Foreign relations: Exotic, invasive applesnails substantially consume taro and other exotic plants

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Foreign relations:
Exotic, invasive applesnails substantially consume taro and other exotic plants

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Abstract:

Plants and invertebrates hold notorious reputations as pests and problematic exotics that quickly spread and become exotic invasive species (EIS). *Colocasia esculenta* [taro], *Eichhornia crassipes* [water hyacinth] and *Myriophyllum spicatum* [Eurasian water milfoil] represent successful EIS aquatic macrophytes that exhibit multiple defenses. Highly fecund and native to South America, *Pomacea insularum*, a channeled applesnail, epitomizes a problematic EIS. To investigate interactions between these EIS, we placed a single early (10-mm) or late (23-mm) juvenile applesnail in enclosures located in pools with or without crayfish (*Procambarus clarkii*) (N=12). Each enclosure held EIS macrophytes in separate compartments. We observed snail growth (as change in operculum or mass), percent plant consumption and habitat preferences over six weeks. Early juvenile snails grew significantly more than late. Presence of *P. clarkii* did not alter snail growth, plant consumption or behavior. Changes in snail mass versus operculum yielded different interpretations. Across all plant species, smaller juveniles consumed more matter per gram than larger snails. Our results suggest juvenile applesnails prefer less defended plants and do not alter plant consumption when predators occur. These results suggest the potential for exotic aquatic macrophytes to facilitate further invasion of *P. insularum* throughout the southeastern United States.

Keywords: *Pomacea insularum*, *Colocasia esculenta*, elephant ear, aquatic macrophytes, mollusks, herbivory, invasion meltdown, *Pomacea canaliculata*, crayfish
Introduction:

Wetland ecosystems provide a myriad of ecosystem services and habitat for both terrestrial and aquatic species. Despite these known attributes, we continue to lose wetland habitat through degradation (Dahl 2006), partly due to introductions of exotic invasive species (EIS) (Maki and Galatowitsch 2004). Simberloff (2006) laments that few studies investigate mechanisms underlying “invasional meltdowns” (sensu Simberloff and Von Holle 1999) or how interactions between EIS may facilitate invasion. Ecosystem shifts caused by macrophyte loss from herbivores (Carlsson et al. 2004a) suggests that both plant and invertebrate EIS in wetlands can increase water turbidity through competition and grazing (Maki and Galatowitsch 2004).

For example, duckweed (Lemna minor) and water hyacinth (Eichhornia crassipes) grow rapidly, overtaking native floating plants and blocking sunlight from penetrating to the bottom of freshwater systems (Holm et al. 1977). This causes further loss in submergent plants, which play critical roles in the structure and function of lake ecosystems (Jeppesen et al. 1997, Burks et al. 2006). This loss leads to severe reductions in species diversity in wetlands and increased turbidity of the ecosystem (Carlsson et al. 2004a). Such macrophyte losses may coincide with the addition of exotic macroinvertebrate species. For example, an introduction of the omnivorous crayfish Procambarus clarkii reduced macrophyte cover from 97% to less than 10% in a Spanish lake (Rodriguez et al. 1993). Furthermore, omnivores like crayfish that consume key herbivores (e.g. aquatic snails, Correia et al. 2005) may have indirect effects on plant consumption by herbivores (Carlsson et al. 2004b, Carlsson and Brönmark 2006).

Estimates place approximately 145 EIS vascular aquatic plants in Texas alone (Gossett et al. 2004), with many flourishing in wetlands throughout the southeastern United States (Fox et al. 2008). Three note-worthy aquatic plant EIS include taro (Colocasia esculenta), water
hyacinth (*Eichhornia crassipes*) and Eurasian water milfoil (*Myriophyllum spicatum*). These EIS inhabit different areas of the water column and present a range of chemical and structural defenses toward herbivores (Burks et al. 2006). Taro, a native to Hawaii and perennial emergent aquatic species, frequently occurs in southern Atlantic and Gulf Coast states (Moore and Lawrence 2003). Water hyacinth, a freely floating perennial aquatic species indigenous to Venezuela, reproduces rapidly from stolons (Madsen 2004) and occurs in California and throughout southern Atlantic and Gulf Coast states. Eurasian milfoil, an evergreen perennial submersed aquatic plant native of Europe and Asia, occurs across the U.S. (Madsen 2004). Taro exhibits little chemical defenses, although it possesses some structural defenses in the form of calcium oxalate crystals that can irritate herbivore epithelial cells (Sunell and Healy 1985). With well-established structural (Casco et al. 2003, Boland et al. 2008) and chemical defenses, herbivores often minimally consume water hyacinth (Holm et al. 1977, Lach et al. 2000). Without a structural defense, Eurasian milfoil defends itself chemically (Gross 2003, Burks et al. 2006, Boland et al. 2008).

