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EFFECT OF PLANT DIET VARIATION AND COMPETITION ON THE FECUNDITY OF TWO CO-OCCURRING SNAILS: A COMPETITIVE QUEST

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Abstract. The invasion success of non-native species depends on their life-history traits and the abiotic and biotic barriers of the recipient ecosystems. Among the biotic factors, competition with native species may restrict the invasion potential of non-native species. Additionally, the presence of macrophytes in freshwater ecosystems may provide food resources that are known to influence the life-history traits of freshwater snails. In this study, we focused on an invasive snail *Physella acuta* and a co-occurring native snail *Racesina luteola* to explore the effect of different plant (garden lettuce, water lettuce, duckweed and eelgrass) diets on their fecundity in intra- and interspecific competitive scenarios. Being a successful invader worldwide, *P. acuta* has demonstrated competitive advantages over co-occurring snails in various regions. The results of this study imply that *P. acuta* laid a significantly higher number of eggs per individual than *R. luteola* under both intra- and interspecific competition and plant diets. Hence, the resource utilization ability of *P. acuta*, even with less productive plant diets (e.g., water lettuce and eelgrass), may potentially lead to the competitive displacement of the native snail *R. luteola*.

INTRODUCTION

Predictive observations regarding the aftermath of non-native species introduction are becoming pivotal as biological invasions represent a significant threat to global biodiversity (Sala et al. 2000; Simberloff et al. 2013). Non-native species establish beyond their native regions through several natural and anthropogenic modes of introduction by overcoming the constraints of the recipient ecosystem (e.g., resource availability, the competitive ability of native neighbours, and the frequency and scale of disturbances in the recipient ecosystems) (Davis et al. 2000; Cowie and Robinson 2003; Blumenthal 2006; Hulme et al. 2008; Blackburn et al. 2011; Banha et al. 2014) and their suitable life-history characteristics (e.g., rapid growth rate, superior reproductive potential), high dispersal ability, phenotypic plasticity, tolerance of various environmental conditions and dietary flexibility (Sakai et al. 2001; Hellmann et al. 2008; Frelich and Reich 2009; Mainka and Howard 2010). Following the invasion of new habitats, non-native species may negatively impact the native ecosystems, biodiversity, local economy and the health of domestic animals and humans (Grosholz 2002; Sanders et al. 2003; Crowl et al. 2008). Meanwhile, the unsuccessful invasion by a non-native species is often modulated by competitive trophic interactions with the native organisms, which are facilitated by traits related to feeding and foraging (Nagelkerke et al. 2018). For instance, several earlier studies have shown that the resource utilization by non-native species is better than by their native neighbours (Byers 2000; Dick et al. 2012, 2017), and they possess an ability to use the available resources at their pinnacle, which generates a battleground for the natives and throw a competitive challenge to the native neighbours (MacArthur and Levins 1967; Tilman 1980). Although few freshwater snails (Mollusca: Gastropoda) show strong preferences towards food sources (Cruz et al. 2015), some invasive snails often exhibit high dietary flexibility, which enables them to adapt in challenging ecosystems (Lach et al. 2000; Kwong et al. 2008). Hence, the potential of resource utilization affects life-history traits, which in turn decide the impact of invasion on the native community.

