehensile labium, we hypothesized that snail body size would influence their vulnerability to odonates, with larger snails being less vulnerable than smaller snails. Therefore, we conducted foraging trials in shoebox containers in order to establish, for two dragonfly species identified in the screening process and field survey as potentially important snail predators (*A. junius* and *P. hymenaea*), which species and size classes of snails the dragonflies were capable of killing. *B. flumineum* was not included in these trials because its ability to forage on snails has already been studied (Kesler and Munns 1989; Chase 1999; Hoverman et al. 2005). Each trial included a single species (*P. acuta*, *H. trivolvis*, or *S. elodes*) and size class of snail. As with the predator screening trials, foraging trials were conducted indoors in plastic shoeboxes filled with 2.8 l of aged well water. Temperature was maintained at 22°C, and lighting was set at 14:10 h day:night. Snails were sorted by shell size into 1-mm size classes. For *S. elodes* and *P. acuta* we measured shell height, for *H. trivolvis* we measured shell width. In each case this dimension represents the longest axis of the shell. Fifteen snails were stocked into each container, and for each predator × snail-species × size class combination, five replicate trials were conducted. Four replicates received predators, and the fifth remained as a no-predator control. Survivorship was measured after 48 h, and method of kill (shell crushed or body extracted) was also recorded. An individual dragonfly was not used more than once in a trial for a particular snail species, though they were in some cases used in predation trials for other species. The effects of predator identity, prey identity, and prey body size on prey mortality were assessed with a 2 × 3 × 7 factorial ANOVA. Analyses were performed with SPSS 11.0.

### Mesocosm study

We hypothesized that insect predation would most affect survivorship of juvenile snails and thus set out to evaluate the effects of insects on snail recruitment from egg to adult. The effect of insect predation on snail recruitment was assessed in large outdoor mesocosms (1.6 m diameter, 0.6 m deep, 1,200 l). Pulmonate snails generally have an annual life history with peak reproductive effort in early summer (Dillon 2000), so our experiment was established

in spring and ran into fall. In May we filled each mesocosm with well water, fertilized the tanks at a rate of 50 µg P l<sup>-1</sup> (added as K<sub>2</sub>HPO<sub>4</sub>, N was added as NaNO<sub>3</sub> so as to maintain a N:P molar ratio of 16:1), added 10 g dry red maple (*Acer rubrum*) leaves to provide physical structure and additional nutrients, and inoculated the tanks with zooplankton and phytoplankton collected from local ponds. Mesocosms were then covered with 50% shade cloth to prevent unwanted insects from colonizing the tanks. In late June, after algae and zooplankton had become established, an assemblage comprising three species of pulmonate snails (*P. acuta*, *H. trivolvis*, and *S. elodes*) was stocked into the tanks as adults (ten of each species for a total of 30 snails) and allowed to oviposit. Adults deposited eggs for 15 days, at which time they were removed and the predators (*A. junius*, *P. Hymenaea*, or *B. flumineum*) were stocked. Hatching time for all three species is approximately 2 weeks, so initiation of hatching coincided with predator stocking. Zooplankton were also abundant in the mesocosms and provided an alternate food source for the odonates. In addition to no-predator controls, we included a treatment of the giant water bug *Belostoma flumineum*, a known predator of snails (Kesler and Munns 1989), in order to establish a benchmark against which to evaluate the ferocity of the dragonfly predators. The three species were stocked at a density of two *A. junius*, four *B. flumineum*, or five *P. hymenaea* per tank, which was aimed at achieving a stocking rate of 2.5 g wet biomass per mesocosm. This stocking rate (1.25 g m<sup>-2</sup>) is about one-quarter of the average overall insect biomass measured in local ponds. There were eight replicate mesocosms for each of the four predator treatments, yielding a total of 32 mesocosms.

