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Antipredator behaviour of the freshwater snail (*Sulcospira hainanensis*) in response to the critically endangered big-headed turtle (*Platysternon megacephalum*)

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Abstract
Predators can trigger antipredator behaviour in their prey, with potential cascading effects on community structure and ecosystem processes. The big-headed turtle (*Platysternon megacephalum*), a critically endangered species, is a key predator of the freshwater snail (*Sulcospira hainanensis*) in Hong Kong hill streams. This study examined the antipredator behaviour of *S. hainanensis* in response to chemical (olfactory) cues from *P. megacephalum* and dead conspecifics. Snails were exposed for 40 min to one of the four treatments: (1) control (no chemical cues), (2) dead conspecific cue, (3) predator cue, and (4) mixed cues (from both dead snails and turtles). We found that snails exposed to the predator cue exhibited the highest refuge use, whereas snails under the dead conspecific treatment showed increased movement at the start of the experiment, which declined over time. These results suggest that *S. hainanensis* exhibits cue-specific behaviours, hiding under refuges (analogous to rock crevices in the wild) as the primary defence strategy against turtles, and increased movement for other potential threats. Such behavioural flexibility may reflect adaptation of *S. hainanensis* to multiple predator types. Our findings demonstrate that *P. megacephalum* influences the behaviour of *S. hainanensis*, the dominant grazer in Hong Kong's hill streams, with a potential cascading effect on habitat and resource use dynamics. Understanding these interactions will advance our knowledge of the ecological roles of Asian freshwater turtles and inform future conservation and environmental education efforts.

Keywords Molluscs, Stream, Trophic cascades, Asian turtles, Kairomones

1 Introduction

Turtles and tortoises perform critical ecological roles, functioning as consumers, seed dispersers, bioturbators, and nutrient cyclers [1]. However, existing literature on the ecological functions of turtles and tortoises have mostly focused on some regions of the world, such as North America [2], while information from other regions remains sparse, despite the fact that they are nearly universally threatened [3]. In Asia, freshwater turtle populations have been heavily impacted by habitat loss and degradation, as well as overexploitation for food, medicinal and pet markets [3], with about 80% of Asian freshwater turtles and tortoises classified as critically endangered, endangered or vulnerable on the IUCN Red List [4]. While there is an urgent need to investigate the ecology of Asian freshwater turtles to better conserve them, the scarcity of wild turtle populations hinders the implementation of systematic ecological studies [5].

One major way in which turtles shape their environment is via predator-prey interactions [6, 7]. In some freshwater ecosystems, carnivorous and omnivorous turtles represent one of the animal groups with the highest biomass, comparable to that of predatory fish [8]. Studies have shown that turtles exert a strong influence on prey communities because they can exploit a wide range of prey [6, 9, 10]. For example, turtles can consume hard-shelled snails that are inaccessible to most other vertebrate predators [10]. The common snapping turtle (*Chelydra serpentina*), for instance, has larger gape sizes than other predators, allowing it to prey on larger prey items such as *Rana sphenocephala* tadpoles [6]. Consequently, the presence of *C. serpentina* has been associated with increased mortality and altered growth patterns of tadpoles [6]. These examples highlight the potential of turtle populations to influence prey population dynamics and community structure.

Turtles can indirectly influence the behaviour of their prey through the release of chemical cues. In snails, chemoreception is highly developed and serves as the primary sensory system [11]. Snails exposed to predator cues alone or together with dead conspecific cues often triggers antipredator behaviours, such as escaping from a predator cue and refuge-seeking above the water surface, within substrates, or under cover [12–15]. These behaviours may change the snail's foraging pattern [12, 16, 17] and reduce their ability to reproduce [18, 19], thereby decreasing activity levels and their population, which could ultimately trigger a top-down trophic cascade affecting the base of the food web—algae and macrophytes [6, 7, 17]. Overall, turtles may indirectly influence ecosystem-level processes (e.g. primary productivity and nutrient dynamics) and community structure (e.g. species composition and total species richness) [6, 7, 20], by suppressing primary consumers, such as snails and tadpoles.

