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Predator avoidance behaviour in response to turtles and its adaptive value in the freshwater snail *Planorbella campanulata*

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ABSTRACT

We investigated predator avoidance behaviours in the freshwater planorbid snail *Planorbella campanulata* when exposed to varied cues of risk of predation by turtles (*Chelydra serpentina*, *Chrysemys picta marginata*, *Trachemys scripta elegans* and *Clemmys insculpta*). Experiments were conducted to address the following questions: (1) What are the behavioural responses of these snails to turtles? (2) What chemical cues elicit responses? (3) How do predator and prey size affect prey vulnerability and reactivity to predators? (4) Are behavioural responses of snails effective in reducing predation by turtles? We found that *P. campanulata* snails responded to turtles by burying in the substratum. Snails buried occasionally (0–30%) in response to cues from nonforaging turtles, but frequently (30–98%) in response to actively-foraging turtles including a nonnative turtle species. Burial was not elicited by chemical cues from injured physid snails (*Physella acuta*). Small snails were more vulnerable to turtle predation and had a commensurately higher propensity to bury. Additionally, the propensity for snails to bury was related to turtle size. Smaller turtles stimulated more burial, perhaps due to the ungainly manner with which they ate snails, which released more snail injury cues compared to larger turtles. However, larger turtles consumed more snails. Buried snails suffered considerably less predation than snails forced to remain unburied. Therefore, the burial response appeared to be adaptive on balance, but imperfectly so.

INTRODUCTION

To survive in sympatry with predators, prey must either escape once encountered by predators or avoid encountering them altogether (Sih, 1987; Lima & Dill, 1990). For many molluscs, active escape is limited by low mobility relative to their predators. Escape *per se* is often a passive matter where shells serve as a last line of defence. Yet shells are energetically costly to produce and the cost reduces growth rate (Palmer, 1992; Brookes & Rochette, 2007). Such costs can be reduced by facultative expression (phenotypic plasticity) or compensated through other traits ('trait compensation'; DeWitt, Sih & Hucko, 1999). For example, molluscs often exhibit predator-induced shell thickening (Leonard, Bertness & Yund, 1999; Auld & Relyea, 2011; Bible, Griffith & Sanford, 2017; Zdelar *et al*., 2018) or form (Appleton & Palmer, 1988; DeWitt, 1998; Krist, 2002; Bourdeau, 2010; Sherker, Ellrich & Scrosati, 2017). Often, vulnerability in shell morphology is compensated by increased antipredator behaviour (e.g. DeWitt *et al*., 1999; Rundle & Brönmark, 2001; Cotton, Rundle & Smith, 2004; Stevison, Kensinger & Luttbeg, 2016). It is not clear as a generality how often morphological and behavioural defences operate independently or in a compensatory or otherwise correlated manner.

To avoid encounters with predators by behavioural means may often be the first line of defence (Sih, 1987; Lima & Dill, 1990). Behaviours used by aquatic molluscs to avoid their predators include crawling to the water surface or out of the water (Snyder, 1967; Alexander & Covich, 1991a, b; DeWitt *et al*., 1999; McCarthy & Dickey, 2002), hiding (e.g. Snyder, 1967; Turner, 1996; DeWitt & Langerhans, 2003), burial (Kempendorff, 1942; Snyder, 1967; Stenzler & Atema, 1977; McCarthy & Fisher, 2000), shell swinging (Tripet & Perrin, 1994; Krupski, Karasek & Koperski, 2017), changing mating or foraging behaviour (DeWitt, 1996; Trussell, Ewanchuk & Bertness, 2003) and active swimming for highly mobile species such as cephalopods and scallops (Stephens & Boyle, 1978; McClintock, 1983; Pitcher & Butler, 1987). The type of behaviour employed may depend not only on a species' mobility, but also on environmental context and individual differences. Behavioural responses of freshwater snails to predators may depend on predator type (e.g. DeWitt, 1998; Turner, Bernot & Boes, 2000; Hoverman & Relyea, 2007), prey size (e.g. Alexander & Covich, 1991a; Levri, 1998; DeWitt *et al*., 1999), cues of predator number, size, proximity and temporal variation

(Turner & Montgomery, 2003; Kain & McCoy, 2016), shell morphology (DeWitt *et al.*, 1999; Rundle & Brönmark, 2001), environmental pollution (Justice & Bernot, 2014), population and species evolutionary history (Bernot & Whittinghill, 2003; Hollander & Bourdeau, 2016), parental environments (Luquet & Tariel, 2016), light regime (Snyder, 1967; Snyder & Snyder, 1971) and individual variation in hunger state (Stenzler & Atema, 1977), parasite status (Levri, 1998; Bernot & Lamberti, 2008) or past experience with predators (Dalesman *et al.*, 2006; Turner, Turner & Lappi, 2006; Aizaki & Yusa, 2010).

