



Article Invasiveness of *Pomacea canaliculata*: The Differences in Life History Traits of Snail Populations from Invaded and Native Areas

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Abstract: Pomacea canaliculata is native to South America and has become a widely distributed agricultural and environmental pest in southern China. Previous studies have primarily focused on the tolerance of P. canaliculata to various environmental factors, and compared non-native invasive P. canaliculata with natives or non-invasive congeners. However, there has been no research concentrated on variation in innate growth and reproductive characteristics between P. canaliculata in its native and invaded areas. To address this gap, we conducted the first comparison experiment between P. canaliculata from their native area (Argentina) and from an invaded area (China). We recorded the temporal dynamics of shell height of male and female P. canaliculata, and investigated the sexual maturation and egg-related indicators in two populations from each country, rearing them under homogeneous temperature, photoperiod and food conditions. Our results showed that the shell growth rate of P. canaliculata in Argentina was significantly lower than that of P. canaliculata in China. Moreover, P. canaliculata exhibited stronger reproductive characteristics in populations from China, mainly reflected in the earlier sexual maturity, larger egg masses, higher hatching success, and a trend of shorter incubation period. These differences probably arose due to contemporary evolution in invaded areas under strong selective pressures in rice fields, and, together with more favorable climates, enable the snail populations to rapidly grow and expand in southern China.

Keywords: Pomacea canaliculata; invasive; native; growth rate; reproduction

1. Introduction

Channeled apple snails (*Pomacea canaliculata*) are native to the Río de la Plata basin in South America [1]. They are mainly found in rivers, lakes, and reservoirs throughout countries such as Argentina, Bolivia, Brazil, Paraguay, Uruguay, and do not pose significant harm to local aquatic crops. However, since they were introduced into China as an edible aquaculture animal in 1981, they have rapidly spread to many provinces and cities in the south of the Yangtze River, including Guangdong, Guangxi, Fujian, Sichuan, as well as to provinces and cities north of the Yangtze River such as Gansu and Liaoning in just a few decades [2]. In the invaded areas, they have widely spread to agro-ecosystems and wetland ecosystems such as paddy fields, vegetable fields, ditches, rivers and lakes. *P. canaliculata* eats large quantities of rice seedlings, which seriously affects rice production in China. Additionally, it is an intermediate host of *Angiostrongylus cantonensis* (rat lung worm),



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Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). which can cause eosinophilic meningitis in humans [3]. *P. canaliculata* has been listed as one of the 100 worst invaders in the world and has the distinction of being the only freshwater snail to appear on this list [4].

The reason why the apple snail (*P. canaliculata*) has become a global invasive species in a short period of time is primarily because it has been widely introduced as an aquaculture animal to many countries and regions. However, once the apple snail arrives in a new environment, how does it settle, spread, and reproduce in the invaded area? What is the invasion mechanism of the apple snail? As a widely known invasive alien species, numerous studies have been conducted to explain the mechanisms of its invasion in terms of its characteristics, including wide habitat requirements [5,6], high resistance to stressors [7,8], high reproductive rate and abundant genetic diversity [2,9], strong defenses and competition against native species [10,11].

Sex ratios of *P. canaliculata* populations are unbiased at the juvenile stage [12,13], but it was usually found that the number of female snails was obviously higher than that of male snails in natural *P. canaliculata* populations. According to the report by Liu et al. [14], the sex ratio of the *P. canaliculata* population, which was reared in the wild and exposed to natural winter conditions, changed from 1:1 to 1:1.54 over a period of three years. In addition, female *P. canaliculata* can store sperm and produce thousands of fertilized eggs even after a single copulation event [15]. A female *P. canaliculata* can spawn hundreds of eggs at a time, which usually hatch within 15 days [16]. The high proportion of female *P. canaliculata* combined with high fecundity results in easier and frequent population breakout, potentially resulting in more harmful damages to crop production and aquatic ecosystems. A higher mortality of males, for instance, as a result of their lower risk avoidance, is a plausible explanation [17].