Mesocosms were periodically inspected, and dead or emerging predators were replaced. After 10 weeks, tanks were drained and all surviving snails were recovered. None of the snails had begun reproduction at the time the experiment was terminated. We tallied the number and dry mass of each species (dry mass includes shell material). Upon draining the tanks we found that one no-predator tank contained several *P. hymenaea*, and data from this tank were deleted from subsequent analyses. The effects of predator treatment on snail biomass, density and body size were analyzed with one-way ANOVA, and pairwise differences among treatments were assessed with Tukey's test. Treatment effects on species composition were evaluated by performing multivariate ANOVA (MANOVA) on the relative abundance matrix and the relative biomass matrix. Because the relative measures of composition sum to 1, there are just two independent variables and we performed MANOVA on vectors of two rather than three species. We also evaluated treatment effects on evenness, using Simpson's formulation (Krebs 1989), by performing

ANOVA on the evenness of biomass and evenness of abundances. All analyses were performed with SPSS 11.0.

## Results

### Insect screening

Of the ten taxa of insects assayed, nine consumed *P. acuta*, with only larval *D. verticalis* (Dytiscidae) failing to kill any snails. Feeding rates varied a great deal, however, among the taxa that consumed snails (Table 1). The most lethal predators were *A. junius*, *B. flumineum*, *E. simplicicollis*, *P. hymenaea*, and *T. lacerata*. The remaining taxa killed fewer than 10% of the snails presented to them (Table 1).

### Field survey

Survey data showed that large insects were quite abundant in local ponds, with an overall average biomass of 4.91 g m<sup>-2</sup>. Libellulid dragonflies were the most prevalent of the insect predators, with a biomass that comprised 46.3% of the overall large-insect biomass (Table 1). Aeshnid dragonflies were the next most abundant group (32% of total biomass), followed by belostomatids and naucorids, with 8 and 7% of the total insect biomass, respectively (Table 1).

### Foraging trials

Dragonflies readily preyed on snails, but the feeding rate depended on predator identity, prey identity, and prey body size, as well as all two-way interactions of these three

factors (Table 2). Most of the variation in mortality (86% of treatment sums-of-squares) was attributable, however, to just two factors: the additive and non-additive effects of predator identity and prey body size (Table 2). Averaged across prey species and size classes, *A. junius* consumed 72% of the snails presented to them (Fig. 1a), whereas *P. hymenaea* consumed 17% of their snails (Fig. 1b), a 4.2-fold difference. Prey size also played a key role in determining vulnerability, as small snails were, on average, much more vulnerable to predators than were larger snails (Fig. 1). The snail size effect was largely dependent on predator species. *Pantala hymenaea* had high feeding rates on the smallest size classes, but was largely unable to consume snails >3 mm body length (Fig. 1b). In contrast, *A. junius* readily consumed all size classes tested (Fig. 1a).

Prey identity and the two-way interactions involving prey identity had small but significant effects on mortality rates (Table 2). *P. acuta* was most vulnerable and *H. trivoltis* the least vulnerable to predators (Fig. 2). Examination of prey identity × body size interaction plots suggests that prey vulnerability rankings were consistent for all size classes >3 mm shell height, but that prey identity did not influence mortality of snails in the 2-mm size class: all were highly vulnerable, regardless of identity. The mortality imposed by *A. junius* depended on prey identity to a greater extent than did the mortality imposed by *P. hymenaea* (Fig. 2).

Dragonflies consumed a snail by extracting its body from the intact shell or by crushing the shell. Averaged across predator species, prey species, and size classes, 69% of all consumed snails were killed by extraction. Dragonflies extracted snails from their shells by first seizing the snail's foot with their labium and then using their

**Table 1** Laboratory assay of feeding rates<sup>a</sup> and abundance of large carnivorous insects in local ponds. SD in parentheses

Order	Family	Laboratory Assay			Field survey <sup>b</sup>	
		Taxa screened	Body size (g)	Consumed (%)	Wet biomass (g m <sup>-2</sup> )	Relative biomass (%)
Coleoptera	Dytiscidae	<i>Dytiscus verticalis</i>	1.36	0	0.03 (0.10)	0.6
Hemiptera	Belostomatidae	<i>Belostoma flumineum</i>	0.37	68 (3)	0.41 (0.46)	8.4
Hemiptera	Nepidae	<i>Ranatra nigra</i>	0.19	5 (3)	0.14 (0.34)	2.9
Hemiptera	Naucoridae	<i>Pelecoris femoratus</i>	0.06	3 (4)	0.35 (0.58)	7.2
Odonata	Lestidae	<i>Lestes vigilax</i>	0.13	3 (4)	0.14 (0.25)	2.8
Odonata	Aeshnidae	<i>Anax junius</i>	1.27	98 (3)	1.56 (1.67)	31.8
Odonata	Libellulidae	<i>Tramea lacerata</i>	0.74	13 (5)	2.27 (2.83)	46.3
Odonata	Libellulidae	<i>Pachydiplax longipennis</i>	0.22	3 (4)		
Odonata	Libellulidae	<i>Erythemis simplicicollis</i>	0.29	55 (6)		
Odonata	Libellulidae	<i>Pantala hymenaea</i>	0.48	17 (7)		