Freshwater gastropods face numerous predators including flatworms, leeches, insects such as water bugs and beetles, fly and dragonfly larvae, as well as crayfish, fish, birds, turtles and mammals (reviewed by Snyder, 1967; Dillon, 2000). Most research has focused on molluscivorous fish and crayfish. However, in most freshwater systems the importance of turtles as major mollusc predators is surprisingly under-appreciated. Biomass of turtles is typically of the order of 20–70 kg ha^{-1} (Iverson, 1982; Congdon, Greene & Gibbons, 1986). Mollusc predation is common in turtles, including specialized species such as musk or map turtles, omnivorous species and juvenile stages of species regarded as herbivorous (Carr, 1995). They are known to impact snail populations heavily (Snyder & Snyder, 1971; Ernst & Barbour, 1972). In one experiment, two modestly-sized (15.5–18.3 cm shell length) Chinese pond turtles, *Mauremys reevesii* (syn. *Chinemys reevesii*; Bickham *et al.*, 2007), consumed an estimated 4,715 *Pomacea canaliculata* in 56 d (Yoshie & Yusa, 2008). Since snails are important in transferring energy and materials into aquatic food webs (Brönmark, Klosiewski & Stein, 1992; Lodge *et al.*, 1994; Bernot & Turner, 2001; Silliman & Zieman, 2001; Trussell, Ewanchuk & Bertness, 2002; Stoler & Relyea, 2016), impacts on snail populations caused by turtles are likely to play a significant role in structuring aquatic communities. It is therefore important to understand the dynamic between these predators and their prey.

We conducted a series of experiments to examine the behavioural response of a freshwater pulmonate snail, *Planorbella campanulata* (Say, 1821) (syn. *Helisoma campanulatum*), to predation by turtles. We investigated: (1) the nature of behavioural responses to turtle predation, (2) the ecological context stimulating the response, (3) effects of predator and prey sizes on prey vulnerability and response and (4) the efficacy of the response for reducing predation by turtles.

METHODS

Study organisms

We investigated responses to predators by *Planorbella campanulata* snails from two populations in Broome County, NY. One snail population was in Finch Hollow Pond (FHP; 42°8′N, 75°58′W), which contained turtles, pumpkinseed sunfish and crayfish as the major snail predators. The second snail population was a laboratory stock (Lab) collected from a single unknown population, but not from FHP (the original collector had never been there). Lab snails had been kept in a predator-free environment for many generations over at least 5 years. Individual snails from FHP were never used more than once, but the lab stock was not large enough to conduct tests without some reuse of snails. The lab stock contained *c.* 200 snails. Lab snails were not reused within any given experiment, but some were used in more than one experiment.

The following species of turtles were obtained from ponds in Broome County, NY: snapping turtle (*Chelydra serpentina*), painted turtle (*Chrysemys picta marginata*) and wood turtle (*Clemmys insculpta*). Red-eared slider turtles (*Trachemys scripta elegans*), which are not native to New York, were obtained from a pet shop. The primarily terrestrial wood turtle and the nonnative red-eared slider were included to test the generality of snail responses to turtles, even those unlikely to have exerted natural selection in these populations.

All experiments were conducted in a laboratory at Binghamton University in Binghamton, NY between 1000 and 1700 h at snail densities between 0.017 and 0.14 per cm^2 of substratum, depending on the experiment, the maximum of which was similar to peak densities we observed in the field. Snails were fed TetraMin conditioning food (Jennings, DeKock & von Eeden, 1970). Turtles were fed snails, supplemented with commercial fish-food pellets or fruit depending on the species (Ernst & Barbour, 1972). Spring water was used for all experiments to ensure we did not introduce latent effects from organic cues in local waterways or unremediated water-treatment chemicals.

Experiment 1: snail response to predation by turtles

Our first experiment investigated behaviour of planorbid snails while under attack by turtles in a seminatural setting. Samples of the two snail populations were established in the laboratory in 38-l aquaria (50 × 25 × 30 cm in length, width and depth) with 30 l water, creating a depth of 25 cm, a 5-cm sand substratum and two piles of rocks. Each pile occupied *c.* 150 cm^2 of the substratum and was composed of rocks that were roughly 5–30 cm^3 in individual volume. Sample sizes used with each snail population are given in Table 1. Air stones were used in each aquarium to circulate water.

Snails were allowed to acclimate in aquaria for 15 min. We counted the initial number of snails exposed (i.e. those in view without obstruction) and then released a small painted turtle (7-cm carapace length, CL) into each aquarium in succession. We counted exposed snails after 15 and 30 min. Three observers recorded behaviour of the turtle and snails for the 30 min of turtle activity in each aquarium. After the experiment, surviving snails were counted and the difference from starting numbers was taken to be the number eaten.

This experiment was intended to be observational. Nonetheless, we follow Snyder (1967) and Snyder & Snyder (1971) in calculating within-trial probabilities using the binomial theorem to identify changes in the magnitude of response before and after treatments were applied in each tank. This approach could be questioned, in the absence of some assurances. However, we found a lack of volatility over time in the absence of new treatment applications, and little between-tank variation within experimental contexts. Also, we found a lack of positive correlation between snail numbers within tanks and responsiveness at the tank level, meaning snails do not seem to influence each other to be more responsive than they would in greater isolation. Thus, the within-trial approach appears to be an effective analytical tool. However, this approach is also combined with conventional statistical analyses as described below.

Experiment 2: behavioural stimuli and size-dependence of behaviour

Antipredator behaviours observed in the first experiment could be stimulated by any number of cues, physical or chemical, because

Table 1. Number of exposed *Planorbella campanulata* snails before and after interaction with turtles.

Population	*n*	Number exposed			Number eaten
		T_0	T_{15}	T_{30}	
Lab	37	34	15****	1****	4
FHP	42	40	24****	21	1

T_i indicates the time at *i* minutes after exposure to free-swimming turtles. Significance tests are binomial exact probabilities of differences in the distribution of snails in sheltered and exposed categories between time intervals T_0 *vs* T_{15} and T_{15} *vs* T_{30}. ****$P < 0.0001$.

predators were in the experimental aquaria with the prey. Experiment 2 was undertaken to examine (1) whether snails reacted differently to chemical cues of different species or sizes of turtles, (2) whether predation was necessary to elicit the response, (3) whether *P. campanulata* snails responded to predation on a different species of pulmonate snail, *Physella acuta* (Draparnaud, 1805) (syn. *P. heterostropha*; Wethington & Lydeard, 2007; Planorboidea: Physidae) and (4) whether reactivity was size-based.