In addition, it has been found that environmental temperature plays an important role in the growth, development and reproduction of *P. canaliculata*, thereby affecting population establishment and distribution [18,19]. The growth rate of *P. canaliculata* is positively correlated with temperatures ranging from 15 to 30 °C [20]. In some invaded areas, the time to reach sexual maturity of *P. canaliculata* significantly reduced. It has been reported that *P. canaliculata* takes up to 25 months to reach sexual maturity in temperate areas in its native Argentina, where the average annual temperature ranges between 9 and 20 °C [21]. In subtropical southern China, *P. canaliculata* can produce 2–3 generations per year, and lay up to 13,764 eggs during its lifetime [14]. However, in Argentina, a female has been reported to produce 4500 eggs in her lifetime [22]. However, it is not known if these differences are due to the different climates and habitats alone, to genetic differences or a combination of the two sources of variation. In the native range, rearing experiments under homogeneous conditions demonstrated that the substantial variation in life history traits among populations from a small stream, a river and a shallow lake is mostly ecophenotypic but also that some of the differences have a genetic origin [22].

Most studies have compared non-native invasive apple snails with non-invasive congeners or with other native snails [23–26], but no research has concentrated on variations in growth and reproductive characteristics of *P. canaliculata* in its native and invaded range. In this study, we aimed to investigate the variations in shell growth, age at sexual maturity and fecundity of *P. canaliculata* from both Argentina (native area) and China (invaded area) and whether their origin is phenotypic or genetic through their experimental rearing under homogenous conditions. We also aimed to compare the intersexual differences between the native and invasive populations, in order to provide a better understanding of the invasion mechanisms of *P. canaliculata*.

2. Materials and Methods

2.1. Experiment Materials

Neonate snails used in the study were hatched from egg masses laid by laboratoryreared females, which were collected from two natural populations both in Argentina and China. In Argentina, one population (A1) was located in an excavated channel that diverts water from the Pigüé stream to the Venado stream $(37^{\circ}11'26'' \text{ S}, 62^{\circ}40'26'' \text{ W})$, and the other population (A2) in the Guaminí stream $(37^{\circ}02'59'' \text{ S}, 62^{\circ}25'26'' \text{ W})$, both in southwestern Buenos Aires Province. In China, the two source populations (C1 and C2) inhabited two rice fields in Guangdong Province $(23^{\circ}17'06'' \text{ N}, 113^{\circ}37'53'' \text{ E} \text{ and } 23^{\circ}24'38'' \text{ N}, 113^{\circ}64'29'' \text{ E}, respectively}.$

The two watercourses from Argentina harbor abundant populations of *P. canaliculata* that have been thoroughly studied [27], the Pigüé and Guaminí, are permanent streams that run through plain areas with extensive agriculture and cattle rearing; they show occasional floods, but are never dry. The water discharge is not controlled artificially, and no control methods are applied to aquatic plants or animals. The climate in the area is mild, warm and temperate, with maximum and minimum monthly mean temperatures of 22.9 and 7 °C, respectively, and total annual rainfall of 814 mm (https://en.climate-data.org/south-america/argentina/buenos-aires/espartillar-145762/; accessed 6 April 2023).

The two rice fields (populations C1 and C2) belong to the same source area in China (Guangzhou) and have similar management measures. The main mechanical labor in these rice fields is ploughing before cultivation. Water management includes field drying for a week after transplanting and for ten days before harvest; when rice is not being grown 3–4 months a year, the rice fields are kept dry. The specific measures to control apple snails in the area are usually applied before transplanting rice to control damage to rice seedlings: removal of apple snail eggs combined with weeding around the paddy fields and the application of a plant-based biopesticide (tea bran containing saponins) and synthetic pesticides (niclosamide ethanolamine salts and metaldehyde). The climate is temperate but warmer and more humid (extreme monthly means of 28.3 and 14.2 °C and annual rainfall of 2123 mm; https://en.climate-data.org/asia/china/guangdong/guangzhou-23 09/; accessed 6 April 2023) than in the source area from Argentina.