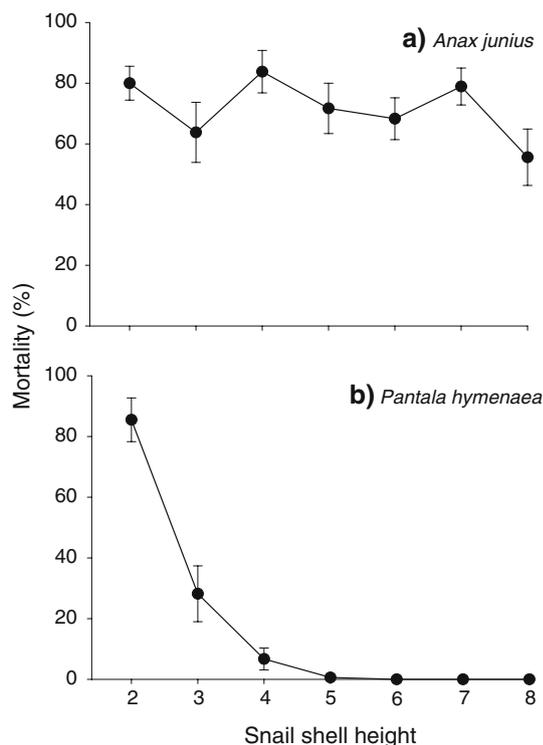
<sup>a</sup> Consumption rates are for late-instar insects feeding on juvenile *Physa acuta* (3.0–6.0 mm shell height) as measured in foraging trails conducted in aquaria and run for 48 h

<sup>b</sup> Field survey results are based on a survey of 12 ponds, each sampled twice. Survey data are organized at the level of family, thus the biomass data for the Aeshnidae, Lestidae, and Libellulidae represent all species in the family pooled together

**Table 2** Effects of predator identity (*Dragonfly species*), prey identity (*Snail species*), and prey body size (*Shell height*) on snail mortality rate in foraging trials.  $\eta^2$  Effect size

Factor	$\eta^{2a}$	df	F	P
Dragonfly species	0.446	1	377.9	<0.001
Snail species	0.033	2	13.9	<0.001
Shell height	0.167	6	23.6	<0.001
Dragonfly species $\times$ Snail species	0.028	2	11.9	<0.001
Dragonfly species $\times$ Shell height	0.119	6	16.8	<0.001
Snail species $\times$ Shell height	0.035	12	2.5	0.006
Dragonfly species $\times$ Snail species $\times$ Shell height	0.023	12	1.7	0.084

<sup>a</sup> For each factor,  $\eta^2$  is the proportion of total variance attributable to the factor, and is calculated as the ratio of the effect variance to the total variance ( $\eta^2 = SS_{\text{factor}} / SS_{\text{total}}$ ). Model  $R^2 = 0.85$

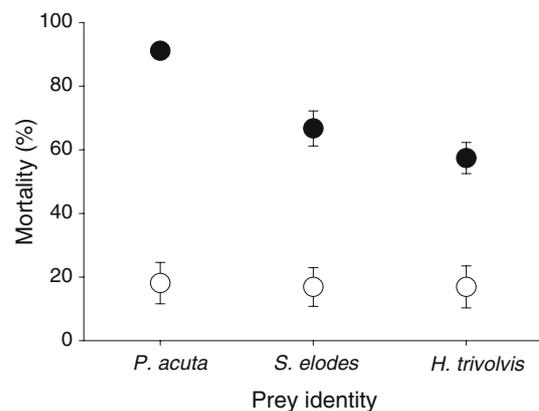


**Fig. 1** Effect of snail body size (shell height, mm) on predation by **a** *Anax junius* and **b** *Pantala hymenaea* as measured in laboratory feeding trials. Each point represents mean mortality ( $\pm 1$  SE,  $n = 12$ ) suffered by each 1-mm size class over 48 h, and is averaged across three snail species