We performed the following experimental survey, repeating a standard assay with several turtle species and both populations of *P. campanulata*. Turtle species, snail sample sizes and number of replicate trials are given in Table 2. Sample sizes varied among trials due to the availability of snails at the time of experimentation.

For each trial, we established between one and eight 6-l acrylic tanks with 4 l of water, a 3-cm layer of sand and 7–20 snails. Lab snails were consistently small, *c.* 8–12 mm shell diameter (SD, maximum diameter in plane of coiling). Sizes of FHP snails varied by availability at the time of collection and often were large (10–17 mm SD), with some exceptions (e.g. trial 6 FHP snails were 8–9 mm SD). Exact size distributions were measured in most (9 of 14) trials and are given with results in Figure 1. Turtles were established without snails in 38-l aquaria with 20 l water for at least 24 h before experimentation to provide chemical cues for the trials. The generalized protocol was as follows. Snails were allowed to acclimate for 30 min. We counted the initial number of exposed and buried snails at a time designated T_0 (time at 0 min) and added 100 ml of water. At T_{30}, we noted snail positions and added nonforaging (NF) predator scent (100 ml of water from a tank containing a NF turtle). Water was removed from the NF turtle tanks and reserved for use in subsequent intervals. Turtles were then fed three crushed 10-mm snails. At T_{60}, we noted snail positions and added NF predator scent to half the tanks and actively foraging (AF) predator scent (100 ml from a tank containing an AF turtle) to the other half (with one exception, trial 2, due to lack of replicates).

Thus, half the tanks lagged 30 min behind in receiving the AF predator scent. This was done as a control measure. If not for this introduced lag, attributing reactivity to AF predator scent at T_{90} would be questionable, as it could be a delayed response to NF predator scent. At T_{90}, positions were noted and AF predator scent was added to the tanks that did not receive AF predator scent at T_{60}. Snail positions were noted again at T_{120}. Some trials were run with multiple water exchanges or multiple turtle-scent exchanges during additional 30-min intervals as added control measures, to be sure that delayed responses to these cues ('lag effects') did not occur on larger time scales. For example, a lag-effect test for AF turtle scent would have compared the responses of snails 30 and 60 min after introduction of the scent to see whether the two time intervals had different levels of snail response (statistical analyses are described below). Control measures used in each trial are indicated along with results in Table 2.

To control for the possibility that reactivity to planorbid injury cues was a generic response to any abrupt change in the chemical environment, rather than one with specific meaning regarding conspecific predation, we also tested for reactivity to physid injury cues. For this test, we set up four 6-l acrylic tanks (tapered cylinders; top diameter 20 cm, bottom diameter 16 cm, depth 24 cm) with 4 l of water (16 cm depth), a 3-cm layer of sand and 10 lab *P. campanulata* (6–8 mm SD). After an initial count of burials, we performed a sham water exchange and counted burials 30 min later. The sham water exchange ensured that behavioural responses were not simply elicited by any disturbance in the water. Next, two tanks received a crushed *P. acuta* (7 mm shell length, measured from the apex to the distal shell margin) and 100 ml from a tank containing a nonforaging snapping turtle (6 cm CL). The remaining two tanks received a crushed *P. campanulata* (6 mm shell diameter) and an identical dose of predator scent. The number of burials was noted 30 min later.

Analysis of reactivity was performed in two ways. When three or more replicate tanks were used in a test, we arcsine square-root transformed the proportion of snails buried in each tank and performed a repeated-measures analysis of variance. This technique treats whole-tank values summed over individuals as the data. For example, to test the turtle-scent effect, we compared the transformed proportion of snails buried in a tank initially (after a sham water addition) with the proportion buried after exposure to NF turtle scent. For tests with one or two replicate tanks (trials 2, 5 and 13; Table 2), too few degrees of freedom were available to use analysis of variance on whole-tank values. Instead, we calculated a Model II two-way table for each tank using a *G*-test with Williams' correction (Sokal & Rohlf, 1995). This analysis assumed that the actions of individual snails in a tank were independent and were unlikely to result from whole-tank effects. For example, the decision of snail A to bury did not depend on what snail B did, and reactivity did not result from conditions peculiar to specific tanks. For tests with two tanks, we tested these assumptions with

Table 2. Burial frequency of *Planorbella campanulata* snails exposed sequentially to the scent of nonforaging and actively-foraging turtles.