Wetlands often contain mixtures of native and EIS invertebrate herbivores. Infamous as one of the 100 most harmful global invasive species (Lowe et al. 2004), the golden or channeled applesnail (GAS, CAS or *Pomacea canaliculata*) now serves as a particular pest in Asian rice fields (Joshi and Sebastian 2006). However, phylogenetic testing of mtDNA showed channeled applesnails actually comprise two separate species – *P. canaliculata* and *P. insularum* (Rawlings et al. 2007). Because high fecundity serves as the best indicator for invasive potential in mollusks (Keller et al. 2007), *P. insularum* may pose a greater EIS threat than *P. canaliculata* because it possesses a longer reproductive season and greater amounts (up to 10x) of eggs per clutch (Cowie et al. 2006, Barnes et al. 2008). Indigenous to Argentina and Brazil, and perhaps
Uruguay, *P. insularum* became established in the U.S. in Texas, Georgia and Florida likely through multiple introductions (Rawlings et al. 2007, Hayes et al. 2008). The potential exists for *P. insularum* to spread throughout the southern U.S. because of their indiscriminate aquatic macrophyte feeding practices. Although, to date, the economic costs of applesnails to rice have not materialized, large reproductive populations of *P. insularum* exist in the bayous around Houston, TX (Harris, Brazoria, Galveston, Waller, Fort Bend and Chambers Counties) (Joshi and Sebastian 2006, Rawlings et al. 2007). Taro, water hyacinth and Eurasian milfoil also occur in sizable populations in these areas (Gossett et al. 2004) and interactions between these species and *P. insularum* could lend understanding to interactions amongst exotic species.

To first explore mechanisms behind a potential invasional meltdown, we examined the extent to which two sizes of juvenile *P. insularum* applesnails consumed exotic macrophytes and whether such consumption differentially impacted behavior and growth of the snails in the presence and absence of a predator. We thought snails would prefer taro as habitat over water hyacinth and Eurasian milfoil because capture of adult *P. insularum* in the field frequently occurs at the base of taro plants (Boland et al. 2008) and water hyacinth contains more physical defenses than milfoil. We also hypothesized that snails would consume more taro than Eurasian milfoil or water hyacinth due to structural and chemical defenses exhibited by those plants (Gross 2003, Burks et al. 2006). Previous experiments by Carlsson and Brönmark (2006) led us to predict that early juvenile applesnails would consume more than older individuals. No literature exists on response of *P. insularum* to predator cues, although we predicted that snails would reduce their feeding in the presence of crayfish (Alexander and Covich 1991). Collectively, our work sought to understand the potential for exotic aquatic macrophytes to facilitate further invasion of *P. insularum* throughout the southeastern United States.
Materials and Methods:

To expose *P. insularum* to cues but prevent predation by crayfish, we constructed 48, mesh-covered (0.025 cm² opening) enclosures from 2 cm thick untreated pine board (external enclosure dimensions 13 cm x 25.5 cm x 37.5 cm) based upon a field design used by Carlsson and Lacoursière (2005). We separated enclosures into three equal volume compartments by adding mesh panels (13 cm x 20 cm; l x w) and secured the mesh flush to the wood with staples and sewed compartmental segments to the mesh sides of enclosures. The panels extended 2/3 of enclosure height (8.5 cm from bottom). This construction allowed snails to move freely but kept plants separated. Tops of each enclosure remained unsecured on three sides to allow easy exchange of organisms. We closed all containers using two 5 cm length binder clips.