In this study, we examined the influence of different food sources (i.e., lettuce and three aquatic macrophytes) on the fecundity of an invasive snail *Physella* (=*Physa*) *acuta* (Draparnaud, 1805) (Gastropoda: Physidae) and a co-occurring native snail *Racesina* (=*Lymnaea*) *luteola* (Lamarck, 1822) (Gastropoda: Lymnaeidae). The invasive snail *P. acuta* has successfully extended its distribution range from North America (native) to different regions of South America, Europe, Asia, Africa and Australia (Brackenbury and Appleton 1993; Albrecht et al. 2009; Vinarski 2017). Following the first report from Kolkata, West Bengal (Raut et al. 1995), the rapid spread of *P. acuta* led to the establishment of stable populations in various regions of India (Devi et al. 2006, 2008; Saha et al. 2016 a, b; Paul and Aditya 2021). Being a successful invader (e.g., rapid growth, earlier sexual maturity and high fecundity), *P. acuta* has managed to outcompete co-occurring snails in different regions, including *Physa fontinalis* (Linnaeus, 1758) in central Europe (Mouthon and Daufresne 2010), *Physastra variabilis* (J. E. Gray, 1843) in New Zealand (Winterbourn 1980) and *Glyptophysa gibbosa* (A. Gould, 1847) in Australia (Zukowski and Walker 2009). In the Indian context, the co-occurring native snail *R. luteola* exhibits similar life-history traits (e.g., attainment of sexual maturity: 24–42 days for *P. acuta*, 32–53 days for *R. luteola*; life span: 21 weeks for *P. acuta*, 15–50 weeks for *R. luteola*) (Taha 1992; Mishra and Raut 1993; Saha et al. 2017; Paul et al. 2022) and shares the same food resources with *P. acuta*, which creates a possible competitive scenario between the two (Saha et al. 2017; Paul and Aditya 2021).

As both snail species are algivorous and graze on aquatic macrophytes, we hypothesized that the outcome of competitive interaction between the co-occurring invasive and the native snails may vary under the influence of different plant diets. To observe the variations, we used the fecundity (eggs per individual) of *P. acuta* and *R. luteola* as the basis for evaluation of the competitive interaction, as the differences in the food resources and competition are known to alter the fecundity of freshwater snails (Qiu and Kwong 2009; Karmakar et al. 2021) and can be used for the risk assessment of non-native freshwater snails (Keller et al. 2007). The results of the present study may provide insights into the management strategies of the invasive snails through the evaluation of the differences in the reproductive output between the invasive and native snails under different plant diets.

MATERIALS AND METHODS

Collection and rearing of snails

We collected the invasive snail *Physella acuta* and native snail *Racesina luteola* from the pond-connected sewage drains and ponds in New Garia, Kolkata, India (22.47423 N, 88.39856 E). To acclimatize the field-collected individuals to the laboratory conditions, we reared *P. acuta* and *R. luteola* separately in the laboratory for seven days in glass aquaria (32 × 36 × 38 cm) filled with 25 L of tap water (pH 7.4–7.9, 25 ± 1 °C) at the density of 10 snails / 1 L water. The snails were fed regularly with decomposing lettuce (*Lactuca sativa*) for that period. We changed the water and removed dead individuals and unconsumed food from each aquarium every 24 hours to maintain hygienic conditions for the snails. The reproductive size class (shell height: 8–10 mm) of both snail species was chosen for the experiment.

Collection and storage of plants

We considered *Lactuca sativa* (garden lettuce) and three freshwater weeds: *Pistia stratiotes* (water lettuce), *Vallisneria spiralis* (eelgrass) and *Lemna minor* (duckweed) as food sources for the experiments. Garden lettuce was commercially available in the local vegetable markets of Kolkata, India, and we collected the freshwater weeds from the shallow ponds in New Garia, Kolkata, India (22.47423 N, 88.39856 E). After collection, we rinsed all plants with tap water to remove the dirt and other organisms, stored them at 4 °C and used within seven days. Among the plants, water lettuce, eelgrass and duckweed are common macrophytes found in the ponds, lakes and wetlands of West Bengal, India, and garden lettuce is proven as a standard diet of freshwater snails for laboratory rearing and experiments, and therefore selected for the experiment.

Experimental design

We placed the snails in conspecific and heterospecific conditions while maintaining a constant density of 10 individuals / 1 l water to observe the effect of competition on fecundity. The ratio of *P. acuta* and *R. luteola* placed in the experimental containers (diameter: 11 cm, height: 13 cm) was as follows: i) 10:0 (intraspecific competition of *P. acuta*), ii) 5:5 (interspecific competition between *P. acuta* and *L. luteola*) and iii) 0:10 (intraspecific competition of *L. luteola*). Among four different plants, i.e., garden lettuce, water lettuce, eelgrass and duckweed, we provided only one type of plant in each experimental container throughout the experiment. A total of 360 snails (i.e., 10 snails per container × 3 competition treatments × 4 plant diets × 3 replicates; 36 experimental containers) were used in the experiment. We placed the experimental containers at 25 ± 1 °C with a 14:10 h light:dark photoperiod. We monitored each container daily and counted the number of egg clutches (and the number of eggs in the clutches) oviposited by

P. acuta and *R. luteola* for 42 consecutive days. The egg clutches laid in the experimental containers were easily distinguishable, as the egg clutch of *R. luteola* was elongated in shape and the egg clutch of *P. acuta* was round, oval or comma-shaped.

