



QUITE THE APPETITE: JUVENILE ISLAND APPLE SNAILS
(*POMACEA INSULARUM*) SURVIVE CONSUMING ONLY EXOTIC
INVASIVE PLANTS

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ABSTRACT

Most aquatic snails derive their energy by grazing periphyton. However, certain species, including the invasive island apple snail, *Pomacea insularum*, readily consume aquatic macrophytes. These snails often overlap in their distribution with other exotic, invasive plants. We sought to discover if juvenile *P. insularum* could survive and grow when fed only three reportedly less palatable food sources: Eurasian watermilfoil (*Myriophyllum spicatum*), wild taro (*Colocasia esculenta*) and water hyacinth (*Eichhornia crassipes*). Snails received nonrooted macrophytes simultaneously in a multiple-resource experiment. Using enclosures with compartments that separated plants but allowed snails full access, we housed individual early (10.7 ± 0.9 mm operculum width; $0.56\text{--}1.11$ g blotted wet weight; mean ± 1 SD) or late (23 ± 2 mm; $4.60\text{--}14.82$ g) juvenile *P. insularum*. We monitored snail survival and growth for 6 weeks. As controls, we placed standardized nonrooted macrophytes in enclosures without snails for 1 week. Replacing plants weekly, we calculated average daily consumption rates. Both size classes of snails grew substantially in terms of operculum width, shell height and blotted wet weight, with early juveniles exhibiting relatively larger gains in size over the 6-week period. No mortality occurred. Both size classes consumed significantly more watermilfoil than taro and more taro than water hyacinth. Collectively, these results translate into the potential for one single 10-g *P. insularum* (i.e. representative of the larger snails used in our experiment) to consume a combined 0.35 g of dried plant matter (or *c.* 3.5 g) of live macrophytes per day. Our study suggests that available resources offered by a community of exotic invasive plants may sustain snail survival.

INTRODUCTION

Aquatic snails may span trophic levels, yet perception of snails as predominately algal grazers remains entrenched among ecologists (Brönmark & Vermaat, 1998; Jones & Sayer, 2003). Herbivorous snails that are not stereotypic algal grazers may pose significant threats to aquatic systems (Burks *et al.*, 2006). Macrophyte consumption gives snails a greater influence on driving shallow lakes towards turbid conditions (Jones & Sayer, 2003; Carlsson, Brönmark & Hansson, 2004). Furthermore, using *Lymnaea stagnalis* as their model, Elger, Barrat-Segretain & Amoros (2002) suggested that large size and long lifespan of certain plant consumers increased their ability to impact macrophyte communities. Advantages of large size and long lifespan also apply to a rising exotic, invasive species, the island apple snail *Pomacea insularum* (d'Orbigny, 1839) from South America (Hayes *et al.*, 2008). Populations of *P. insularum* now extend across the Gulf Coast of the USA (Karatayev *et al.*, 2009; Burks, Kyle & Trawick, 2010).

As in other successful invasive molluscs, apple snails possess high fecundity and reproduce rapidly (Keller, Drake & Lodge, 2007; Barnes *et al.*, 2008). Juvenile snails that consume macrophytes pose a threat that is at least equivalent to that from adult snails. Although the golden apple snail, *P. canaliculata* (Lamarck, 1828), remains the best studied of the apple snail species (Joshi & Sebastian, 2006), *P. insularum* exhibits a higher reproductive capacity (Barnes *et al.*, 2008) and thus potentially poses a bigger threat to aquatic ecosystems worldwide (Keller *et al.*, 2007). In addition, the distribution of *P. insularum* often overlaps with ranges of multiple exotic aquatic plants (ISSG, 2009).

Despite its history as a successful invasive species with severe economic impact (Joshi & Sebastian, 2006), only a handful of studies have quantitatively documented feeding trends, survival or growth of *P. canaliculata* on aquatic macrophytes (Carlsson & Lacoursière, 2005; Carlsson & Brönmark, 2006; Fang *et al.*, 2009; Qiu & Kwong, 2009). Early invasions that

establish reproducing populations of *P. insularum* also appear to have occurred under the radar of the ecological community. Recent spread, particularly into the Florida Everglades, has been accompanied by a small surge in papers on plant consumption by *P. insularum* (Boland *et al.*, 2008; Gettys *et al.*, 2008; Burlakova *et al.*, 2009; Baker, Zimmanck & Baker, 2010; Morrison & Hay, 2010). However, many of these studies have focused on the impact of the exotic snail on native plants.