To create “predator-cued” versus “predator-free” environments, we filled and maintained two plastic inflatable pools (2.62 m x 1.60 m x 0.46 m; l x w x h) with approximately 460 L of water. One pool contained 10 *P. clarkii* obtained from local groceries (HEB) while the other pool lacked *P. clarkii*. We placed two water pumps (1000 L/h, Fluval 305 multi-stage filter) in each pool and circulated water for 24 hours. Every two days during data collection, we exchanged our 10 *P. clarkii* from the crayfish pool to a feeding tank (Figure 1).

Because it best predicts weight and shell height (Youens and Burks 2008), we used operculum width (mm) measurements of 48 laboratory-raised juvenile *P. insularum* to categorize them as early (10.7 ± .9 mm; mean ± 1 SD) or late (23 ± 2 mm). For initial placement, we standardized operculum width of early versus late juveniles across pools (with and without *P. clarkii*) using ANOVA (F₁,ₓ = 0.120, *P* = 0.733). Each enclosure housed one snail, which we gave one week to acclimate to experimental conditions before six weeks of data collection.
began. We measured operculum width, snail position and added and removed plant mass weekly and also rotated placement of enclosures in pools to ensure water flow did not affect the results. To investigate how *P. insularum* interacted with exotic macrophytes, we offered each snail three plant choices. Each compartment offered different plant species with specific initial wet weights (6 g taro, 20 g water hyacinth or 9 g Eurasian water milfoil). We replaced plant matter weekly. We obtained water hyacinth from Hornsby Bend (Austin, TX) and Armand Bayou (Clear Lake, TX; Harris County) and Eurasian milfoil from Emma Long Park (Austin, TX). We grew taro in a greenhouse at 78-84°F from locally-obtained bulbs obtained. After each week, we placed all recoverable plant matter by species into individual brown paper bags.

To convert recovered wet plant material to dry plant mass, we dried bags using a 60°C oven for 24-48 hours and recorded dry mass of each plant. Due to the small size of Eurasian milfoil, we dried each sample in a small envelope for weeks 3-6. To account for the envelope’s dry weight, we submerged 15 envelopes in tap water for 10 minutes, and then dried them at 60°C for 24 hrs. We calculated average standard envelope mass and subtracted this value from the end mass of each sample for weeks 3-6. Using the enclosures without snails, we determined natural plant loss and wet to dry mass conversions for each plant species. After one week, we dried plants as before and ran all data analysis with plant dry mass.

To assess habitat choice of snails, we recorded compartmental position of each snail weekly and analyzed these data using a Chi-square test (SPSS 13.0). We ran separate Chi-square tests to ensure that snail size and crayfish presence did not significantly affect habitat choice. Percent consumption of each plant species depended on a function of the total amount of that species’ dry mass consumed divided by the total dry amount of that plant species offered. For total consumption, we combined the consumed plant matter and offered plant matter per snail
and performed the same calculation. Due to extrapolation, some consumption values exceeded 100% and we considered these as 100% for analysis. For each plant species and total plant consumption, we conducted two-way ANOVAs (factors equal snail size and crayfish presence) on three sets of calculations using percent consumption (regardless of snail size, per snail mass (g), and per snail operculum (mm)). We based calculations of snail mass on the equation $y = 5.372 \ln(x) + 11.896$, where $x$ is mass and $y$ is operculum width (Youens & Burks 2008).

Finally, we tested whether snail size or crayfish cue presence affected snail growth (weekly changes in operculum width) using a repeated measures two-way ANOVA (SAS, V. 8.0).

**Results:**

Overall, applesnails tended to prefer taro ($X^2 = 5.725, P = 0.057$) compared to water hyacinth and milfoil. Neither crayfish cue presence ($X^2 = 0.840, P = 0.359$) nor snail size category ($X^2 = 0.804, P = 0.062$) showed any effect on snail habitat choice. Unadjusted for snail size, late juveniles consumed significantly more total macrophytes than early ones, although crayfish presence had no effect (Table 1, Figure 2A). With respect to plant species, late juveniles also consumed more Eurasian milfoil, taro and water hyacinth than early snails when unadjusted for size effects (Table 1, Figure 2B-D). Only for Eurasian milfoil did snails consume more in the presence of crayfish cue than in its absence (Table 1, Figure 2B).