Trial	Turtle species and size[†]	Snail population	Number of tanks	Snails per tank	% burial initially	% burial for NF turtle[‡]	% burial for AF turtle[‡]	Size-based burial[‡]	Lag test[‡][§]
1	SN-6	FHP	6	7	7.3	4.9	82.9***	ns	NF
2	SN-6	Lab	1	15	6.7	40.0*	86.7**	–	–
3	SN-6	Lab	4	10	0	27.5**	87.5**	ns	NF, AF
4	SN-18	FHP	6	11	0	9.2*	40.0**	–	W, NF, AF
5	SN-18	Lab	2	20	0	2.6	38.5***	–	W, NF, AF
6	PA-7	FHP	6	11	3	12.1*	66.7**	**	NF, AF
7	RE-17a	FHP	6	10	3.3	6.7	55.0**	**	NF, AF
8	RE-17a	Lab	6	10	21.7	35	88.3**	*	NF, AF*
9	RE-17b	FHP	8	10	12.5	21.3	70.0**	***	NF, AF
10	RE-17b	FHP	6	10	8.3	13.3	51.7**	ns	NF, AF
11	RE-17b	Lab	6	10	30	55.0**	98.3**	–	NF, AF
12	WO-19	FHP	6	7	7.1	11.9	38.1**	ns	NF, AF
13	WO-19	Lab	2	20	2.5	7.5	30.0**	ns	NF, AF

[†] Species designations: SN, snapping turtle; PA, painted turtle; RE, red-eared slider; WO, wood turtle; numbers give carapace lengths (cm); lower case letters indicate individual identities of turtles of same size. [‡] Statistical results from per-trial ANOVAs: *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$; ns, $P \geq 0.05$; –, not tested. [§] Lags tested in each trial: NF, nonforaging turtles; AF, actively foraging turtles; W, sham water treatment; –, no lag periods tested.

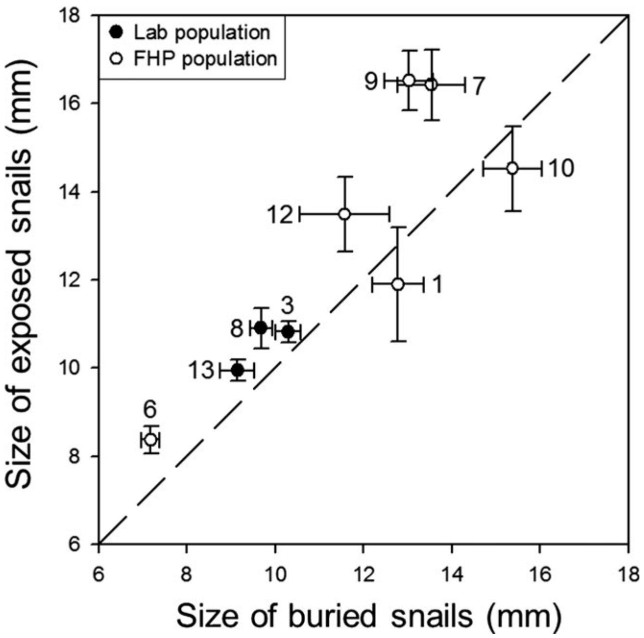

Figure 1. Sizes (mean shell diameter ±1 SE) of buried and exposed snails for nine trials in which we took size data. Trial number (following Table 2) is given next to each point. Points above the diagonal represent experiments in which buried snails were smaller than exposed snails. Trial 10 had several relatively small snails that crawled above the waterline and these were considered "exposed" in this figure. Had we categorized these snails as reactive, the mean for trial 10 would have fallen on the diagonal, rather than below it.

heterogeneity G tests (Sokal & Rohlf, 1995). No heterogeneity of response was noted for either pair of tanks for which we could perform this test (for trials 5 and 13: $G_{adj} = 0.56$ and 3.08, $P \geq 0.08$).

To contrast the sizes of buried and exposed snails, we pooled snails across tanks (within trials) and used t-tests if the size distribution was approximately normal, or else we used Mann-Whitney U tests. Pooling across tanks was more convenient for measurement, but assumed that tanks received snails of similar size at the start and that size-based responses did not differ among tanks. We tested this assumption for trials in which we did measure snails from each tank separately. No tank effects were noted (for trial 1: $F_{5,29} = 0.35$, $P = 0.88$; for trial 6: $F_{5,60} = 0.79$, $P = 0.56$), nor did the size-based response differ among tanks (for trial 1: $F_{5,29} = 0.89$, $P = 0.50$).

We additionally examined the nature of size-based responses using trial means. Since mean sizes in trials were normally distributed, we performed an ANOVA (randomized block analysis) to compare mean sizes of buried *vs* exposed snails. To test for association between snail responses and turtle size, we calculated a correlation between mean snail reactivity (by trial) and turtle CL. We hypothesized that snails might exhibit greater burial responses to the more threatening predator or the predator that caused a greater release of alarm cue.

Experiment 3: size-dependent predation

Three snapping turtles of various sizes were each established in a 38-l aquarium with 32 l of water. We placed eight small (6–8 mm SD) and eight large (16–17 mm SD) *P. campanulata* from FHP in each aquarium. Burial behaviour by snails was precluded because no sand or other material was provided. Behavioural observations of turtles were taken for 15 min. The number of remaining snails in each size class were counted (noting injuries) the following day and again each day until the fifth day after introduction of turtles. Using these data, we defined three elements of prey selectivity on the part of the turtles. First, the behavioural observations indicated prey selected for attack (*sensu* Sih, 1987). Second, the prey consumed on the first day indicated prey selected for ingestion while alternative choices were available. Third, counts in subsequent days indicated the absolute abilities of the turtles to prey on each size class of snail, assuming that hunger drove the turtles to consume all possible prey. The distribution of surviving snails did not change after the third day.

Experiment 4: efficacy of snail behavioural response

To test the efficacy of burial as an antipredator behaviour, we established four 38-l aquaria with 32 l of water, each with 20 snails (5–12 mm SD) from FHP. Two aquaria contained a 5-cm layer of sand, allowing for snail burial. The other two tanks had only 0.5 cm of sand, precluding effective burial. We hereafter refer to tanks with deep-sand as 'burial tanks' and tanks with shallow sand as 'no-burial tanks'.