Tropical and temperate South America, including Uruguay and southern Brazil, include the native range of both *P. insularum* and water hyacinth, *Eichhornia crassipes*. Water hyacinth is a formidable invasive species, forming dense mats that disrupt ecosystem function and cost millions of dollars to control worldwide (ISSG, 2009). Curiously, although many studies of apple snail herbivory include water hyacinth, no consistent consumption pattern has emerged from past investigations. For example, Lach *et al.* (2000) published one of the first studies that demonstrated that *P. canaliculata* failed to grow when restricted to its least preferred resource, water hyacinth. However, Fang *et al.* (2009) recently found that *P. canaliculata* successfully fed on the roots of water hyacinth in a field enclosure experiment, although they did not examine the impact on the snails.

While water hyacinth and apple snails coexist in their native environments, other invasive plants, such as wild taro (*Colocasia esculenta*) and Eurasian watermilfoil (*Myriophyllum spicatum*) have invaded wetlands across the Gulf Coast (Lester & Gonzalez, 2004) and commonly overlap with established exotic populations of *P. insularum* (Kyle, Kropf & Burks, 2011). Most studies have looked at consumption of individual species. For *P. canaliculata*, Qiu & Kwong (2009) found that snails fed watermilfoil or water hyacinth alone exhibited very low survivorship, grew only marginally and failed to reproduce. Snails fed wild taro exclusively also did not reproduce and ultimately died in the experiment (Qiu & Kwong, 2009). Given their different architecture (i.e. submerged, freely floating and emergent), these plants conceivably co-occur in systems with areas of open water surrounded by a riparian zone. However, no study has examined how apple snails respond when presented with milfoil, water hyacinth and taro simultaneously.

Many successful herbivore invaders manage to survive even when provided with plant resources considered less desirable, palatable or nutritious (Carlsson & Lacoursière, 2005). Consequently, the minimal nutrition supposedly offered by exotic or invasive plants may still play an important role in sustaining reproductive populations and promoting spread (Kwong *et al.*, 2009). Reproducing populations of *P. insularum* became established in Texas as early as 2000. However, it was not until 2008 that snails near the size assumed necessary for reproduction were found (Kyle *et al.*, 2009). We sought to discover if exotic juvenile *P. insularum* could survive and grow when fed only Eurasian watermilfoil, wild taro or water hyacinth, all plants exotic in North America.

MATERIAL AND METHODS

Study organisms

We selected juvenile *P. insularum* to investigate growth of smaller life stages as emphasized in previous studies of *Pomacea* (Carlsson & Brönmark, 2006). The term 'juvenile' requires explanation. No standardized size classes exist for this species. Because it best predicts both weight and shell height and can be easily and reliably measured (Youens & Burks, 2008), we measured operculum width of 48 laboratory-raised *P. insularum*. To test if snail growth differed between size classes, we measured snail size using a digital micrometer at the beginning of the experiment and every week for 6 weeks. We chose to use

operculum width (in mm; OW) because, with multiple investigators measuring the snails, it is most repeatable (Youens & Burks, 2008). To convert OW to snail mass (in g; *M*) and shell height (in mm; *H*), we used the equations $M = 5.372 \ln(\text{OW}) + 11.896$ ($R^2 = 0.978$) and $H = 0.834(\text{OW}) + 1.284$ ($R^2 = 0.967$), respectively (Youens & Burks, 2008). We used the natural logarithm relationship because it yielded the highest R^2 value over the size range (Youens & Burks, 2008). Mass was measured as blotted wet weights of snails, because we did not sacrifice individuals.

We categorized snails as early (10.7 ± 0.9 mm OW; mean \pm 1 SD) or late (23 ± 2 mm OW) juveniles, without distinguishing males from females. Our late-juvenile category exhibited a larger range in size (20.09–26.38 mm OW; 18.04–23.28 mm SH; 4.60–14.82 g *M*) than the early-juvenile group (8.78–12.45 mm OW; 8.61–11.67 mm SH; 0.56–1.11 g *M*). However, these classes differed significantly in initial size (Mann–Whitney *U*-test, $Z = -5.983$, $P < 0.001$). No snails deposited egg clutches during our study, indicating that they had not attained sexual maturity.

To investigate how *P. insularum* interacted with the three macrophytes, we offered each snail a choice of all plants (6 g taro, 20 g water hyacinth or 9 g Eurasian watermilfoil; blotted wet weight), in a design in which each plant occupied a separate compartment of similar volume. Macrophytes came from three different locations: water hyacinth from Hornsby Bend (Austin, TX, USA) and Armand Bayou (Clear Lake, TX, USA) and Eurasian watermilfoil from Emma Long Park (Austin, TX, USA). Taro was grown in the Southwestern University greenhouse at 25–29°C from commercial bulbs.