mouthparts to pull the snail's body from its shell. The foraging mode employed by dragonflies depended on snail body size, however, as 76% of the consumed snails in the 2- and 3-mm size classes were killed by shell crushing, but only 2% of the consumed snails >3 mm were crushed.

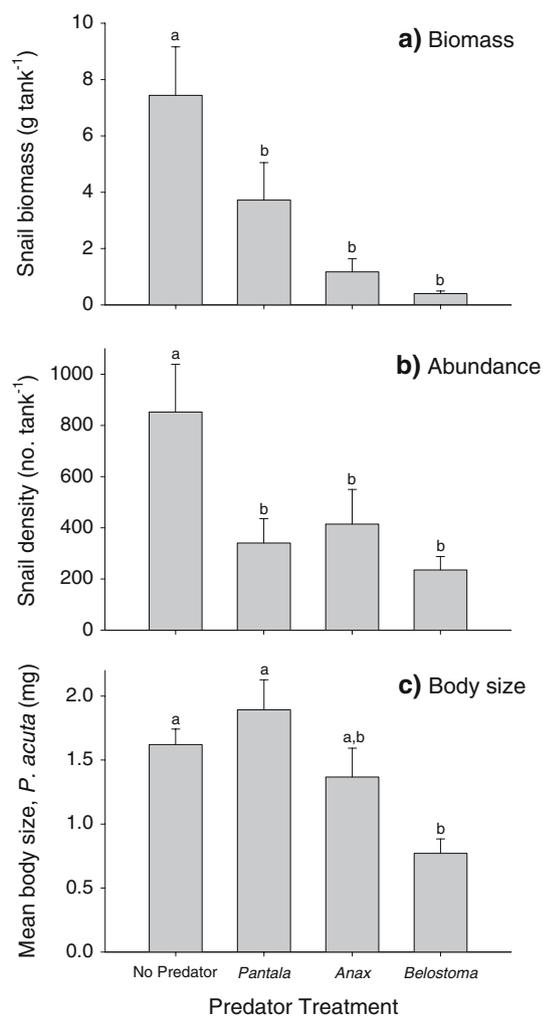
#### Mesocosm study

Insect predators had a strong negative effect on snail recruitment, with biomass of recovered snails substantially



**Fig. 2** Effect of prey identity (*Physa acuta*, *Stagnicola elodes* and *Helisoma trivolvis*) on predation by *A. junius* (filled circle) and *P. hymenaea* (open circle) as measured in laboratory feeding trials. Each point represents mean mortality ( $\pm 1$  SE,  $n = 28$ ) suffered by each species over 48 h, and is averaged across size classes

and significantly lower in all three predator treatments than in no-predator controls (ANOVA,  $F_{3,27} = 35.8$ ,  $P < 0.001$ ; all pairwise comparisons of predator treatments with no-predator control significant at  $P < 0.05$ ). The effects of *P. hymenaea*, *A. junius* and *B. flumineum* on snail biomass were not statistically distinguishable from one another (Fig. 3a). Insect predators also depressed total snail abundance (ANOVA,  $F_{3,27} = 4.60$ ,  $P = 0.01$ ). *P. hymenaea*, *A. junius*, and *B. flumineum* each had similar negative effects on snail abundance, as all three reduced snail density relative to no-predator controls but were not significantly different from each other (Fig. 3b). Predators had a significant effect on mean body size of *P. acuta* (ANOVA,  $F_{3,27} = 4.75$ ,  $P < 0.01$ ), with mean body mass in the presence of *B. flumineum* reduced by more than 50% relative to the no-predator control (Fig. 3c). Mean body size of *P. acuta* in other predator treatments was not significantly different from controls ( $P > 0.10$ ), and predator effects on body size of *H. trivolvis* and *S. elodes* were not significant ( $P > 0.10$ ).