Two 10-mm snails were crushed in 75 ml of water and 10 ml of the mixture was added to each tank. After 30 min, most snails, *c.* 90%, had buried in the tanks with deep sand and the few snails that remained exposed were manually buried by pushing them into the sand and covering them lightly. We introduced a relatively 'large' snapping turtle (12–14 cm CL) into a burial tank and another large snapping turtle into a no-burial tank. Similarly, we introduced one 'small' snapping turtle (5–6 cm CL) into each type of tank. Surviving snails were counted after 24 and 48 h. Data were analysed using G tests because the experimental design fitted a Model II two-way table (column totals were fixed by the number of snails in a tank, but row totals were allowed to vary with differential predation; Sokal & Rohlf, 1995). We applied Williams' correction because $n < 100$.

RESULTS

Experiment 1: snail response to predation by turtles

We did not observe change in snail behaviour immediately after the introduction of the small (7 cm CL) painted turtle into experimental aquaria. Turtle foraging occurred within minutes after placing each one in experimental aquaria. In each trial, the turtle failed to consume the first few snails they attacked. First, each turtle took a snail into its mouth and attempted to crush it, usually starting with the larger snails in sight. When not immediately successful, each moved to other snails.

Snails that were attacked and rejected usually responded immediately with burial or moved rapidly away until a solid object was encountered, such as a rock, tank wall or large conspecific, and then buried. Crawlout behaviour (Snyder, 1967; Alexander & Covich, 1991a, b) was not observed in this experiment.

Once the turtle had successfully consumed snails, widespread reactivity (production of any response) was noted. Snails often released from the tank walls and dropped to the substratum before burial, as has been described by Kempendorff (1942) and Snyder (1967). Releases were especially common if turtles disturbed snails, no matter how slightly. On no occasion were buried snails observed to be attacked.

Burial took the form of the snail moving its foot into the substratum a few mm at a time and drawing the shell in, often while moving the shell to the left and right. Repeated contractions in this manner rendered a snail entirely buried in 5–15 min (see also Kempendorff, 1942). Once fully buried, or nearly so, snails extended their antennae from the substratum as if to monitor the environment for signs of risk or safety.

Table 1 shows a summary of the number of exposed snails (i.e. those in view that could be counted) before and after turtle introduction. Both populations exhibited reactivity. Burial increased from 8% to 97% for the lab population and from 5% to 49% for the FHP snails.

Experiment 2: behavioural stimuli and size-dependence of behaviour

We observed reactivity of *Planorbella campanulata* in response to the scent of all actively foraging turtles, even for a nonnative turtle and a terrestrial species (Table 2). The form of reactivity was primarily self burial, although occasional crawlout behaviour was observed (up to 10% for one test, although the modal value was 0%). Weaker reactivity was noted in response to the scent of NF turtles. Of the 25 control measures applied to test for lag effects, only one was significant (trial 8, for AF turtle scent). Generally, it appears that responses to chemical stimuli occurred in full within 30 min.

No reactivity was observed for snails exposed to the scent of snapping turtle and crushed physid snails (for both tanks, $G_{adj} = 0$, df = 1, $P = 1$), whereas the two simultaneous control tanks that received the scent of snapping turtle and crushed planorbid snails were highly reactive (for both tanks, $G_{adj} \geq 10.03$, df = 1, $P < 0.0001$).

For trials in which size was measured, buried snails were generally smaller than those that remained exposed. Within-trial contrasts for size of buried and exposed snails were significant in 4 of 9 tests ($P < 0.05$). Using trial means, this trend was also evident ($F_{1,8} = 5.28$, $P = 0.05$)—mean size of buried snails was typically less than that of exposed snails (Fig. 1). Snail responses also depended on predator size. Burial response frequency in *P. campanulata* was inversely related to turtle size, regardless of turtle species ($r = -0.81$, $P = 0.0008$; Fig. 2). Reactivity was greatest in response to the scent of small turtles (65–88% for small snapping and painted turtles), moderate for intermediate-sized turtles (43–68% for medium red-eared sliders) and least in response to the largest turtles (28–40% for large wood and snapping turtles).

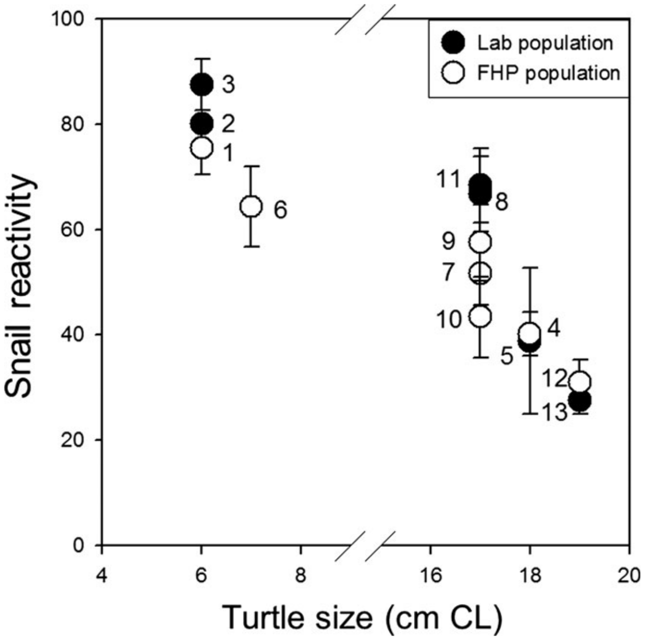

Figure 2. Snail reactivity in the 13 trials (mean ± 1 SE) as a function of turtle carapace length (CL). Snail reactivity was calculated as the difference between percent of snails buried in response to actively-foraging (AF) turtles and percent of snails buried initially. Trial numbers (following Table 2) are given next to each point.