Data analysis

We calculated eggs per individual (E/I) from the observed fecundity data of *P. acuta* and *R. luteola* and applied descriptive statistics to obtain mean ± SE eggs per individual (E/I) per day. As the data did not comply with normal distribution, we applied the non-parametric Kruskal-Wallis test with multiple pairwise comparisons using Dunn's procedure and Bonferroni correction using XLSTAT software (Lumivero 2023) to find any significant variations in the E/I of *P. acuta* and *R. luteola* due to competition and types of foods provided in the experiment.

RESULTS

Although the reproductive output (eggs/individual) of *P. acuta* and *R. luteola* varied with different plant diets, the E/I of both snails was higher on the *L. sativa* diet, followed by the *L. minor* diet, and was low on *P. stratiotes* and *V. spiralis* diets. In all plant diets, *P. acuta* laid a significantly higher E/I than *R. luteola* in intraspecific and interspecific competitions (Figure 1). In *L. minor* diet ($k = 106.965$, $df = 3$, $p < 0.0001$) (Figure 1a), no significant difference was found between E/I in intraspecific (5.79 ± 0.42) (mean ± SE) and interspecific (5.18 ± 0.30) competition of *P. acuta* as well as E/I in intraspecific (2.06 ± 0.28) and interspecific (2.08 ± 0.19) competition of *R. luteola*. Similarly, in *L. sativa* diet ($k = 149.567$, $df = 3$, $p < 0.0001$) (Figure 1b), no significant difference was observed between E/I in intraspecific (11.16 ± 0.63) and interspecific (11.93 ± 0.72) competition of *P. acuta* and E/I in intraspecific (4.19 ± 0.56) and interspecific (4.20 ± 0.39) competition of *R. luteola*. In *P. stratiotes*