Enclosure design

We constructed 48 mesh-covered (1.6-mm mesh) enclosures (1 × w × h: 37.5 × 13 × 25.5 cm; total volume equal to 0.01 m³) from 2 × 2 cm untreated pine. With one juvenile *P. insularum* in each enclosure, the snail density was one per 487.5 cm² or about 20 snails per m² (this was twice the density of a similar design by Carlsson & Lacoursière, 2005). The cage design allowed snails to move freely, but kept plants separated. We divided each enclosure into three compartments of equal volume by adding mesh panels (13 × 20 cm); these extended vertically 2/3 of enclosure height at 8.5 cm from the bottom. Compartmental panels were sewn to the mesh sides of enclosures to prevent movement between compartments other than at the bottom. To allow easy exchange of organisms but prevent snail escape, large binder clips temporarily secured tops of each enclosure on three sides.

We placed 24 enclosures in each of two plastic inflatable pools (1 × w × h: 2.62 m × 1.60 m × 0.46 m) with *c.* 460 l of water at ambient temperature (27°C). We used two water pumps (1,000 l/h, Fluval 305 multi-stage filter) to maintain continuous water flow. To examine impact of a potential predator, our design exposed half of the single *P. insularum* juveniles to crayfish cues by adding 10 red swamp crayfish (*Procambarus clarkii*) to one pool. We exchanged each crayfish every 2 days.

Snail growth and survival

Before disturbing the snails each week, we recorded their position in the compartments to document habitat preference, and analysed these data using χ^2 tests. We then removed each enclosure to confirm snail viability, measured snail OW and collected the remains of each plant species. An immediate withdrawal of the snail's operculum indicated survival. We replaced fresh plant material in the enclosures before they were returned to the holding pools. We examined snail growth using repeated-measures analysis of variance (rmANOVA; SPSS 16.0).

Controls and wet to dry weight conversions

As controls for our experiment, we placed standardized non-rooted plant samples ($n = 12$) in enclosures without snails for 1 week before wet-weighing, drying and reweighing. This allowed us to determine natural plant loss and wet to dry mass conversions for each plant species. We measured only dry mass of the plants after exposure to snails, because of the high variation associated with wet-plant mass (Elger & Willby, 2003; Qiu & Kwong, 2009). Plant matter was dried in brown paper bags at 60°C for 48 h. Water hyacinth lost the most mass when dried (96%), followed by watermilfoil (91.1%) and wild taro (90.6%). We calculated average standard envelope mass after submersion in water and oven drying at 60°C for 24 h ($n = 15$; 1.307 ± 0.013 g). We then subtracted this value from the total dry mass of each sample, to determine dry mass of plant remains. Based on the large quantity of samples and limited time, we did not preweigh envelopes.

Plant consumption

We measured consumption of the three plant species each week. We did not employ repeated-measures analysis for plant

consumption because snails received fresh plant material each week. Because consumption trends remained consistent across analyses and weeks, we chose to present our results as grams of dry-plant mass consumed adjusted for wet (i.e. blotted-dry) snail mass (g plant/g snail/day) (as done by Burlakova *et al.*, 2009; Qiu & Kwong, 2009). To calculate daily consumption rates, we divided average weekly consumption by 7 and used *t*-tests to examine differences in consumption between early and late juveniles. Snail mass measurements were log-transformed and daily consumption rates square-root transformed to meet normality criteria. We achieved normality for all dependent variables except watermilfoil consumption and snail mass at week 3 ($\chi = 1.443$ and 1.405, $P = 0.031$ and 0.039, respectively). However, we proceeded with the parametric analysis because of the robustness of this test to nonnormally distributed data (Zar, 1999).