Experiment 3: Size-dependent predation

Results from this experiment demonstrated two size refuges from predation: one a refuge from the predator's preference, the other from the predator's abilities. The first days in which predators were left with their prey indicate the predator's behavioural preference among prey items, whereas limitations on the predator's abilities were evident by the end of the experiment (day 5). Upon introduction of the two snail size-classes, all turtles (snapping turtles of 6, 12 and 18 cm CL) were observed to strike only large snails. However, small- and medium-sized turtles were often unable to crush shells of large snails (Fig. 3A, B). Four large snails were injured by the medium-sized turtle in the first 24 h but were never eaten. One snail was fatally injured. The large turtle ignored the majority of small snails during the first days of the experiment, but ate them eventually. No other food was available. After 24 h of predation, small snails suffered greater predation from small- and medium-sized turtles, but larger snails suffered greater predation from large turtles (Fig. 3A). Thus, predation was size-dependent: larger snails were at greater risk of attack, but were only susceptible to larger turtles; smaller snails were not attacked preferentially, but eventually sustained more predation.

Experiment 4: Efficacy of snail behavioural response

More snails were consumed in tanks with insufficient substratum to allow burial than in tanks allowing burial. This asymmetry was most pronounced for trials in which small turtles were used. Specifically, the small turtle in the no-burial tank consumed 14 of

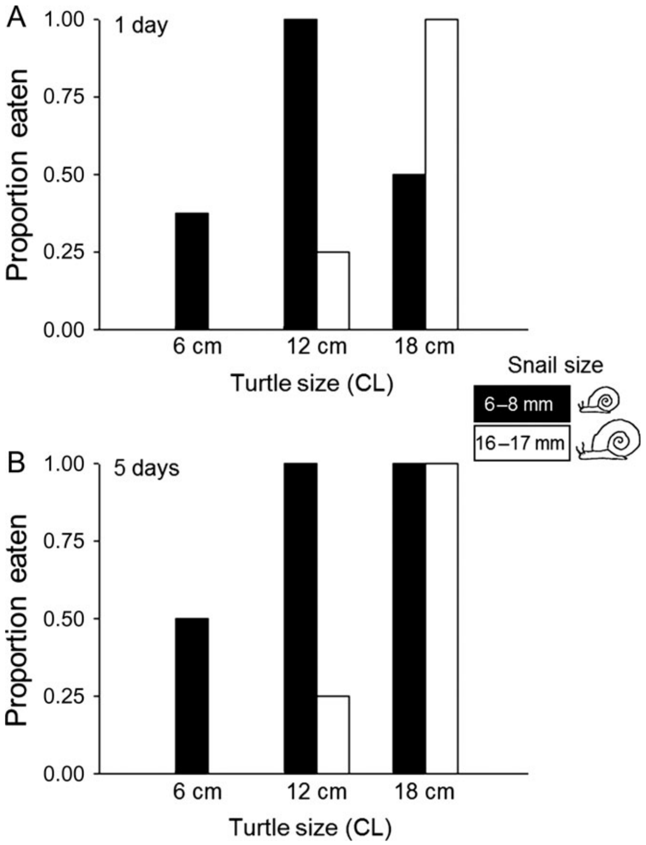

Figure 3. Size-dependent predation. **A.** After 24 h. **B.** After 5 d. The largest turtle (18 cm carapace length, CL) consumed all snails, beginning on the first day with the largest snails. The smallest turtle (6 cm CL) consumed only small snails, whereas the medium-sized turtle (12 cm CL) ate all the small snails, but appeared unable to eat many of the larger snails.

40 snails available over 2 d (6 on day 1; 8 on day 2). In contrast, the matched-size turtle in the burial-tank consumed no snails ($G_{adj} = 19.8$, df = 1, $P = 0.0001$). Similarly, the large turtle in the no-burial tank ate more snails (40 of 40 on day 1) compared to the matched-size turtle in the burial tank (30 of 40: 18 on day 1; 12 on day 2; $G_{adj} = 14.6$, df = 1, $P = 0.0001$). Although these results seem to indicate that burial was not very effective against large turtles (because 75% of snails were consumed), we noticed that the tank size and water volume left larger turtles on the substratum where they shoved the sand about as they moved. This action did not appear to be deliberate searching, but it did expose snails that had buried. Our observations of turtles during several experiments indicated that the turtles detected prey visually and did not actively search in the sand for snails.