Research on predator-prey dynamics among Asian freshwater turtles are mostly limited to interactions with the invasive apple snail (*Pomacea canaliculata*) [18, 19, 21, 22]. Researchers found that the Chinese softshell turtle (*Pelodiscus sinensis*) and Reeve's terrapin (*Mauremys reevesii*) can be effective biological control agents of apple snails, given the large number of snails they consume [22, 23]. The effects of turtles on native prey species in Asia, however, remain largely unknown. For example, in Hong Kong's mountain streams, a native freshwater snail (*Sulcospira hainanensis*) [24] is the primary prey of the big-headed turtle (*Platysternon megacephalum*) [25], yet we know very little about the dynamics of their predator-prey interaction, and its broader consequences on the ecosystem. Nevertheless, reduced *S. hainanensis* populations have been shown to result in sharp increases in algal biomass, total species richness and insect biomass and density [26]. This means that changes in predator-prey dynamics between the snail and its major predator would likely have major cascading effects [7, 17, 27], warranting closer investigation.

In this study, we assess if *P. megacephalum* elicits measurable antipredator responses in its primary prey, *S. hainanensis*. We addressed the following questions: (1) Do the snails hide when exposed to the chemical cues mimicking turtle presence? (2) Do the snails' responses intensify when chemical cues from both dead conspecifics and turtles are present, indicating that turtle predation poses a greater threat than their mere presence? The results of this research will help fill the vast knowledge gaps regarding the ecological roles of freshwater turtles in Asia. Addressing these knowledge gaps is vital for informing conservation efforts and raising public awareness about the importance of freshwater turtle conservation.

2 Materials and methods

2.1 Study animals

Between September and October 2022, we collected two batches of *S. hainanensis* (Fig. 1a) in two separate trips (240 in each batch, a total of 480 snails) from a river in the New Territories of Hong Kong, where *P. megacephalum* (Fig. 1b) occurs in the higher reaches of the river. The snails [mean ± SD: snail width = 10.9 ± 1.2 mm] were acclimatised for 2–3 days before the experiment and released to the collection site after the experiment, within one week of collection. They were allotted randomly to two large holding tanks (40 cm × 40 cm × 61 cm) in densities that mirror the wild, i.e., between 100 and 200 individuals per m^2 [28]. The tanks were filled with de-chlorinated, aerated aged tap water (24 °C) with a water filter (filtering capacity: 200 L hr^{-1}). The snails were provided shelters constructed out of rocks that were collected from the river and fed algae wafers (Brand: OTTO – Sinking Bottom Fish Food) three times a week. Four wild *P. megacephalum* were temporarily held in the laboratory and kept individually in separate tanks with a shelter, a basking lamp and a water filter. Turtles were fed twice a week with chicken breast, turtle pellets (Brand: Zoo Med – Natural Aquatic Turtle Food – Maintenance Formula) and blueberries.

2.2 Treatment design

We tested snail behaviour under four experimental treatments: (1) control—without additional chemical cues; (2) dead conspecific treatment—chemical cues from dead snails; (3) predator treatment—chemical cues from a turtle; and (4) mixed treatment—chemical cues from both dead snails and a turtle predator. For each experimental treatment, we added 150 mL of the corresponding cue mixtures to an experimental tank