**Fig. 3** Mesocosm study showing effects of three insect predators on snail **a** biomass, **b** abundance, and **c** body size. Bars represent treatment means (+1 SE),  $n = 8$  replicate mesocosms per treatment, except for no-predator, for which  $n = 7$ . Lower case letters above bars denote treatment means not significantly different from each other ( $P < 0.05$ , Tukey's test)

*H. trivolis* dominated the snail biomass of the mesocosms, comprising on average 66% of the total biomass, and *P. acuta* was the most abundant species, comprising 51% of the total snail abundance. There was, surprisingly, no significant effect of predator treatment on species composition, measured either as patterns of relative biomass or relative abundance (MANOVA; relative biomass, Wilk's  $\lambda = 0.686$ ,  $F_{6,52} = 1.80$ ,  $P > 0.10$ ; relative abundance, Wilk's  $\lambda = 0.795$ ,  $F_{6,52} = 1.05$ ,  $P > 0.10$ ). An analysis of Simpson's evenness, as calculated from the relative biomass and relative abundance matrices, also found no treatment effects (ANOVA; evenness of relative biomasses,  $F_{3,27} = 1.73$ ,  $P > 0.10$ ; evenness of relative abundances,  $F_{3,27} = 1.30$ ,  $P > 0.10$ ).

## Discussion

Lodge et al. (1987) hypothesized that given adequate Ca, snail assemblages in lakes will be regulated by fish and crayfish predators, whereas snails in shallow, fishless ponds will be structured largely by competition, and snail assemblages in temporary ponds will be limited by the frequency and severity of desiccation. The hypothesis that predation by fish and crayfish limits snails residing in lakes has been tested repeatedly (e.g., Brown and DeVries 1985; Osenberg 1989; Weber and Lodge 1990; Brönmark et al. 1992; Martin et al. 1992; Osenberg et al. 1992; Lodge et al. 1994; Nyström and Perez 1998; Lewis 2001), but the mechanisms structuring the snail assemblages of fishless ponds remains little studied (but see Eisenberg 1966; Kesler and Munns 1989; Chase 2003). While admitting that there are very few data regarding the abundance and feeding rates of invertebrate predators, Lodge et al. (1987) argued that competition will predominate in fishless ponds, as the available data suggest that invertebrate predators have low feeding rates on snails and thus are ineffective predators relative to fish and crayfish.

Here we show that insects common in fishless ponds are effective predators of snails and can suppress the abundance of species with which they co-occur. Thus, these results do not support the hypothesis that predation will be unimportant in governing the snail assemblages of fishless ponds. A number of insects fed on snails in laboratory feeding trials, with the anisopteran *A. junius*, the hemipteran *B. flumineum*, and the anisopteran *E. simplicicollis* scoring the highest predation rates. Our mesocosm study showed, in a semi-natural setting and using a realistic predator biomass, that odonates and *B. flumineum* can suppress the recruitment of snails with which they commonly co-occur. Our survey data show that insects are both widespread and abundant in the marshes and ponds of northwestern Pennsylvania. Thus, our data, especially when taken together with the results of Kesler and Munns (1989), provide evidence that snail abundances in fishless ponds are likely governed in part by insect predation, especially by dragonflies.

Other inhabitants of fishless ponds known to be snail predators include tiger salamanders (*Ambystoma tigrinum*; Brophy 1980; Benoy et al. 2002), red-spotted newts (*Notophthalmus viridescens*; Burton 1976), turtles (Mahmoud 1968), sciomyzid fly larvae (Eckblad 1976), leeches (Brönmark and Malmqvist 1986; Brönmark 1992), and waterfowl (Krapu and Reinecke 1992). In the ponds of our region, these taxa are much less abundant than insects and thus less important as predators, but these studies do further support the general idea that predators can limit snail populations in fishless ponds.