DISCUSSION

Extensive research has shown that turtles are major predators of molluscs (Serrouya, Ricciardi & Whoriskey, 1995; Silliman & Bertness, 2002; Yoshie & Yusa, 2008). Yet studies of mollusc defense against turtles have been uncommon in recent decades, especially given the proliferation of research on other predators (reviewed above). In the present study, the predominant predator-induced response elicited in *Planorbella campanulata* in the presence of turtles was burial. Burial increased from a median frequency of 6.7% in the absence of turtle or injured-snail cues to 12.1% in response to turtle scent alone and 66.7% in response to turtle scent coupled with cues of conspecific snail injury. Prey responses to predator scent alone are common for terrestrial organisms (Kats & Dill, 1998), but aquatic species very often rely on the scent of injured prey to condition their responses (e.g. Kempendorff, 1942; Turner, 1996; 2008). As well, induction cues used by aquatic prey are often trait-specific (e.g. McCarthy & Fisher, 2000; Bourdeau, 2010) or otherwise complex. One species of apple snail, *Pomacea paludosa*, predictably and overwhelmingly buries in response to *Sternotherus minor* turtle scent without requiring snail injury cues, whereas *P. glauca* responds only for a short period in early ontogeny and *P. dolioides* is unresponsive without co-exposure to snail-injury cues (Snyder & Snyder, 1971). Such complexities limit the generalizations that can be drawn even in the restricted context of freshwater snail–turtle interactions. Further results from a multiplicity of snail–turtle pairings and observational contexts are needed to define the diversity and generality of the outcomes.

Snail burial in response to turtle scent as observed in the present study appears unlikely merely to be a nonspecific response to any sudden change in the local environment, because no burial resulted from sham water additions or scent from injured physid snails. The half-life of *P. campanulata* alarm substance is only 12 h in spring water and it is essentially gone by 18 h (T.J. DeWitt, T.M. McCarthy, D.L. Washick & J.D. Arendt, unpublished). Thus, it is unlikely that turtles retained residual scent of injured snails from trials on previous days, unless the snail alarm substance is more stable in the gut of turtles than in spring water. This suggests an innate capacity on the part of the snails to respond to turtles. However, we cannot exclude an intriguing alternative possibility as demonstrated in fish (Chivers, Wisenden & Smith, 1995; Korpi & Wisenden, 2001), damselflies (Wisenden, Chivers & Smith, 1997) and more recently in snails (Dalesman *et al.*, 2006, Turner *et al.*, 2006; Aizaki & Yusa, 2010). Wisenden *et al.* (1997) found that damselflies, *Enallagma boreale*, from a fishless site initially lacked reactivity to fish. After a single trial in which they paired the scent of northern pike fish, *Esox lucius*, with that of injured damselflies, damselflies exposed to the cue pairing learned the association and subsequently reacted to pike scent alone. To our knowledge, three snail species have been shown to possess both innate reactivity to injured conspecific scent and capacity for a secondary learned response to predators. Dalesman *et al.* (2006) showed that another pulmonate snail, *Lymnaea stagnalis*, could learn to associate injured conspecific scent with the scent of nonforaging fish, *Tinca tinca*. In *Physella acuta*, Turner *et al.* (2006) found that the response to pumpkinseed sunfish (*Lepomis gibbosus*) scent was modified based on prior co-exposure to crayfish (*Procambarus clarkii*) scent. Aizaki & Yusa (2010) demonstrated that the ampullariid *P. canaliculata* learned to associate injured conspecific scent with the scent of nonforaging fish (*Cyprinus carpio*) and turtles (*Chinemys reevesii*). The implication for the present study is that many of our experimental snails may have been preconditioned to respond to turtle scent. Because snails from FHP were collected from the wild, they may have already learned an association between turtle scent and injured conspecific cue, as shown in research by Turner *et al.* (2006). Snails from the lab population had not experienced turtle scent prior to our experimentation, but were sporadically reused after early experiments. Therefore, the lab snails may have become conditioned early in the present study to associate turtle scent with danger. Distinguishing innate from learned responses to predator scent requires multigenerational rearing with at least '3-generations-naïve' prey run through control and conditioning trials and subsequently compared for their reactivity to predator scent. Multiple generations are necessary to eliminate transgenerational predator environment effects known in diverse taxa such as plants (Sultan, Barton & Wilczek, 2009), zooplankton (Walsh *et al.*, 2015) and snails (Luquet & Tariel, 2016; Beaty *et al.*, 2016).

Whether our snails had evolved or learned responses to nonforaging turtles, it is interesting that we found responses to the nonnative red-eared slider and primarily-terrestrial wood turtle. Having no evolutionary history or ecological experience with these turtle species, it was surprising that the snails responded. Because burial entails costs such as energy and opportunity losses for feeding and mating (Turner *et al.*, 2000; Koch, Lynch & Rochette, 2007), responding unnecessarily is maladaptive. Some snails differentiate among predator species and adjust antipredator behaviours accordingly; *Physa fontinalis* exhibits a shell-swinging behaviour in response to predatory leeches but not to an abundant nonmolluscivorous leech (Townsend & McCarthy, 1980). Two congeneric *Acmaea* limpets respond to four species of predatory starfish, but not to a nonpredatory or a micro-allopatric starfish (Phillips, 1976). In other cases, prey fail to distinguish threatening from nonthreatening species, such as *Physa virgata*, which induce rotund shells and growth reduction in response to six sunfish species, including molluscivorous and nonmolluscivorous and native and nonnative species (Langerhans & DeWitt, 2002). Additional cases in marine molluscs have been reviewed by Hollander & Bourdeau (2016). While it would seem beneficial for *P. campanulata* to distinguish between turtle species, the generalized response of treating all turtles alike, especially when combined with use of prey-injury cues, may be an optimal compromise given the sensory mechanisms available to *P. campanulata* (Kempendorff, 1942).