RESULTS

Snail growth and survival

Throughout the 6-week study, presence of crayfish produced few detectable influences on the six response variables tested

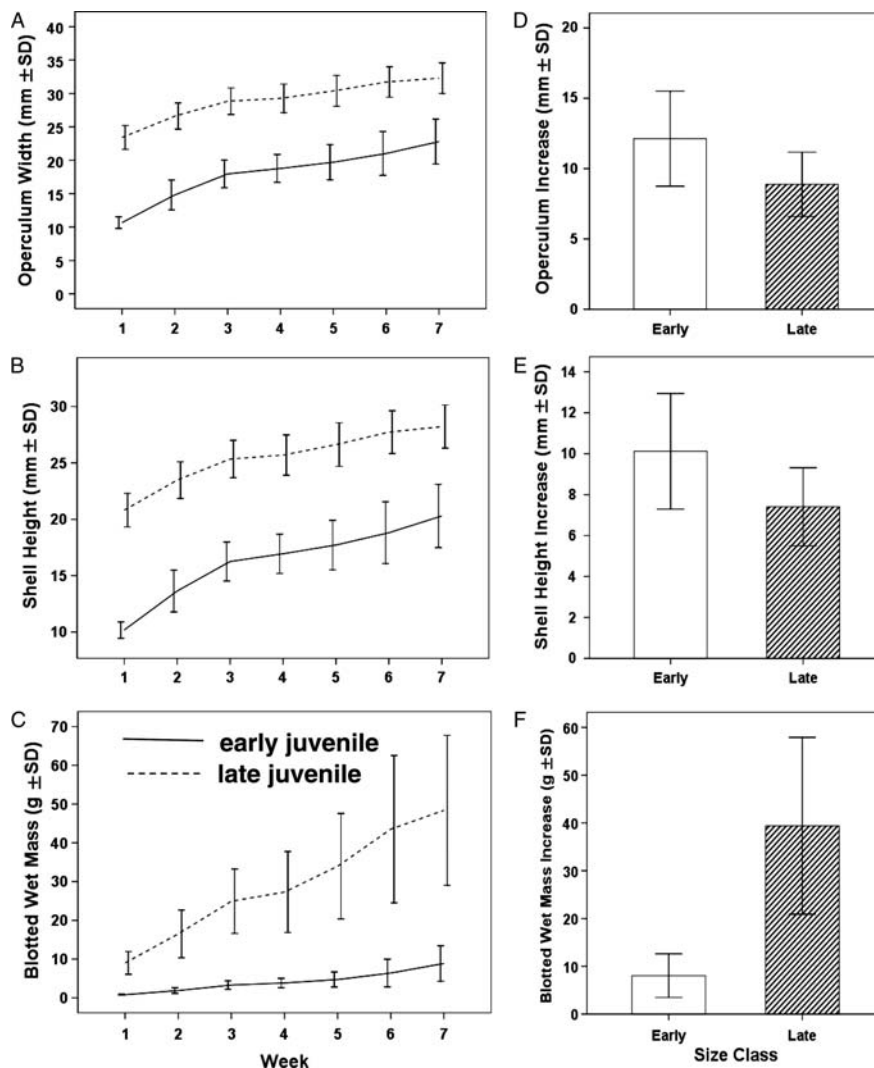


Figure 1. The left column of graphs show mean growth of early juvenile (solid lines) and late juvenile (dotted lines) *Pomacea insularum* over the course of 6 weeks, as measured by operculum width (A), shell height (B) and blotted wet mass (C). The right column of graphs show total change in operculum width (D), shell height (E) and blotted wet mass (F) over 6 weeks for early juveniles (open bars) and late juveniles (shaded bars). All error bars are ± 1 SD.

Table 1. Overall rmANOVA results for snail growth of two size classes (early and late) over time (i.e. 6 weeks).

	Operculum width (mm)			Shell height (mm)			Mass (g)		
	F	Df	P	F	df	P	F	df	P
Week	105.277	(6, 41)	<0.001	105.277	(6, 41)	<0.001	29.430	(6, 41)	<0.001
Size	10,114.451	(1, 46)	<0.001	399.989	(1, 46)	<0.001	142.505	(1, 46)	<0.001
Week × size	3.715	(6, 41)	0.005	3.715	(6, 41)	0.005	13.326	(6, 41)	<0.001

Three dependent variables were operculum width (mm), shell height (mm) or mass (g). We specified main effect and error degrees of freedom (df).

each week (i.e. habitat choice, snail growth rate, consumption rates of milfoil, taro, water hyacinth and all plants combined). The three exceptions were early juveniles consuming more *Myriophyllum* in Weeks 2 and 6, and an overall average in the presence of crayfish ($P = 0.015$, <0.001 and <0.018 , respectively). Owing to an absence of a consistent effect of crayfish, we pooled our results and only compared consumption of macrophytes between snail size classes.