The incubation of egg masses and subsequent rearing experiments (see below) were carried out at National University of the South in Argentina and South China Agricultural University in China. The same standardized procedure for apple snail experimental rearing [28,29] was maintained in both countries.

2.2. Species Identification

Initially, species identification of apple snails relied on their physical characteristics [1]. However, due to the significant diversity present within the *Pomacea* genus, species misidentification is frequently observed. To more accurately classify Pomacea species, P. canaliculata was identified according to the COI gene sequence in mitochondrial genomic DNA [30–32]. The cytochrome *c* oxidase subunit I (*COI*) gene, which exhibits notable genetic diversity in *P. canaliculate*, is a more dependable molecular identification marker. The genomic DNA from the preserved foot tissue was extracted by using the TIANamp Genomic DNA kit (Macherey Nagel, Beijing, China). PCR was conducted using $2 \times$ SuperTaq PCR StarMix (GenStar, Beijing, China), and the primers for *P. canaliculata* (F: 5'-TGG GGT ATG ATC AGG CC-3', R: 5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3'), and for P. maculata (F: 5'-ATC TGC TGC TGT TGA AAG C-3', R: 5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3'). The amplified region was a mitochondrial COI gene segment (666 bp for P. canaliculata, 390 bp for P. maculata). PCR conditions consisted of 94 °C for 2 min, 35 cycles of 94 °C for 30 s, 50 °C for 30 s, and 72 °C for 1 min, and a final extension of 72 °C for 5 min. The PCR products were then separated and analyzed by 2% agarose gel electrophoresis and banded using the ultraviolet method.

2.3. Experiment Procedure

Neonate snails hatched from the egg masses (up to 100 from each population) were supplied with fresh lettuce ad libitum and reared collectively in 1.5 L tap water saturated with CaCO₃, and maintained under a photoperiod of 14/10 h (light/dark) at 25 ± 2 °C. This temperature is thought to be optimum for the survival and growth of *P. canaliculata* [33,34]. We measured the basic chemical properties of the tap water used in Argentina and China.

The properties of the aerated tap water used in Argentina were as follows: Ca: 24.0 mg/L, K: 6.0 mg/L, Mg: 6.9 mg/L, Na: 73.1 mg/L, SO₄: 31.2 mg/L; PO₄: <0.1 mg/L; CL⁻: 42.1 mg/L; HCO₃: 308 mg/L; CO₃: <0.1 mg/L; pH: 7.4; conductivity: 0.51 mS/cm; hardness: 88.3 mg/L. The properties of the aerated tap water used in China were as follows: Ca: 29.89 mg/L, K: 3.664 mg/L, Mg: 2.0945 mg/L, Na: 8.321 mg/L, SO₄: 20.775 mg/L; PO₄: 0.0075 mg/L; CL⁻: 13.24 mg/L; HCO₃: 40.685 mg/L; CO₃: 0 mg/L; pH: 7.055; conductivity: 0.2445 mS/cm; hardness: 85.375 mg/L. After 7 days for the neonates from the snail population (A1), and 10 days for the neonates from the other three populations (A2, C1 and C2), 50 neonate snails were randomly selected from each population respectively. Each one was transferred to an individual plastic case with 150 mL tap water, and maintained under the same culture conditions as described above.

Food supplies were checked every day and supplemented if necessary. Water was changed once a week, and the shell heights of all the snails were measured during the water change. To avoid damage to the snails and facilitate the measurements, we obtained a digital photograph in dorsal view after the water was removed and the snail was placed on the bottom center of the plastic case by a soft-bristled brush. On the outside of the translucent plastic case a 1 cm bar was drawn, which served as a scale in each photograph to estimate the shell height, defined as the distance from the apex to the farthest point of the aperture of the snail [28].