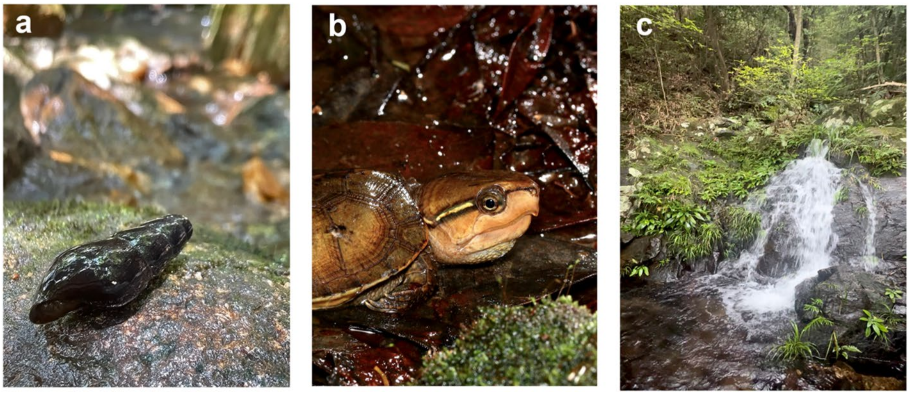

Fig. 1 This study examined the antipredator behaviour of the freshwater snail *Sulcospira hainanensis* (**a**), triggered by the chemical cues of the critically endangered big-headed turtle *Platysternon megacephalum* (**b**). Both species coexist in rocky mountain streams in Hong Kong (**c**)

containing 500 mL of aged tap water. In the control treatment tank, we added 150 mL of aged tap water from a bucket aerated with an air pump for over 48 h. For the dead snail treatment, the cue mixture was prepared by adding five homogenised *S. hainanensis* (total weight ± SD = 6 ± 0.5 g) to 3 L of aged tap water. The mixture was stirred for 30 s and allowed to sit for one minute before filtering debris (shells and snail tissues) through a 212 µm sieve. The concentration was approximately 2 g of snail tissue per litre of water [29]. We then added 150 mL of the resulting filtrate to the experimental tank. Snails used for cue preparation were frozen intact and stored at -20 °C until use, then thawed before homogenisation. For the predator treatment, a *P. megacephalum* (mean ± SD: head width = 29.8 ± 9.7 mm; plastron length = 78.7 ± 19.5 mm) was placed in 3 L of aged tap water for two hours. The turtle was then removed, and 150 mL of the water, containing turtle chemical cues, was added to the experimental tank. For the mixed treatment, 75 mL of the dead snail treatment mixture was mixed with 75 mL of the predator treatment mixture, and the resulting 150 mL of combined mixture was added to the experimental tank.

2.3 Experimental procedure

The experiment was conducted in four sessions, held on 26 September, 29 September, 3 October, and 5 October 2022, between 12:00 noon and 2:00 pm. Each session involved 120 snails, randomly chosen and assigned to 12 experimental groups of 10 individuals. Each group was randomly assigned to one of the four treatments, resulting in three replicate groups per treatment per session. Each snail was tested only once. Each group of 10 snails was placed in a glass tank (12.5 cm × 7 cm × 17 cm), containing 500 mL of aged tap water and a 10 × 10 cm tile was completely submerged and propped against the glass to provide a refuge underneath. Snails were acclimatised in experimental tanks for 30 min before the addition of treatment mixture (150 mL). All tanks were positioned on the same bench under uniform lighting and temperature conditions. To prevent potential effects of food on snail behaviour, both snails and turtles were not fed on the day of the experiment or during treatment preparation.

We conducted a pilot experiment with 120 snails and observed snail behaviour for two hours after exposure to the control and predator treatment mixture. We identified five distinct behaviours: (1) hiding under refuge—stationed under a refuge and not visible from above; (2) emerging from water—climbed up the wall of the tank and completely out of water; (3) retreating into shell—retreated into the shell and aperture sealed by operculum; (4) scanning environment—sweeping movement of antennae while stationary; and (5) travelling around— moving actively in the water. We found that most snail behaviour ceased to change after 40 min, consistent with similar studies [14, 21, 29, 30]. Therefore, in this study, we observed snails for 40 min and recorded the number of snails exhibiting each behaviour at the 10th, 20th, 30th and 40th minute.