Feeding on only three invasive plants, snails of both size classes grew significantly in terms of operculum width (Fig. 1A), shell height (Fig. 1B) and blotted wet weight (Fig. 1C) over the 6-week period (Table 1; Fig. 1). For both size classes, operculum width and shell height increased most in the first 2 weeks and then increased gradually throughout the remaining 4 weeks (Fig. 1A and B). On average, early juvenile snails approximately doubled their operculum widths and shell heights over the 6-week period. This significantly exceeded the growth exhibited by late juvenile snails (Fig. 1D and E), which only increased operculum widths and shell heights by a factor of 1.4 (t -test, $t_{1, 46} = 3.891$, $P < 0.001$). Changes in mass showed different patterns between size classes; late juvenile snails gained mass at a faster rate (Fig. 1C) and exhibited a significantly greater overall weight gain (Fig. 1F; t -test, $t_{1, 26} = -8.060$, $P < 0.001$).

Consumption of three invasive macrophytes

Early juvenile snails consumed significantly more plant matter per gram of snail per day of all three plants (Fig. 2A–C; $t_{46} = 18.00$, $t_{27} = 10.354$ and $t_{29.5} = 8.009$, respectively, for watermilfoil, taro and hyacinth; P -values all <0.001). Collectively, average weekly per cent consumption of watermilfoil by all snails was 71% (± 13), followed by taro at 62% (± 21) and water hyacinth at only 25% (± 9.5). No mortality occurred in our experiment. Snails showed consistent activity in all compartments (active exploration, siphon extension, feeding), maintained their dark colouring and added shell material week to week. Both early and late juveniles exhibited similar trends in compartment choice (χ^2 contingency table, $\chi^2_2 < 0.001$, $P = 1.00$). Forty per cent of our observations showed snails in the taro compartment, followed by 31% for milfoil and 28% for water hyacinth, but these were not statistically different ($\chi^2_2 = 5.725$, $P = 0.057$).

Both early and late juveniles consumed higher amounts of watermilfoil (Fig. 2A; for early juveniles, $c.$ 0.02 g plant/g snail/day) than the other two plants. Snails within both of these size classes consumed $c.$ 50% less wild taro (Fig. 2B; 0.01 g plant/g snail/day) and 75% less water hyacinth (Fig. 2C; only 0.005 g plant/g snail/day) than watermilfoil. Collectively, these results translate into one single 10-g *Pomacea insularum* (e.g. representative of the larger snails used in our experiment), consuming a combined 0.35 g of dried plant matter per day. Given that aquatic plants frequently lose at least 90% of their mass when dried, such a juvenile snail would remove $c.$ 3.5 g of live macrophytes daily.