Adjusted for snail operculum size (mm), snail size no longer affected the percentage of all plants consumed (Table 1, Figure 3A-D). When measuring consumption per mm in operculum width, snails significantly consumed more total plant matter, driven by their consumption of water milfoil, in the presence of crayfish cue versus its absence (Table 1, Figure 3A-B). Again considering operculum width, both snail size and the presence of crayfish showed no significant effect on either taro or water hyacinth consumption (Table 1, Figure 3C-D).
When we adjusted plant consumption for snail mass (g), consumption still depended upon size (Table 1, Figure 4A-D). Early juveniles consumed more plant matter per gram of body mass than late juveniles and the presence of crayfish showed no effects (Table 1, Figure 4A-D). Consumption trends by both size classes remained consistent when we broke down consumption by week (data not shown).

Snail size independently influenced applesnail growth ($F = 5.78$, df = 1, $p > 0.0209$; Figure 5) as early juveniles grew more than late. As expected, snails grew significantly over time ($F = 9.49$, df = 5, $p < 0.001$). Although crayfish did not clearly influence snail behavior, consumption or growth (insert p), inconsistencies in growth between treatments during weeks 2, 5 and 6 resulted in an unexpected significant interaction between time, crayfish and snail size ($F = 4.05$, df = 5, $p > 0.0052$).

**Discussion:**

For both size classes, we found substantial consumption of three exotic plant species by *P. insularum*. Juveniles consumed between 80 and 100% of the amount of taro and water milfoil offered. Although noticeably less consumption occurred for water hyacinth, *P. insularum* juveniles still removed between 40 and 60% of hyacinth biomass offered. Our study offers the first quantification of the amount of exotic plants that exotic *P. insularum* individuals are capable of consuming. In addition, our study demonstrated a close habitat association between two invasives, taro and *P. insularum*. Furthermore, adult *P. insularum* seem to preferentially lay their eggs on taro stalks in the field and laboratory (Kyle and McDonough, unpublished data).

Collectively, these interactions suggest that taro may facilitate *P. insularum* invasion. In addition, availability of other exotic macrophytes does provide potentially important food
sources for the invasive snail. Identifying habitats where these plants dominate may indicate areas prone to future invasion.

Combined with field position observations, the consumption of taro by *P. insularum* and its habitat choice provides a potential example of invasional meltdown. Because our “snapshot” approach to snail behavior (i.e. weekly habitat choice; N = 6 observations) yielded a clear result, we feel that this supports our hypothesis that snails prefer taro. Most often, capture of adult *P. insularum* occurs at the base of taro plants in the Houston region (Boland et al. 2008). However, taro does not occur in the native range of *P. insularum* (Moore and Lawrence 2003, Rawlings et al. 2007). Possibly, the relationship revealed in our experiments exists because taro did not evolve to prevent consumption by such a major aquatic herbivore as *P. insularum*. However, from the standpoint of the snail, the structure of taro may provide shelter from predators as well as a reliable oviposition site. In contrast, native ranges of water hyacinth and *P. insularum* overlap (Burks et al. 2006, Rawlings et al. 2007). In contrast to taro, water hyacinth populations may have evolved strong physical and chemical defenses to deter consumption by *P. insularum* as well as *P. canaliculata*. Thus, differential resource consumption by exotic snails may depend on prior interactions, or the lack thereof, within native habitats.

In natural field conditions where applesnails occur, crayfish may indirectly alter macrophyte consumption by one of three mechanisms: 1) consuming applesnails and freeing the macrophyte from snail herbivory; 2) directly consuming the plant; or 3) altering the consumption behavior of applesnails via predator avoidance. We did not see many consistent impacts of crayfish presence on macrophyte consumption, snail behavior or growth. Crayfish cue presence only affected Eurasian milfoil consumption, possibly because Eurasian milfoil is a submergent, therefore rooted in benthic areas which crayfish inhabit. Yusa et al. (2006) showed *P. clarkii*
consumed *P. canaliculata* less than 16 mm in shell height. However, no comparable data exists for *P. insularum*. Some prey species fail to respond to non-natural predators (Shave et al. 1994), possibly explaining the absence of combined effects of crayfish cue upon macrophyte consumption in our experiments. Vulnerable size-classes of *P. canaliculata* have reacted based on chemical cues from injured conspecifics or predator presence (Ichinose 2002). In our study, our snails likely surpassed the vulnerability stage to crayfish and crayfish did not have direct access to either snails or macrophytes. Overall, our results with *P. insularum* agree with Carlsson et al. (2004b) which found *P. canaliculata* fed substantially despite predator presence.