When the age of the snails around 8 weeks in Argentina and 6 weeks in China, the shell heights were more than 10 mm for a vast majority of the snails, and we transferred the snails to individual 3 L glass aquaria with 2.5 L tap water. Water was also changed once a week and shell height was measured with a caliper during the water change. The sex of all the snails was determined when the shell heights were more than 25 mm, because smaller snails lack external sexual dimorphism. We first identified their sex based on operculum morphology, because the opercula at a particular site of males become convex when they tend to mature, which is different from the opercula of females, which remain concave after sexual maturity [35]. Additionally, we further examined a visible albumin gland through the shell (to identify mature females) or testes (to identify mature males).

From the time they reached a mean size of 25 mm in shell height, all the snails (except some individuals less than 20 mm) from the same population were numbered with paint markers, and placed once a week in an 18 L collective container with water at 25 °C for 8 h, in order to give them the possibility to copulate. When the mating behavior was started, the date was recorded and regarded as a mark of sexual maturity, the female and male snails were gently transferred to a 3 L glass aquarium to allow them to mate. After the mating finished, the female was weighed and maintained in its individual aquarium to keep record of egg laying. The weight of each snail was recorded after each female had crawled onto a dry plastic surface to drain water from the pallial cavity. Once a female laid three egg masses with only one mating, the female was weighed again, and five females from each population were killed by immersion in boiling water in Argentina or immediately frozen at -40 °C in China, then kept frozen at below -18 °C until further processing. Other snails from each population continued feeding, mating and laying egg-masses for at least one month, then euthanized or used in other experiments.

The egg masses were carefully removed to plastic cases, respectively, then incubated at 25 ± 2 °C, more than 30 egg masses from each population in China were collected, and their mothers only mated once before laid these egg masses. The incubation periods of these egg masses were calculated from the day they were laid to the day of the first hatching [36]. In order to determine hatching success, the number of hatchlings in each egg mass was counted, and the remaining non-hatched eggs were counted after they were dispersed in 2% sodium hydroxide solution for 1.5 h [37]. The fertilization rate of each egg mass was investigated, based on the undeveloped eggs which remained red.

2.4. Data Analysis

Shell height and incubation period were analyzed using the linear mixed model examining the population nested in the country. The number of egg masses, egg mass size and age at sexual maturity, fertilization rate, and hatching success were analyzed by generalized linear mixed model with population nested in country. Poisson distribution was used for egg masses, egg masses size, and age at sexual maturity. Binomial distribution was used to examine the fertilization rate and hatching success. Mixed models were built using the R package lmerTest [38]. Significance level was set at p < 0.05. Plots were generated using the R package ggplot2 [39].

3. Results

3.1. Variations in Growth

There were dramatic differences in growth and reproductive patterns between Chinese and Argentinean snail populations; however, there were no significant differences between the populations within each country (p > 0.05 in all cases). Henceforth, the snails from each country will be treated as a homogeneous group. Chinese snails exhibited rapid growth, with females and males reaching average shell heights of 37.59 ± 0.68 mm and 36.96 ± 0.61 mm, respectively, at 15 weeks (two weeks after sexual maturity). By contrast, the Argentinean snails grew more slowly than the Chinese ones, were not sexual mature at 15 weeks, and attained average shell heights of 26.90 ± 0.39 mm and 25.17 ± 0.43 mm for females and males, respectively (Figure 1). At weeks 6, 7, 8, and 9, the population in China demonstrated a significant difference in shell height between males and females (p < 0.05), with females exhibiting greater height. However, there was no significant sex difference in the rest of the experiment. In contrast, in Argentina, female shell heights were significantly higher than male shell heights from week 13 until the end of the experiment (p < 0.05) (Figure 1).



Figure 1. Temporal changes of shell height (mean \pm SD) of female (circles) and male (triangles) *P. canaliculata* from populations in China (red) and Argentina (blue).

3.2. Variations in Reproduction

Regarding the changes of shell height at sexual maturity, the results of the two-way analysis indicated that country (i.e., native and invaded area) (p = 0.039), sex (p < 0.001) and their interaction (p = 0.024) significantly influenced the shell height at sexual maturity (Figure 2). Specifically, female snails in China exhibited a significantly lower shell height at maturity ($37.64 \pm 0.32 \text{ mm}$) than that in Argentina ($41.27 \pm 0.63 \text{ mm}$), whereas no significant difference was found in male snails between the two countries (China: $34.2 \pm 0.58 \text{ mm}$, Argentina: $35.55 \pm 0.90 \text{ mm}$, Figure 2).