2.4 Statistical analysis

We used generalised linear mixed models (GLMMs) with a binomial distribution to analyse the effects of treatment on snail behaviour [31]. The proportion of snails exhibiting each behaviour was used as the response variable (e.g. a value of 0.4 for hiding means that four out of ten snails were hiding under refuge), with treatment, time (10, 20, 30, and 40 min), and their interactions included as fixed factors. We included snail group and experimental date as random factors. We carried out separate GLMMs for each type of behaviour. Our statistical analysis examined each behaviour separately, assuming independence among behaviours. This was necessary because we recorded the number of snails performing each behaviour at the tank level rather than tracking individuals. As a result, some behaviours may not be completely independent, and potential correlations among behaviours within groups could not be addressed in our analyses. As few snails emerged from the water, this behaviour was excluded from the statistical analysis. The full models with interaction terms did not converge for the scanning environment, so the interaction terms were removed from this model. All analyses were conducted using R software [32]; GLMMs were performed using the lme4 package, and model diagnostics (checking residual patterns and for overdispersion) were done using the DHARMa package [33, 34].

3 Results

Among the five behaviours observed, hiding under refuge was most frequently observed (mean number of snails per tank ± SE = 4.4 ± 0.2), followed by travelling around (2.7 ± 0.2), retreating in shell (1.4 ± 0.1), and scanning environment (1.3 ± 0.1). Few snails emerged from the water (0.2 ± 0.1). The predator treatment significantly increased the proportion of snails hiding under refuge compared to the control ($p = 0.004$; Fig. 2a; Table 1), while neither the dead snail nor the mixed treatments differed from the control. No significant temporal change or interaction with time was detected, indicating that the predator effect remained stable throughout the experiment (Fig. 3a). The proportion of snails travelling around declined significantly over time in the dead snail treatment compared to the control ($p = 0.01$; Fig. 3b; Table 1). There were no significant treatment effects on the proportion of snails retreating into shell ($p \geq 0.16$ for all treatments; Table 1).

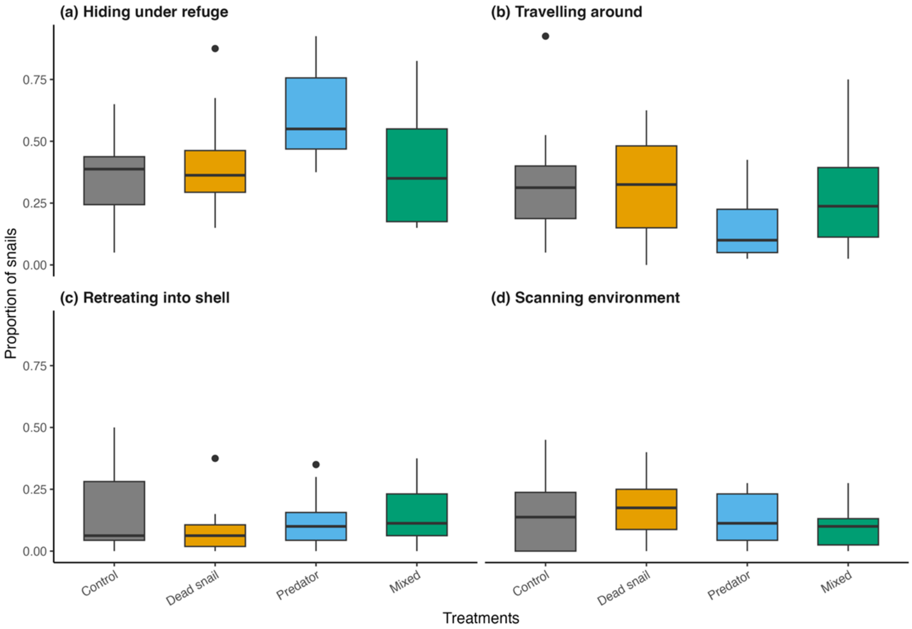

Fig. 2 Box-and-whisker plots showing the proportion of snails (*Sulcospira hainanensis*) exhibiting different behaviours (**a**: hiding under refuge; **b**: travelling around; **c**: retreating into shell; and **d**: scanning environment) under four treatments with different chemical cues (control, dead snail, predator, and mixed) in a laboratory experiment. Boxes represent the interquartile range, horizontal lines indicate medians, whiskers show the range of non-outlier values, and points denote outliers