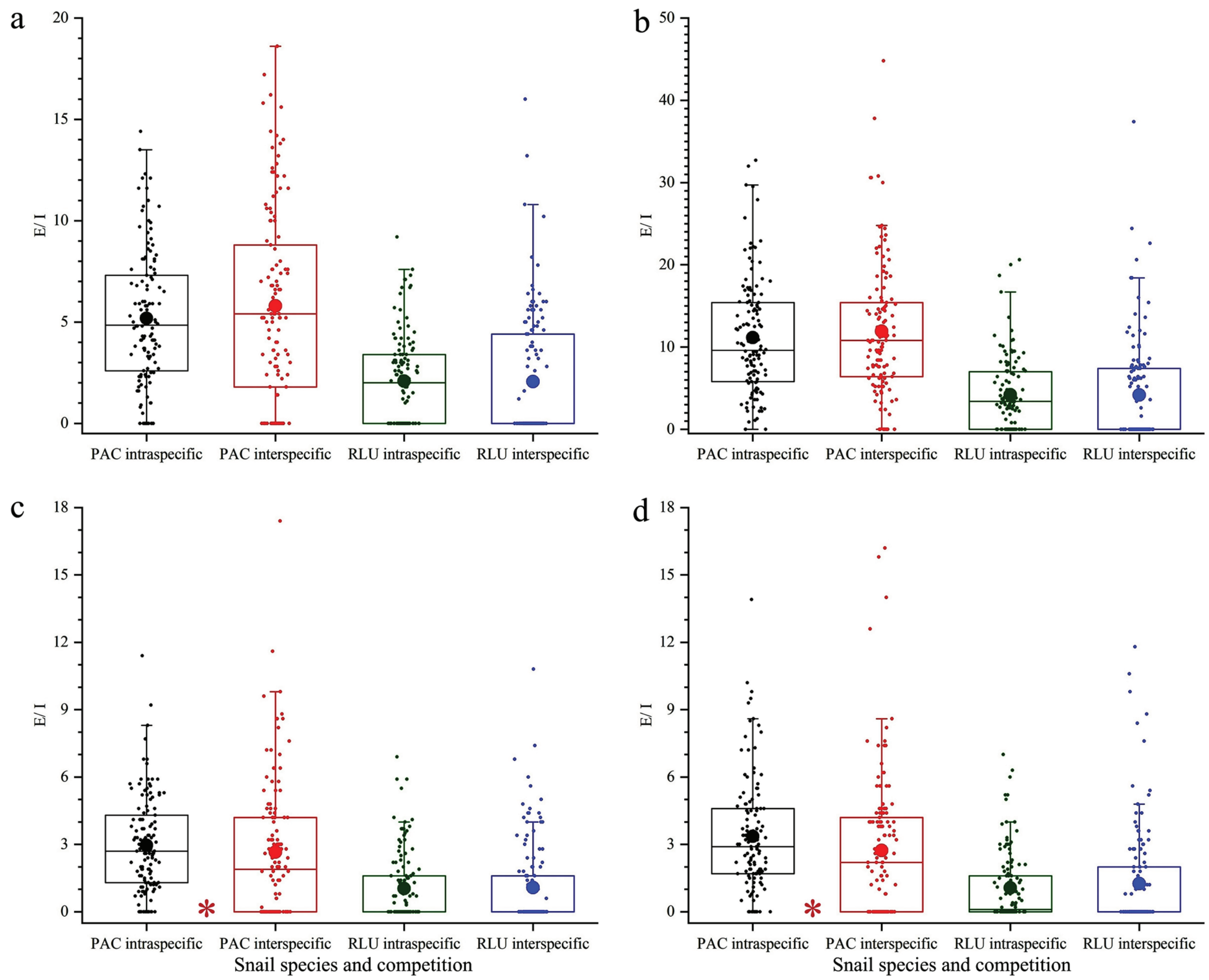

Figure 1. Eggs/individual/day (E/I) of the invasive snail *Physella acuta* (PAC) and the native snail *Racesina luteola* (RLU) on the diet of (a) *Lemna minor*, (b) *Lactuca sativa*, (c) *Pistia stratiotes* and (d) *Vallisneria spiralis*. * indicates significant difference between the E/I of intraspecific and interspecific competition at $p < 0.05$.

diet ($k = 88.997$, $df = 3$, $p < 0.0001$) (Figure 1c), there was a significant reduction in the E/I of *P. acuta* in interspecific (2.66 ± 0.30) than intraspecific competition (2.97 ± 0.19), but no such difference was observed between intraspecific (1.08 ± 0.17) and interspecific (1.04 ± 0.14) competition of *R. luteola*. Similar to the *P. stratiotes* diet, in *V. spiralis* diet ($k = 96.387$, $df = 3$, $p < 0.0001$) (Figure 1d), *P. acuta* showed a significant reduction in E/I in interspecific (2.73 ± 0.29) compared to intraspecific (3.36 ± 0.22) competition, and no significant difference was observed between intraspecific (1.26 ± 0.21) and interspecific (1.07 ± 0.14) competition in *R. luteola*.

DISCUSSION

The previous studies hypothesized that the invasion success of non-native species is associated with either occupying the empty niche or with competitive superiority (Lekevičius 2009; Fridley and Sax 2014; Turetsky et al. 2017). The globally invasive snail *P. acuta* largely relies on the second criterion, with an outstanding capability to outcompete the native snails of the recipient ecosystem (Winterbourn 1980; Zukowski and Walker 2009; Mouthon and Daufresne 2010). The competitive interactions of invasive species with their native neighbours are often affected by a few abiotic and biotic factors, and resource availability is one of such significant factors (Holway et al. 2002; Fobert et al. 2011). In this context, dietary flexibility and the ability to utilize a variety of foods by non-native species can be a significant factor behind invasion success (Matsuzaki et al. 2009).