For reactivity to predators to be adaptive, it must enhance prey fitness. Innate responsiveness to conspecific injury or the ability to learn associations between conspecific injury and predator scent could clearly represent adaptive strategies. Additionally, responding to injury cues of heterospecific species that are ecologically similar might prove beneficial as well (Snyder, 1967; Stenzler & Atema, 1977; Chivers *et al.*, 1995; Wisenden *et al.*, 1997). Cross-reactivity between physid and planorbid snails (members of separate families within the Planorboidea) could be adaptive because they frequently co-occur. We found, however, that planorbid snails from FHP, where they co-occur with physid snails, did not react to injured physid snails. Alexander & Covich (1991b) found that the reverse of this cross-reactivity was also absent: physids lacked reactivity to injured planorbids. Similarly, Turner (2008) found that neither physid nor planorbid snails reacted behaviourally to the scent of the other. Snyder (1967), in his broader five-species context, found no evidence for physid–planorbid cross-reactivity, although he found that the caenogastropod ampullariid

P. paludosa reacted to injury cues from the pulmonate *Lymnaea columella*. Although physid and planorbid snails frequently co-occur, injured to one may not imply risk to the other. For example, physids are readily crushed by tench fish, *Tinca tinca*, but their predation is meaningless to most planorbids, which have much greater crush-resistance (Rundle & Brönmark, 2001). Even injured planorbids do not necessarily imply risk to physids; the leech *Glossiphonia complanata* attacks planorbids with an eightfold greater frequency than physids (Brönmark & Malmqvist, 1986). Also, there may often be microhabitat segregation between physids and planorbids (Alexander & Covich, 1991a). Therefore, conservative cross-species reactivity with respect to costly antipredator responses is not unexpected.

Smaller planorbid snails were individually more vulnerable to predation from turtles and they also buried more frequently (Figs 1, 3). Thus, the individuals at greater risk of predation performed antipredator behaviour with greater frequency. Alexander & Covich (1991a) found a similar result in *Planorbella trivolvis*, using crayfish as predators and focusing on crawlout as the prey response. Smaller snails were both more vulnerable to predation and more responsive to cues of predation. One way to view these results is that snails lacking one type of defence (large size) compensated by increasing the frequency of an alternative defence (hiding). These results support recent studies suggesting that behavioural 'trait compensation' may be a common and important strategy used by prey in complex communities. Trait compensation was originally defined and demonstrated in molluscs (DeWitt *et al.*, 1999; Rundle & Brönmark, 2001; DeWitt & Langerhans, 2003; Cotton *et al.*, 2004; Bourdeau, 2012; Stevison *et al.*, 2016), but has since been shown in zooplankton (Hansson, Hylander & Sommaruga, 2007), insects (Mikolajewski & Johansson, 2004), fish (Sillett & Foster, 2000; cf. Lacasse & Aubin-Horth, 2012) and tetrapods (López *et al.*, 2005; Arendt, 2007). Such positive correlations between risk and defensive responses strongly suggest adaptive evolution.

Burial response was inversely related to turtle size (Fig. 2). It appeared to us that greater reactivity to smaller turtles stemmed from the way in which the turtles foraged. Larger turtles quickly consumed the snails, whereas smaller turtles more fully crushed the snails and tore the body into pieces during consumption. The increased handling presumably released more snail odours, which likely serve as a cue. Similarly, mode of predation was thought by Stenzler & Atema (1977) to result in the differential responses to two predator species in *Nassarius obsoletus*. In their study, snails buried in response to predation by crabs, *Carcinus maenas*, which fed sloppily by cracking the shell and tearing the snail tissue into pieces. The snails did not respond to predation by the large molluscivorous naticid snail *Lunatia heros*, which neatly drilled a hole in the shell of prey while sealing the site of attack with its large foot. Studies that measured reactivity in response to different concentrations of alarm substance, rather than contrasting reactivity to individual predators, have demonstrated that dose-dependency is the rule for most reactive species (reviewed by Chivers & Smith, 1998). In freshwater snails, Turner & Montgomery (2003) found that increasing cue age and distance to cue source (caged fish) reduced refuge use in a physid snail. Alexander & Covich (1991b) demonstrated dose-dependent reactivity in planorbid snails by showing that reactivity correlated with the number of snails consumed by crayfish. Thus, dose dependency has been documented in three ways: (1) by alarm substance concentration *per se*, (2) by the number of snails being consumed and (3) by the voracity of predators and their feeding differences (both within and among predator species).

For prey, dose-dependency is adaptive when greater cue dose correlates with greater risk. In the present study, it appeared that dose-dependency led to greater response to less voracious predators (i.e. the smaller turtles in experiment 3), which was maladaptive in this context. In natural environments, however, greater alarm-cue dose may not only arise from inefficient predation. It could arise from multiple, more recent or more proximal predation events (as discussed above). Therefore, the lack of correspondence between cue concentration and risk for some predators may be compensated by alternative, positively correlated indications of risk. This implies that the maladaptive response to less voracious turtles is better viewed in a broader evolutionary context as part of an overall adaptive response. For predators, dose-based responses by prey imply selection for them to consume prey neatly, because poor or extended handling increases both the release of chemicals that stimulate escape reactions of prey and the time prey have to enact antipredator behaviour, thereby increasing the search time for subsequent prey (DeWitt, Robinson & Wilson, 2000).

In this study, burial by planorbid snails in response to turtles appeared to be an imperfect but generally effective adaptation. Burial effectively reduced predation and was contingent on individual vulnerability, wherein smaller, more vulnerable snails exhibited more behavioural defence (i.e. trait compensation). The propensity to bury appeared to be dose-dependent, which on balance would likely be adaptive, although in our study this propensity resulted in failure to respond to the most voracious predators.

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