Figure 2. Comparisons of the shell height and age at sexual maturity between male and female *P. canaliculata* in China and Argentina between males and females in the same country. (**a**): Shell height at sexual maturity; (**b**): age at sexual maturity. Different capital letters indicate significant differences (p < 0.05) in height and age at sexual maturity between males and females in the same country, Different lowercase letters indicate significant differences (p < 0.05) in shell height and age of the same sex at sexual maturity in different countries.

The age at sexual maturity was significantly lower in China than in Argentina for both female (94.58 \pm 2.23 and 206.33 \pm 3.85 days, respectively) and male snails (90.09 \pm 7.65 and 205.36 \pm 10.87 days, respectively). Country (p < 0.001) was the only significant factor affecting age at sexual maturity, with neither sex (p = 0.393) nor the interaction between country and sex (p = 0.190) being significant (Figure 2).

Additionally, there was a significant difference in the number of egg masses per female between the Chinese and Argentinean populations (5.11 ± 0.39 and 3.00 ± 0.14 egg masses, respectively, p < 0.001). In Argentina, on average, 334 ± 50.43 eggs per female were produced, which was barely half the level of eggs produced in China (693.58 ± 57.40 , p = 0.005). The fertilization rate was 79.91 \pm 1.97% in China, significantly higher than that in Argentina ($34.81 \pm 6.42\%$, p < 0.001). Correspondingly, the hatching success rate of the snail eggs was 53.17 \pm 12.71% in China, also significantly higher than that in Argentina ($25.27 \pm 6.68\%$, p = 0.012). The egg hatching success rate of *P. canaliculata* was found to be highly variable, ranging from 46.85% to 98.50% in the 36 randomly selected egg masses from Chinese populations. In contrast, the highest hatching success rate of Argentinean populations was 69.55%, and 35% of the egg masses did not hatch at all. The snail incubation period was not significantly different in China (13.90 ± 0.09 days) and Argentina (16.74 ± 0.81 days, p = 0.074). The statistical analysis did not include the seven unhatched egg masses in Argentinean populations (Figure 3).



Figure 3. Comparisons of the reproductive characteristics between the Chinese and Argentinean apple snails. (**a**): Number of egg masses; (**b**): egg mass size; (**c**): fertilization rate; (**d**): hatching success rate; (**e**): incubation period. Stars indicated the significance level (*, p < 0.05; **, p < 0.01; ***, p < 0.001; ns, no significant difference). Empty circles and black bars represent the mean \pm SE.

4. Discussion

4.1. Growth of the Snail Populations from the Invaded and Native Areas

Somatic growth rates are important population characteristics that are influenced by various factors, including body size, fecundity, hatches per season, longevity, etc. [40,41]. Studies have also found that growth rates are typically enhanced in invasive populations compared with native populations [42–45]. Therefore, investigating the difference in growth rates of *P. canaliculata* in invaded and native areas is an important step towards understanding its invasions more comprehensively [45,46].

In this study, we investigated the variation in shell heights of both male and female P. canaliculata in their native (Argentina) and invaded (China) areas. Our analysis of the comparative data revealed that *P. canaliculata* exhibited significantly accelerated growth in their invaded area when compared with the native one. In the invaded areas, both male and female snails reached a shell height of more than 35 mm in 16 weeks, whereas in the native areas it took at least 24 weeks for the snails to reach the same shell height. Furthermore, the repeated measures analysis of variance of shell height data from the first 1–15 weeks also indicated that the growth rate of *P. canaliculata* was significantly higher in invasive populations than in native populations. The results of this study are generally in support of the evolution of increased competitive ability (i.e., the EICA hypothesis), which is one mechanism that has been proposed to explain the relatively greater success of invasive populations [47]. The EICA hypothesis was developed through the research of invasive species [48–50] and it suggests that invasive species are able to reallocate resources from defense (in the absence of co-evolved predators) to growth and reproduction [47]. Even if some predators and a few parasites attack apple snails in invaded areas [51], they are lower in species number and less specific than in the native range, and after attaining 20 mm, they are almost invulnerable to most predators in the invaded range [52].