In the mesocosm study, *B. flumineum* had a stronger effect on snail biomass than did *A. junius* and *P. hymenaea*. Recall, however, that predator treatments in the mesocosm study were matched for biomass. The degree to which different predator taxa in a pond will each govern snail biomass depends not just on differences in mass-specific feeding rates, but also on the biomass density of each predator taxa (Peters 1983; Yodzis and Ennis 1992). We can generate an index of predator impact on snail biomass, and compare the importance of the three taxa tested here, by constructing a simple model incorporating our field survey data. Let the mass specific interaction strength of predator (*i*) be defined as the additive reduction in snail biomass as observed in the mesocosm study, standardized by predator biomass (2.5 g in all cases):

$$a_i = (\text{snail biomass, no predator trt.}(g) - \text{snail biomass, predator trt } i(g)) / \text{predator biomass}(g) \quad (1)$$

$a_i$  is a dimensionless coefficient representing the reduction in snail biomass per unit predator biomass added. Predator impact, the predicted reduction of snail biomass in the field ( $\text{g m}^{-2}$ ) attributable to predator taxa (*i*), is then:

$$r_i = (\text{Biomass density predator taxa } i(\text{g m}^{-2})) \cdot a_i. \quad (2)$$

Because the mesocosms differ from ponds in a number of ways, including initial snail biomass,  $r_i$  is an index of predator impact and not a quantitative estimate of predator impact. This analysis suggests that aeshnid dragonflies are the most important of the three predators considered, with  $r_i = 3.94 \text{ g snails m}^{-2}$  (Table 3). Libellulids are the second most important predator taxa, with a predicted predator impact 85% as large as that of the aeshnids (Table 3). Belostomatids, despite having the highest mass specific interaction strength ( $a_i$ ), have a predicted predator impact just 29% that of the aeshnid  $r_i$ , due to the lower abundance of belostomatids in the field survey (Table 3). Thus, these

**Table 3** Relative impact of three predator taxa on snail biomass.  $a_i$  Mass specific interaction strength of predator *i* as measured in the mesocosm experiment, e.g., the additive reduction in snail biomass (g) per gram of predator biomass added to mesocosms;  $r_i$  predator impact—the predicted reduction of snail biomass in the field ( $\text{g m}^{-2}$ ), taking into account predator biomass measured in field surveys, attributable to predator *i*

Taxa	$a_i$	$r_i$
Aeshnidae	2.52	3.94
Libellulidae	1.48	3.36
Belostomatidae	2.82	1.16

results support the notion that anisopteran odonates (dragonflies, including aeshnids and libellulids), relative to other insect taxa, are the most important predators of snails in fishless ponds.

Insect predators in the mesocosm study had substantial effects on snail abundance and biomass, but there was little evidence that predators caused a shift in species composition. Although high variability in snail abundance among tanks may have limited our power to detect subtle effects, it is clear that insect predators did not induce a large shift in species composition. Thus, in the relatively natural environment of outdoor mesocosms the three species are of similar vulnerability to predators. This result contrasts with the laboratory foraging trials where *P. acuta* was more vulnerable to predators that were *H. trivoltis* and *S. elodes*. The small spatial and temporal scale of the laboratory foraging trials are designed to maximize predator–prey encounters and preclude the use of inducible defenses, so the predation trials measure the ability of predators to capture and consume prey. In contrast, the larger spatial scale, physical complexity, and temporal scale of the mesocosm study allow for the employment of behavioral defenses which lower encounter rates with predators and morphological trait shifts which lower vulnerability to predators (e.g., DeWitt et al. 2000; Turner and Montgomery 2003; Hoverman et al. 2005; Turner et al. 2006).

Insect predators are patchy at the landscape scale, reaching their greatest abundance in shallow, fishless ponds and marshes (McPeck 1990; Skelly 1996). Their role in structuring snail assemblages at large spatial scales remains an open question as the snail species used in our study are those that most typically coexist with insect predators in small ponds and marshes. However, most of the 30-odd gastropods species found in northwestern Pennsylvania do not occur in these ponds and their vulnerability to insect predators is not yet known. Studies of predation in lentic systems generally find that regardless of a predator's short-term effects on coexisting prey, predators can shape among-lake distribution of prey through local exclusion of vulnerable prey species, thereby restricting community membership (Wellborn et al. 1996). Thus, it is possible that odonates play an important role in determining species composition of snails in ponds by excluding more vulnerable species, but this hypothesis has not been tested.