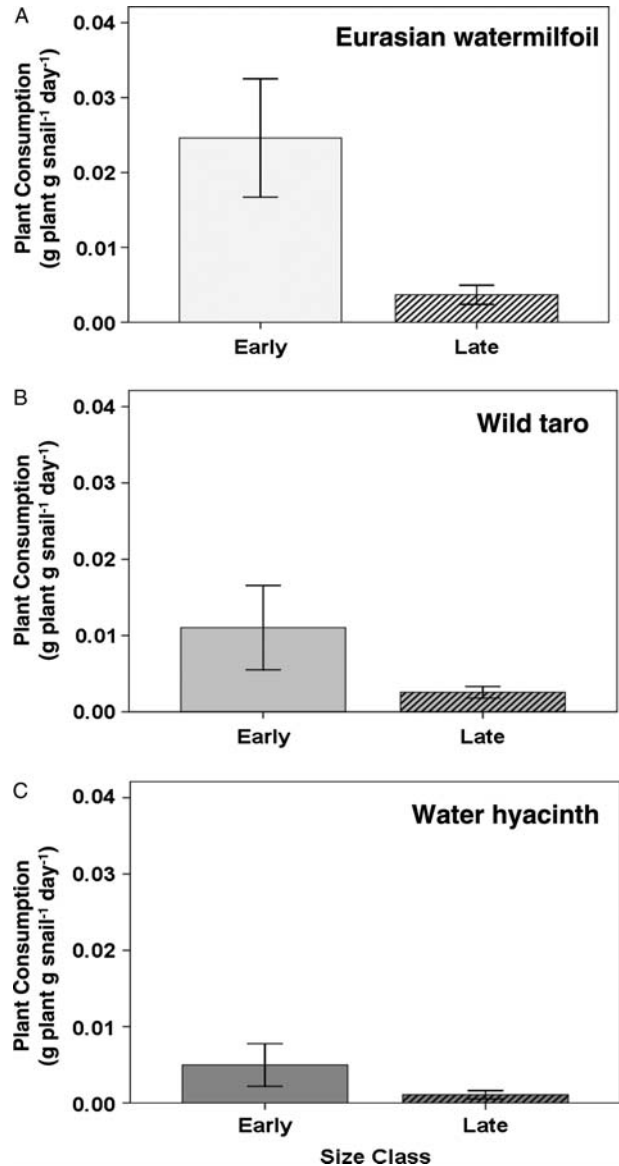


Figure 2. Average daily consumption of three exotic plants Eurasian watermilfoil (A), wild taro (B) and water hyacinth (C) by early juvenile (open bars) or late juvenile (shaded bars) *Pomacea insularum*. Snails had simultaneous access to all three plant resources. Values are per capita consumption expressed as dry weight (g) of plant resource consumed per blotted wet weight of snail per day. Error bars are ± 1 SD.

DISCUSSION

Our study revealed that *Pomacea insularum* juveniles survived and grew on subpar resources when offered in conjunction. We

define these resources as subpar because a recent analysis revealed that wild taro, water hyacinth and *Myriophyllum aquaticum* (a close relative of Eurasian watermilfoil) all contained markedly lower amounts of sodium, nitrogen and phosphorus than most other plant species tested (Qiu & Kwong, 2009). These plant species also possess physical or chemical defences (Sunell & Healy, 1985; Burks *et al.*, 2006) likely to deter herbivory. We observed a significant effect of age as early juveniles increased their shell size substantially more than late juveniles, although the latter added more mass. Our study failed to record any extreme costs of consumption of subpar resources such as mortality or absence of growth.

Our results of 100% juvenile survival and notable growth contrast dramatically with other studies performed with the same plants presented alone to less mature snails (i.e. hatchlings or neonates). In laboratory experiments lasting 8 weeks, an exclusive (nonchoice) diet of any one of the three plants species we used failed adequately to support growth, survival or reproduction of neonate golden apple snails (*P. canaliculata*) (Lach *et al.*, 2001; Qiu & Kwong, 2009). Regardless of snail species, neonates may not be able to tolerate plant defences as well as larger snails. We speculate that the provision of multiple exotic plants in our experiment improved survival. In 24-h nonchoice feeding experiments with similar-sized *P. insularum* (15–30 mm SH compared with 18–23 mm in this study), Baker *et al.* (2010) reported a low feeding rate (0.053 g/g/day) on water hyacinth and a complete lack of taro consumption. When Qiu & Kwong (2009) fed hatchling *P. canaliculata* only taro, they grew poorly, failed to reproduce and ultimately died. Our observations of *P. insularum* interactions with taro suggest a different outcome. Based on our results, a 50-g (i.e. medium-sized) *P. insularum* could consume 0.5 g of dried taro or nearly 4.5 g of live plants per day. This result is surprising as we rarely see evidence of extensive leaf damage on taro in the field.

Preferential consumption may be affected by plant choice and snail species. Comparison of preferences in feeding studies can be difficult because of the different approaches or species used. When we offered snails a simultaneous choice of three macrophytes, we saw the most frequent rejection (0% consumption) of water hyacinth. In contrast, Carlsson & Lacoursière (2005) actually found a complete loss of water hyacinth from field enclosures with *P. canaliculata*. However, this loss took 21 days. Consequently, time-dependent, size-specific interactions between plant defences and apple-snail survival warrant further investigation.

Our study demonstrated that early *P. insularum* juveniles consumed more plant material per gram body mass than their older counterparts and that all juveniles survived when fed only invasive exotic plants. In agreement with Carlsson & Brönmark (2006), we found no evidence of ontogenetic diet shifts over the size range we used. Regardless of age or growth rate, all juvenile apple snails showed preferential choice. Early and late snails combined consumed c. 60–70% of the watermilfoil and taro offered, but only 25% of the water hyacinth.

While snails may choose more palatable plants when available in the field, the presence of these exotic species could sustain populations in areas that lack more preferred resources. Field studies need to be performed to test this prediction. Overall, the ability of juvenile *P. insularum* to grow quickly on subpar food resources does not bode well for controlling population growth. Unlike most aquatic snails, apple snails are not primarily algal grazers, but instead have quite the appetite for a range of aquatic macrophytes. Based on our results, any warm, freshwater system containing *C. esculenta*, *E. crassipes* and *M. spicatum* could support a vigorous *P. insularum* population. Consequently, aquatic systems already invaded by exotic

plants may serve as a holding reservoir for developing snails, from which further spread may occur.

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