The initial phases of the experimentation did not reveal any significant difference between the shell height of female and male populations, as neonate snails were used in the experiment. However, differences in shell height between females and males became more apparent over time. Both native and invasive populations exhibited significant differences in shell height between males and females at sexual maturity. Previous studies have found that female *P. canaliculata* tend to grow faster than males, mainly due to their higher feeding rate and food conversion rate [53]. The reason for this difference can be explained by the relationship between size and reproductive success in each sex. The male P. canaliculata size does not play a significant role in copulation probability [54,55]. In males, the primary pressure is to copulate as soon and as frequently as possible while maximizing sperm transfer during each copulation [55–57]. In the case of *P. canaliculata*, this last selective pressure may have resulted in a much bigger testicle size relative to that of the ovary, which reduces the mid-gut gland size and its capacity to process food. In contrast, fecundity is proportional to body size in females since they bear high reproductive costs and need to produce large, elaborate egg masses [54,58]. Thus, a selection to maximize growth rates is more likely to be observed in females. In China, the difference in shell height between male and female snails gradually decreases between 10 and 15 weeks, with no significant differences observed (p > 0.05). This phenomenon could be attributed to the fact that females allocate more energy to reproduction, resulting in an additional cost that affects their growth.

4.2. Reproduction of the Snail Populations from the Invaded and Native Areas

Normally, the reproductive capability of *P. canaliculata* is proportional to their shell height [59]. However, both male and female *P. canaliculata* in invaded areas exhibited sexual maturity at smaller shell height compared with their counterparts in native areas. Notably, Chinese females reached sexual maturity at significantly smaller shell heights than their Argentinean counterparts, whereas the difference between male shell heights was not significant. This suggests that in China, females may have undergone an evolutionary adjustment to balance mortality risks and fecundity costs: faster growth rates probably compensate only partially for an earlier sexual maturity that reduces pre-reproductive exposure to high mortality risks [58], although at the expense of a somewhat smaller size.

In response to the survival pressures of the novel environment, the strategy of invasive populations was characterized by earlier reproduction and extended reproductive lifespan [60]. Invasive populations tend to grow exponentially in the early stages of an invasion, which often gives them an advantage, allowing them to reproduce earlier than other species [61]. In this study, the average age at sexual maturity was 90.09 d and 94.58 d for male and female *P. canaliculata* from invaded areas, compared with 205.36 d and 206.33 d for male and female *P. canaliculata* from native areas. The results suggest that the age at sexual maturity has significantly shortened for *P. canaliculata* in invaded areas, probably due to the strong selective pressures represented by control measures against the apple snail in rice fields [62–64]. Early reproduction probably contributes greatly to the success of the invasion, minimizing pre-reproductive risk exposure and unnecessary costs [65]. Previous studies have found that the age to reach sexual maturity in this apple snail is greatly reduced in warmer regions [8,21,55,66], which, coupled with the selected reproductive precocity, could have enhanced its invasive potential in many invaded regions.

Research in Asia has found that a mature female *P. canaliculata* can lay 50–500 eggs at a time and the incubation period is often less than 15 days [67]; moreover, the females can store sperm and lay thousands of eggs after a single copulation [15]. In the present study, it was found that the number of egg masses laid by each female in the invaded area was significantly higher than that in the native area. There was also a significant difference in egg mass size, being approximately 50% in the native area of that in the invaded one. Furthermore, the hatching success and fertilization rate of egg mass in the native area were also significantly lower than that in the invaded area. The combination of the hatching rate and number of eggs laid by female allows us to estimate that the number of neonates produced by a recently matured female is 3.97 times higher in China than in Argentina (369 and 93, respectively). High mortalities provoked by control and culture practices in the rice fields may have promoted an earlier energetic and nutritional investment in

reproduction after maturity, similar to that proposed to occur in intermittent streams in the native range [55].