Table 1 Estimated effects from binomial generalised linear mixed models (GLMMs) analysing the proportion of snails (*Sulcospira hainanensis*) exhibiting different behaviours (hiding under refuge; travelling around; retreating into shell; and scanning environment] under four treatments (control, dead snail, predator, and mixed) over time in a laboratory experiment

Fixed factors	Estimate	SE	z	*p*
Hiding under refuge				
Dead snail	0.48	0.49	0.99	0.32
Predator	**1.40**	**0.49**	**2.89**	**0.004**
Mixed	0.48	0.49	0.99	0.33
Time	0.00	0.01	0.54	0.59
Dead snail x Time	−0.01	0.01	−0.51	0.61
Predator x Time	−0.01	0.01	−0.67	0.51
Mixed x Time	−0.01	0.01	−0.74	0.46
Travelling around				
Dead snail	0.69	0.55	1.27	0.20
Predator	−0.56	0.58	−0.96	0.34
Mixed	0.41	0.56	0.75	0.46
Time	0.01	0.01	0.99	0.32
Dead snail x Time	**−0.03**	**0.01**	**−2.46**	**0.01**
Predator x Time	−0.03	0.02	−1.79	0.07
Mixed x Time	−0.03	0.01	−1.93	0.05
Retreating into shell				
Dead snail	−0.75	0.53	-1.41	0.16
Predator	−0.17	0.52	-0.33	0.74
Mixed	0.03	0.51	-0.06	0.95
Time	**−0.01**	**0.01**	**-2.14**	**0.03**
Scanning environment				
Dead snail	0.39	0.50	0.78	0.44
Predator	−0.13	0.51	−0.26	0.79
Mixed	−0.44	0.51	−0.86	0.39
Time	**0.03**	**0.01**	**5.01**	**< 0.001**

Fixed factors included treatments, time, and their interaction. The control treatment was used as the reference level. Bold rows indicate significant effects.

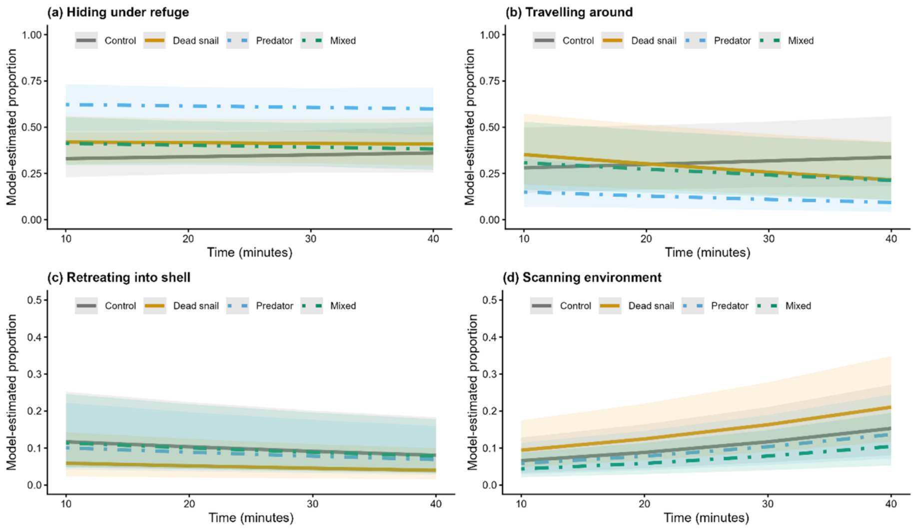

Fig. 3 Model-estimated proportion of snails (*Sulcospira hainanensis*) exhibiting different behaviours (**a**: hiding under refuge; **b**: travelling around; **c**: retreating into shell; and **d**: scanning environment) under four treatments with different chemical cues (control, dead snail, predator, and mixed) over time (10 to 40 min) based on binomial generalised linear mixed model (GLMMs). Shaded areas indicate 95% confidence intervals