Twenty years ago, Lodge et al. (1987) pointed out that we have little understanding of the factors governing among-lake variation in snail species composition and abundance, and made the valuable suggestion that it would be profitable to examine how regulating mechanisms shift across the lake size gradient. Subsequent work with other aquatic taxa (e.g., amphipods, amphibians, and odonates) adopted such an approach and showed that there is a predictable pattern of species replacement along the lake-

size continuum, driven in large part by shifts in the identity of the top predator and tradeoffs involving traits conferring safety against predators (Wellborn 1994; Skelly 1997; McPeck 1998; McPeck et al. 2001). Behavioral, physiological, or morphological traits that confer protection against the predators of larger ponds and lakes often incur costs that put the bearer of those traits at a disadvantage in ponds lacking predators or with different sorts of predators (e.g., Wissinger et al. 1999; Wellborn 2002; McPeck 2004). Unfortunately, less is known about the role of such mechanisms in structuring gastropod assemblages. Our results suggest that predation is an important limiting factor even in ponds lacking fish and crayfish, but field experiments conducted across the lake size gradient are necessary in order to more completely understand the factors governing the landscape-scale distribution of freshwater snails.

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## References

- Benoy GA, Nudds TD, Dunlop E (2002) Patterns of habitat and invertebrate diet overlap between tiger salamanders and ducks in prairie potholes. *Hydrobiologia* 481:47–59
- Brönmark C (1992) Leech predation on juvenile freshwater snails: effects of size, species, and substrate. *Oecologia* 91:526–529
- Brönmark C, Malmqvist B (1986) Interactions between the leech *Glossiphonia complanata* and its gastropod prey. *Oecologia* 69:268–276
- Brönmark C, Klosiewski SP, Stein RA (1992) Indirect effects of predation in a freshwater benthic food chain. *Ecology* 73:1662–1674
- Brophy T (1980) Food habits of sympatric larval *Ambystoma tigrinum* and *Notophthalmus viridescens*. *J Herpetol* 14:1–6
- Brown KM (1991) Mollusca: Gastropoda. In: Thorp JH, Covich AP (eds) *Ecology and classification of North American freshwater invertebrates*. Academic Press, San Diego, Calif., pp 285–314
- Brown K, DeVries D (1985) Predation and the distribution and abundance of a pond snail. *Oecologia* 66:93–99
- Burton T (1976) An analysis of the feeding ecology of the salamanders (Amphibia: Urodela) of the Hubbard Brook Experimental Forest, New Hampshire. *J Herpetol* 10:187–204
- Chase JM (1999) To grow or to reproduce? The role of life-history plasticity in food web dynamics. *Am Nat* 154:571–586
- Chase JM (2003) Strong and weak trophic cascades along a productivity gradient. *Oikos* 101:187–195
- DeWitt TJ, Robinson BW, Wilson DS (2000) Functional diversity among predators of a freshwater snail imposes an adaptive tradeoff for shell morphology. *Evol Ecol Res* 2:129–148
- Dillon RT Jr (2000) *The ecology of freshwater mollusks*. Cambridge University Press, New York
- Dunkle SW (1989) *Dragonflies of the Florida Peninsula, Bermuda, and the Bahamas*. Scientific Publishers, Gainesville, Fla.
- Eckblad J (1976) Biomass and energy transfer by a specialized predator of aquatic snails. *Freshwater Biol* 6:19–21
- Eisenberg RM (1966) The regulation of density in a natural population of the pond snail, *Lymnaea elodes*. *Ecology* 47:889–906
- Hoverman JT, Auld JR, Relyea RA (2005) Putting prey back together again: integrating predator-induced behavior, morphology, and life history. *Oecologia* 144:481–491
- Jokinen E (1987) Structure of freshwater snail communities: species–area relationships and incidence categories. *Am Malacol Bull* 5: 9–19
- Kesler DH, Munns WR Jr (1989) Predation by *Belostoma flumineum* (Hemiptera): an important cause of mortality in freshwater snails. *J N Am Benthol Soc* 8:342–350
- Krapu GL, Reinecke KJ (1992) Foraging ecology and nutrition. In: Batt BDJ, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL (eds) *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, Minn., pp 1–29
- Krebs CJ (1989) *Ecological methodology*. Harper and Row, New York
- Lewis DB (2001) Trade-offs between growth and survival: responses of freshwater snails to predacious crayfish. *Ecology* 82:758–765
- Lodge DM, Brown KM, Klosiewski SP, Stein RA, Covich AP, Leathers BK, Brönmark C (1987) Distribution of freshwater snails: spatial scale and the relative importance of physicochemical and biotic factors. *Am Malacol Bull* 5:73–84
- Lodge DM, Kershner MW, Aloï JE, Covich AP (1994) Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecology* 75:1265–1281
- Mahmoud I (1968) Feeding behavior in kinosternid turtles. *Herpetologica* 24:300–305
- Martin TH, Crowder LB, Dumas CF, Burkholder JM (1992) Indirect effects of fish on macrophytes in Bays Mountain Lake: evidence for a littoral trophic cascade. *Oecologia* 89:476–481
- McPeck MA (1990) Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. *Ecology* 71:83–98
- McPeck MA (1998) The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecol Monogr* 68:1–23
- McPeck MA (2004) The growth/predation risk tradeoff: so what is the mechanism? *Am Nat* 163:88–111
- McPeck MA, Grace M, Richardson JML (2001) Physiological and behavioral responses to predators shape the growth/predation risk trade-off in damselflies. *Ecology* 82:1535–1545
- Mower C, Turner AM (2004) Behavior, morphology and the coexistence of two pulmonate snails with molluscivorous fish: a comparative approach. *Am Malacol Bull* 19:39–46
- Nyström P, Perez JR (1998) Crayfish predation on the common pond snail (*Lymnaea stagnalis*): the effect of habitat complexity and snail size on foraging efficiency. *Hydrobiologia* 368:201–208
- Osenberg CW (1989) Resource limitation, competition, and the influence of life history in a freshwater snail community. *Oecologia* 79:512–519
- Osenberg CW, Mittelbach GG, Wainwright PC (1992) Two-stage life histories in fish: the interaction between juvenile competition and adult performance. *Ecology* 73:255–267
- Peters RH (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge
- Pip E (1986) The ecology of freshwater gastropods in the central Canada region. *Nautilus* 100:56–66
- Skelly DK (1996) Pond drying, predators, and the distribution of *Pseudacris* tadpoles. *Copeia* 1996:509–605