The performance of invasive species relative to native species can differ with environments. In the case of apple snails, temperature plays an important role in determining their growth and reproductive patterns [55,66]. The *P. canaliculata* in Argentina where the average temperature throughout the year is 9–20 °C during spring and summer (October to April in southern South America). However, in many parts of China, including Guangzhou, the reproduction occurred all the year round, only fewer occurred in January and February. This suggests that the annual reproductive output of these apple snails in China is much higher than that of their Argentinean conspecifics and that this may have enhanced their invasive potential.

A plausible reason why *P. canaliculata* in invaded areas exhibit higher fecundity may be due to the reduced natural enemies [51,52] and other burdens. The previous studies confirmed a much lower haplotype diversity of *P. canaliculata* in populations of China than that in their native countries Argentina and Brazil [2,9,68]. In some invasive species, a decrease in genetic diversity promotes successful invasion. For example, *Linepithema humile*, an Argentine ant, invaded North America. The decrease in its genetic diversity reduced the intra-population struggle, thus improving the survival and reproduction ability of the population and gaining a numerical advantage, thus forming behavioral characteristics conducive to competition in the new environment [69]. Furthermore, invasive populations and native populations typically have different gut microbial communities. Changes in host–microbe relationships may also lead to improved host fitness and may facilitate the host's invasion of new environments [70,71].

5. Conclusions

The results of this experiment under homogeneous conditions showed that *P. canaliculata* exhibited differences in life history traits between populations from the invaded (China) and native (Argentina) range, mainly reflected in the accelerated growth rate, earlier sexual maturity, higher fecundity and higher hatching success. The direction of the changes suggests a process of contemporary evolution during the transcontinental invasion and an adaptation to the new selective pressures represented by pest control, culture labors and water management. These changes in life history traits allow *P. canaliculata* to rapidly develop populations and form dominant populations in the invaded sites, probably enhanced by a warmer climate and enemy release. These findings will be helpful to better understand the invasion mechanisms of *P. canaliculata* in China.

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Data Availability Statement: The data for the analysis in this study are available upon request from the corresponding author.