However, the proportion of snails retreating into shell decreased significantly over time across treatments ($p = 0.03$; Fig. 3c; Table 1). The proportion of snails scanning the environment did not differ among treatments ($p \geq 0.39$; Table 1) but increased significantly over time ($p < 0.001$; Fig. 3d; Table 1).

4 Discussion

In this study, we found that *S. hainanensis* exhibited clear antipredator behaviour in response to chemical cues from *P. megacephalum*, consistent with previous studies on freshwater snails and their predators [15, 29, 30]. Snails are known to adopt a range of antipredator strategies depending on predator type or environmental conditions [13, 29, 35, 36]. Several studies have shown that hiding in substrate is a common and effective defence against visually hunting turtles [15, 19, 29, 37]. In our experiment, *S. hainanensis* displayed a similar strategy by seeking refuge under the tile provided, which is likely analogous to hiding in rock crevices in the mountain streams where *S. hainanensis* and *P. megacephalum* coexist. Such behaviour is advantageous in Hong Kong hill streams, where abundant cobbles and boulders provide ample refuges year-round (> 60% coverage in both wet and dry seasons) [38]. This is further supported by our field observations of wild *S. hainanensis* detaching from rock surfaces and dropping into rock crevices when subjected to strong taps, which they may have associated with predatory risk. Similar drop-and-escape behaviour has been observed in other snail species exposed to turtle predators [15]. Retreating into the shell or leaving the water would be ineffective because *P. megacephalum* can crush the shells of snails and emergent plants are rare [25]. Unlike habitats for other studied snail species [7, 14, 29, 36], sandy substrates and submerged plants are scarce in these streams whereas rock crevices are abundant [38]. Therefore, seeking refuge among rocks is likely the most effective defence against *P. megacephalum*.

Many previous studies have shown that snails also respond to the chemical cues from dead or injured conspecifics [14, 29, 39, 40], sometimes more strongly than to predator cues [39, 40]. In contrast, we did not detect a significant main effect of the dead snail treatment (Table 1), although we found a significant interaction between time and treatment where snails under the dead snail treatment travelled more initially but reduced their movement over time (Table 1; Fig. 3b), whereas snails exposed to predator cues showed the lowest level of movement (Fig. 2b). These results suggest that *S. hainanensis* may adopt different strategies depending on cue type—refuge use in response to turtle cues, and increased movement when exposed to dead conspecifics. Cue-specific strategies have been observed in other freshwater snails, particularly in relation to predators differing in size, risk level and predation strategy [29, 30, 35, 39, 40].

Besides *P. megacephalum*, *S. hainanensis* is also prey for smaller benthic predators such as shrimps (e.g., *Macrobrachium hainanensis*) [41, 42]. Given the much smaller size and manoeuvrability of shrimps and other potential benthic predators (e.g. crabs) in small space compared to turtles, hiding in crevices may be less effective against these benthic predators [41, 43]. The adult snails used in this experiments are realistically larger than snails that are subject to predation under natural conditions [41]. However, anti-predator responses can persist across different snail size classes, and may even be transgenerational for some species [44, 45]. This may help explain why snails used in this experiment increased movement under the dead snail treatment which may signal risks from a broader range of predators, including small benthic predatory shrimps and crabs.

Such behavioural flexibility may allow snails to balance the trade-off between avoiding large, shell-crushing predators and small, benthic predators capable of entering small rock crevices. Further experiments testing responses of *S. hainanensis* to cues from different predators, including shrimps and crabs (e.g. *Cryptopotamon anacoluthon* and *Eriocheir japonica*), would help test this hypothesis and clarify the plasticity of their antipredator behaviour and its associated evolutionary implications [30, 39, 40]. In addition, it is possible that the intensity of anti-predatory responses may vary, and be diminished in larger snails, so future experiments comparing predator-avoidance behaviour across a range of snail sizes is warranted.