Overall, our findings suggest many parallel feeding trends between *P. insularum* and *P. canaliculata*. Our experiments with *P. insularum* concur with a study by Carlsson et al. (2004a) that showed *P. canaliculata* consume substantial amounts of macrophytes regardless of size. Carlsson and Brönmark (2006) later demonstrated that smaller *P. canaliculata* consumed more per capita, which also happens with *P. insularum*. In addition, we found lower consumption of water hyacinth than either taro or Eurasian milfoil. Correspondingly, with *P. canaliculata*, Carlsson and Lacoursière (2005) found lower water hyacinth consumption than other plant species offered. Boland et al. (2008) also found preferences for Eurasian milfoil consumption over water hyacinth by both *P. insularum* and *P. canaliculata*. Too many disturbing similarities exist between our recently invasive snail, *P. insularum*, and its highly invasive relative *P. canaliculata*, suggesting that *P. insularum* possesses comparable potential for detrimental economic and ecological impacts (Joshi and Sebastian 2006, Rawlings et al. 2007).

Our investigations regarding plant consumption by *P. insularum* suggest that ecologists must consider what they are measuring to adequately assess impact. In the case of *P. insularum*, as with other species of applesnails, a linear relationship exists between the mass of the snail and
its operculum width when it is a hatchling, but this relationship deteriorates as it ages (Youens & Burks 2008). *P. insularum* operculum width changes less in later life stages as more mass is added, a possible function of the way snails grow (Youens & Burks 2008). This could explain the disappearance of the significant effect of snail size when considering consumption rates by operculum changes. We think that significant effects occurred when we adjusted consumption by snail mass because snail size correlates more accurately with mass (Youens & Burks 2008). However, the data unadjusted for snail size suggest that late juvenile snails do more physical plant damage than early juvenile snails simply because they are larger. Although some weeks showed inconsistent combined consumption per plant species, consistent relationships existed between factors affecting plant consumption per week and by combining weeks. We believe that our 6-week study adequately described trends in plant consumption.

Due to their rapid growth and high consumption rates of plant matter with small effects of predator cue upon macrophyte consumption rates, *P. insularum* possesses great potential to damage existing wetland habitats. Although we restricted our study to the lab due to the invasive nature of the snails, our results likely reflect occurrences in the field. *Pomacea insularum* consumption of exotic aquatic macrophytes provides new insight to invasive exotic species interactions as suggested by Simberloff (2006). Although more work is needed to fully demonstrate an invasional meltdown in this system, our results warn that such a phenomenon remains possible. In management terms, removal of invasive taro from exotic habitats may cause a subsequent decline in *P. insularum* populations. Without taking such interactions between exotic species into account, researchers may overlook key steps in controlling major agricultural and economic pests.
Acknowledgements:

We’d like to thank Ken Strickland for constructing mesocosms and providing advice, Roshni Ghandi for aiding in experimental execution and the Department of Biology at Southwestern University for funding and use of their facilities.

Literature cited:


Table 1: Summary of significant factors affecting consumption of plant species across data unadjusted for snail size and adjusted for operculum width (mm) and mass (g). C = crayfish cue presence, S = snail size category and I = crayfish by size interaction. N.S. = non-significant. Greater impact column notes which treatment consumed more plant matter.