- Skelly DK (1997) Tadpole communities: pond permanence and predation are powerful forces shaping the structure of tadpole communities. *Am Sci* 85:36–45
- Turner AM, Montgomery SL (2003) Spatial and temporal scales of predator avoidance: experiments with fish and snails. *Ecology* 84:616–622
- Turner AM, Trexler JC (1997) Sampling aquatic invertebrates from marshes: evaluating the options. *J N Am Benthol Soc* 16:694–709
- Turner AM, Turner SL, Lappi HM (2006) Learning, memory, and predator avoidance by freshwater snails: effects of experience on predator recognition and defensive strategy. *Anim Behav* 72:1443–1450
- Weber LM, Lodge DM (1990) Periphytic food and predatory crayfish: relative roles in determining snail distribution. *Oecologia* 82:33–39
- Wellborn GA (1994) Size based predation and the evolution of prey life histories: a comparative study of freshwater amphipod populations. *Ecology* 75:2104–2017
- Wellborn GA (2002) Trade-off between competitive ability and antipredator adaptation in a freshwater amphipod species complex. *Ecology* 83:129–136
- Wellborn GA, Skelly DK, Werner EE (1996) Mechanisms creating community structure across a freshwater habitat gradient. *Annu Rev Ecol Syst* 27:337–363
- Wissinger SA, McGrady J (1993) Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. *Ecology* 74:207–218
- Wissinger SA, Whiteman HH, Sparks GB, Rouse GL, Brown WS (1999) Foraging trade-offs along a predator-permanence gradient in subalpine wetlands. *Ecology* 80:2012–2116
- Yodzis P, Innes S (1992) Body size and consumer–resource dynamics. *Am Nat* 139:1151–1175
- Zaret TM (1980) *Predation and Freshwater Communities*. Yale University Press, New Haven, Conn.