Another potential explanation for the weaker response to the dead snail cue is that the stimulus may not have been strong enough to trigger consistent alarm responses, as compared to the predator treatment. In some studies, dead snail cues were prepared by crushing live snails [14, 40], while others did not specify whether live snails were used [29, 39]. If the snails are alive during cue preparation, they would likely have released alarm pheromones [46]. In this study, however, our cues were made from frozen carcasses stored at -20 °C. Because chemical cues can degrade over time [47], future studies should consider using live snails to trigger the release of alarm pheromones and exposing experimental snails to cues immediately after preparation.

We also found that the mixed cue of dead snails and predators did not produce an additive effect, unlike findings from other studies [39, 48]. Snail responses under the mixed treatment were similar to those under the dead snail treatment for both hiding under refuge and travelling around (Fig. 2a and b). This pattern may be explained by cue dilution because dead snail and predator cues were each diluted to half of the original concentration in the mixed treatment. While the impact of predator on hiding behaviour was significant under the predator treatment, the reduced predator cue concentration in the mixed treatment may have fallen below the threshold that triggers a strong antipredator response in *S. hainanensis*.

Behavioural responses of snails also changed over time. The effect of the predator treatment on hiding under refuge remained consistent throughout the 40-minute experiment (Fig. 3a), while other behaviours, including retreating into shell and scanning environment (Fig. 3c and d), varied significantly over time, including the control treatment. This likely reflects the impacts of initial disturbance at the start of the experiment which faded over time, as snails shifted from retreating into shell to scanning environment when they became acclimated to the experimental tanks [49–51].

The ecological roles of Asian freshwater turtles remain poorly understood because wild populations are scarce [5]. In this study, we documented the behavioural impact of *P. megacephalum* on *S. hainanensis*, an ecologically important species that serves as the dominant grazer in mountain streams in Hong Kong [26]. The observed antipredator responses to turtle cues may influence how snails utilise habitat and exploit resources, potentially leading to cascading ecological effects. For example, by seeking refuge under cover in the presence of turtle cues, snails may concentrate their grazing activity in sheltered microhabitats such as rock crevices, reducing resource consumption in open areas and indirectly benefiting other grazing macroinvertebrates [16, 17, 26]. To address this knowledge gap, future research should investigate if such cascading effects occur and how *P. megacephalum* affects *S. hainanensis* populations in areas where robust *P. megacephalum* populations still exist. This will help us to understand the broader ecological consequences of turtle population decline. Such knowledge will enhance our understanding of their ecological roles which is valuable for informing conservation and environmental education efforts.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1007/s44338-025-00157-9.

Supplementary material 1.

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Declarations

We confirm that this manuscript has not been published elsewhere and is not under consideration by another journal. All authors have approved the manuscript and agree with its submission to Discover Animals.

Author contributions

A.W.L.F. and Y.H.S. acquired funding and wrote the main manuscript text. A.W.L.F. implemented the experiment and collected the data. A.W.L.F., J.H.L., and Y.H.S. assessed the accuracy of the data analysis methods, validated the methodology, and reviewed the manuscript.

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Data availability

All data supporting the findings of this study are available within the paper and its Supplementary Information.

Declarations

Ethics approval and consent to participate

The methods used in this study were approved by the Department of Health [Permit number: (20–51) in DH/HT&A/8/2/8 Pt.1] and the Agriculture, Fisheries and Conservation Department [Permit number: (95) in AF GR CON 09/51 Pt. 8] of the Hong Kong Special Administrative Region Government, China. All procedures involving the protected turtles in this study were approved by the Agriculture, Fisheries and Conservation Department, Hong Kong SAR Government (AF GR CON 09/51 Pt 6).

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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