In this study, the invasive snail *P. acuta* was observed to be reproductively superior (in terms of eggs per individual per day) to the native snail *R. luteola* under the diet of garden lettuce, water lettuce, duckweed and eelgrass. Similarly, in an earlier experiment, the invasive snail *P. acuta* laid a higher E/I than the native snail *R. luteola* exposed to different temperatures (Karmakar et al. 2021). However, in heterospecific conditions (i.e., interspecific competition), the reproductive output of *P. acuta* declined significantly in *P. stratiotes* and *V. spiralis* diets. Although the decline in the growth and reproductive output of *P. acuta* was more evident in their higher intraspecific densities than in the presence of interspecific snails (Cope and Winterbourn 2004; Paul et al. 2022), the present observation may be attributed to competitive interactions with *R. luteola* and low nutrient contents in *P. stratiotes* and *V. spiralis* diets. An earlier study reported similar results where the fecundity of *Physella gyrina* (Say, 1821) decreased significantly upon interspecific competition with *Lymnaea elodes* (Say, 1821) (both snails are native to the United States of America) (Brown 1982).

Among four plant varieties, the garden lettuce diet was the most suitable one, as the fecundity of both snails was highest in conspecific and heterospecific conditions, which could be due to higher nutritional and lower physical (i.e., toughness) and chemical defences in lettuce leaves compared to other macrophytes. A similar observation was made in China, where another invasive snail, *Pomacea canaliculata* (Lamarck, 1822), showed high fecundity when fed with cultivated semi-aquatic macrophytes yet lower fecundity and smaller egg clutches when fed with wild semi-aquatic macrophytes (Qiu and Kwong 2009). Similarly, an earlier study reported the maximum fecundity of the native snail *R. luteola* when fed with lettuce (Aziz and Raut 1996). The fecundity of *R. luteola* and *P. acuta* declined when fed with other macrophytes compared to garden lettuce, which showed similarity with an earlier study where the reproductive output of *P. canaliculata* was poorest when provided with a macrophyte *Phragmites australis* (Yam et al. 2016). Based on our observation, the lower E/I in the macrophyte diets can be attributed to the lower consumption rates of the aquatic macrophytes than of garden lettuce by both snail species and may depend upon the nutrient content of the selected plant diets. An earlier study demonstrated that the survival and growth of the invasive snail *Pomacea canaliculata* depends upon plant nutrient content and phenolics, and low levels of phenolic content and high levels of nutrients in the food, irrespective of whether decaying or fresh, increased survival and growth which turned them into a successful invader (Qiu et al. 2011).

In the present study, the invasive snail *P. acuta* overpowered the native snail *R. luteola* in terms of fecundity even when fed with aquatic macrophytes in which the productivity of both snails was poor. This finding proves the greater resource utilization ability of *P. acuta* and may result in the local competitive displacement of the native snail *R. luteola* (Paul and Aditya 2021). Apart from temperature and food resources, other abiotic (e.g., pollution, disturbance) and biotic (e.g., presence of predators and other competitors) factors may influence the invasion success of *P. acuta*. Hence, further studies should be conducted to understand the effects of these factors behind the invasion success of *P. acuta* and perceive the potential impact of its invasion. Similarly, the growth rate, fecundity, resource allocation and other life-history traits may vary with different environmental factors, which can be examined in future studies.

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Declarations

Author contribution

Debjit Mondal: Investigation, Writing – Original Draft, Writing – Review & Editing. **Pranesh Paul**: Investigation, Visualization, Formal analysis, Writing – Original Draft, Writing – Review & Editing. **Sujeeta De**: Investigation. **Chilka Saha**: Investigation. **Rupsha Karmakar**: Investigation. **Gautam Aditya**: Conceptualization, Supervision, Writing – Review & Editing.

Data availability

The data of this experiment can be made available upon authentic and reasonable request.

Conflict of interest

We declare that we do not have any conflict of interest.

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