<table>
<thead>
<tr>
<th>Plant Factor</th>
<th>Plant</th>
<th>Unadjusted % Plant consumption</th>
<th>% Plant consumption / operculum width (mm)</th>
<th>% Plant consumption / snail mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>p-value</td>
<td>Greater Impact</td>
</tr>
<tr>
<td>Eurasian milfoil</td>
<td>C</td>
<td>20.093</td>
<td>0.001</td>
<td>In presence</td>
</tr>
<tr>
<td>S</td>
<td></td>
<td>10.095</td>
<td>0.003</td>
<td>Late juvenile</td>
</tr>
<tr>
<td>I</td>
<td></td>
<td>1.146</td>
<td>0.290</td>
<td>N.S.</td>
</tr>
<tr>
<td>Taro</td>
<td>C</td>
<td>0.211</td>
<td>0.649</td>
<td>N.S.</td>
</tr>
<tr>
<td>S</td>
<td></td>
<td>46.471</td>
<td>0.001</td>
<td>Late juvenile</td>
</tr>
<tr>
<td>I</td>
<td></td>
<td>0.307</td>
<td>0.583</td>
<td>N.S.</td>
</tr>
<tr>
<td>Water hyacinth</td>
<td>C</td>
<td>1.042</td>
<td>0.313</td>
<td>N.S.</td>
</tr>
<tr>
<td>S</td>
<td></td>
<td>12.534</td>
<td>0.001</td>
<td>Late juvenile</td>
</tr>
<tr>
<td>I</td>
<td></td>
<td>0.615</td>
<td>0.437</td>
<td>N.S.</td>
</tr>
<tr>
<td>Overall</td>
<td>C</td>
<td>2.143</td>
<td>0.150</td>
<td>N.S.</td>
</tr>
<tr>
<td>S</td>
<td></td>
<td>69.820</td>
<td>0.001</td>
<td>Late juvenile</td>
</tr>
<tr>
<td>I</td>
<td></td>
<td>0.182</td>
<td>0.672</td>
<td>N.S.</td>
</tr>
</tbody>
</table>
**Figure 1:** Elements of experimental design including two pools, one with crayfish and one without, that each housed 24 enclosures. Each enclosure contained a compartment for each of the three plant species. This figure shows remaining plant matter after one week.

**Figure 2:** Combined percent plant consumption for Eurasian milfoil, taro, water hyacinth and total plant species unadjusted for snail size. A) Eurasian milfoil; B) Taro; C) Water hyacinth; and D) Total plant consumption. Average consumption of Eurasian milfoil relative to the initial amount offered (85 ± 20 %, mean ± SD), taro (86 ± 14%), water hyacinth (54 ± 16 %).

**Figure 3:** Combined percent plant consumption for Eurasian milfoil, taro, water hyacinth and total plant species adjusted for operculum width (mm). Panels reflect same order as Figure 2. Consumption appears relative to plant offered.

**Figure 4:** Combined percent plant consumption for Eurasian milfoil, taro, water hyacinth and total plant species adjusted for mass (g). Panels reflect same order as Figure 2. Consumption appears relative to plant offered.

**Figure 5:** Additive growth (mm/wk) of late and early juvenile snails as a function of treatment type over six weeks. Arranged by average growth per treatment per week. Early juvenile snails grew more than late, all *P. insularum* grew over time.
Figure 1:

Snails:
12: Early (10-11mm)
12: Late (24-25mm)

+ 0 Crayfish

+ 10 Crayfish

Submerged
Water milfoil
Myriophyllum spicatum

Emergent
Taro
Colocasia esculenta

Water hyacinth
Eichhornia crassipes
Figure 2:

A) Combined percent eurasian milfoil consumption unadjusted for small size

B) Combined percent taro consumption unadjusted for small size

C) Combined percent water hyacinth consumption unadjusted by small size

D) Combined total plant consumption unadjusted for small size
Figure 3:

A) Combined eurasian milfoil consumption adjusted for snail operculum width (mm)

B) Combined taro consumption adjusted for snail operculum width (mm)

C) Combined water hyacinth consumption adjusted for snail operculum width (mm)

D) Combined total plant consumption adjusted for snail operculum width (mm)
Figure 4:

A) Combined eurasian milfoil consumption adjusted for snail mass (g)

B) Combined taro consumption adjusted for snail mass (g)

C) Combined water hyacinth consumption adjusted for snail mass (g)

D) Combined total plant consumption adjusted for snail mass (g)
Figure 5:

Additive growth (mm/wk) of late and early juvenile snails as a function of treatment type over six weeks

- **size**: $F = 5.78$, $p > 0.0209$
- **time**: $F = 9.49$, $p < 0.001$
- **time*cray*size**: $F = 4.05$, $p > 0.0052$