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References

- 1. Hayes, K.A.; Cowie, R.H.; Thiengo, S.C.; Strong, E.E. Comparing apples with apples: Clarifying the identities of two highly invasive Neotropical Ampullariidae (Caenogastropoda). *Zool. J. Linn. Soc.* **2012**, *166*, 723–753. [CrossRef]
- Yang, Q.-Q.; Liu, S.-W.; He, C.; Yu, X.-P. Distribution and the origin of invasive apple snails, *Pomacea canaliculata* and *P. maculata* (Gastropoda: Ampullariidae) in China. *Sci. Rep.* 2018, *8*, 1185. [CrossRef] [PubMed]
- Lv, S.; Zhou, X.-N.; Zhang, Y.; Liu, H.-X.; Zhu, D.; Yin, W.-G.; Steinmann, P.; Wang, X.-H.; Jia, T.-W. The effect of temperature on the development of Angiostrongylus cantonensis (Chen 1935) in *Pomacea canaliculata* (Lamarck 1822). *Parasitol. Res.* 2006, 99, 583–587. [CrossRef] [PubMed]
- Lowe, S.M.; Browne, S.; BoudjelaS, S.; De Poorter, M. 100 of the World's Worst Invasive Alien Species: A Selection from the Global Invasive Species Database, in The Invasive Species Specialist Group; van der Weijden, W., Leewis, R., Bol, P., Eds.; IUCN: Auckland, New Zealand, 2000; pp. 206–208.
- 5. Qin, Z.; Yang, M.; Zhang, J.-E.; Deng, Z. Effects of salinity on survival, growth and reproduction of the invasive aquatic snail *Pomacea canaliculata* (Gastropoda: Ampullariidae). *Hydrobiologia* 2020, *847*, 3103–3114. [CrossRef]
- 6. Yusa, Y.; Wada, T.; Takahashi, S. Effects of dormant duration, body size, self-burial and water condition on the long-term survival of the apple snail, *Pomacea canaliculata* (Gastropoda: Ampullariidae). *Appl. Entomol. Zool.* **2006**, *41*, 627–632. [CrossRef]
- Wada, T.; Matsukura, K. Linkage of cold hardiness with desiccation tolerance in the invasive freshwater apple snail, *Pomacea canaliculata* (Caenogastropoda: Ampullariidae). *J. Molluscan Stud.* 2011, 77, 149–153. [CrossRef]
- Lach, L.; Britton, D.K.; Rundell, R.J.; Cowie, R.H. Food Preference and Reproductive Plasticity in an Invasive Freshwater Snail. *Biol. Invasions* 2000, 2, 279–288. [CrossRef]
- Lv, S.; Zhang, Y.; Liu, H.X.; Hu, L.; Liu, Q.; Wei, F.R.; Guo, Y.H.; Steinmann, P.; Hu, W.; Zhou, X.N.; et al. Phylogenetic evidence for multiple and secondary introductions of invasive snails: *Pomacea* species in the People's Republic of China. *Divers. Distrib.* 2013, 19, 147–156. [CrossRef]
- 10. Guo, J.; Martín, P.R.; Zhang, C.; Zhang, J.-E. Predation risk affects growth and reproduction of an invasive snail and its lethal effect depends on prey size. *PLoS ONE* **2017**, *12*, e0187747. [CrossRef] [PubMed]
- Guo, J.; Zhang, J.-E.; Zhao, B.; Luo, M.; Zhang, C. The role of spotted green pufferfish *Tetraodon nigroviridis* in controlling golden apple snail *Pomacea canaliculata*: An effective biological control approach involving a new agent. *Biocontrol Sci. Technol.* 2016, 26, 1100–1112. [CrossRef]
- 12. Yusa, Y.; Suzuki, Y. A snail with unbiased population sex ratios but highly biased brood sex ratios. *Proc. R. Soc. B Boil. Sci.* 2003, 270, 283–288. [CrossRef] [PubMed]
- Yusa, Y. Nuclear Sex-Determining Genes Cause Large Sex-Ratio Variation in the Apple Snail Pomacea canaliculata. Genetics 2007, 175, 179–184. [CrossRef]
- 14. Liu, J.; He, Y.-J.; Tan, J.-C.; Xu, C.-X.; Zhong, L.; Wang, Z.-G.; Liao, Q.-G. Characteristics of *Pomacea canaliculata* reproduction under natural conditions. *Chin. J. Appl. Ecol.* 2012, 23, 559–565.
- 15. Burela, S.; Martín, P.R. Evolutionary and functional significance of lengthy copulations in a promiscuous apple snail, *Pomacea canaliculata* (Caenogastropoda: Ampullariidae). *J. Molluscan Stud.* **2011**, *77*, 54–64. [CrossRef]
- 16. Seuffert, M.E.; Saveanu, L.; Martín, P.R. Threshold Temperatures and Degree-Day Estimates for Embryonic Development of the Invasive Apple Snail *Pomacea canaliculata* (Caenogastropoda: Ampullariidae). *Malacologia* **2012**, *55*, 209–217. [CrossRef]
- 17. Xu, W.; Zhang, J.; Du, S.; Dai, Q.; Zhang, W.; Luo, M.; Zhao, B. Sex differences in alarm response and predation risk in the fresh water snail *Pomacea canaliculata*. *J. Molluscan Stud.* **2014**, *80*, 117–122. [CrossRef]
- Yang, Q.Q.; Li, J.N.; Zhao, X.X.; Pu, J.J.; Qiao, D.D.; Yu, X.P. Temperature on biological charaterstics and adaptive mechanisms of the apple snails. *Acta Hydrobiol. Sin.* 2022, 46, 1754–1760.
- 19. Seuffert, M.E.; Martín, P.R. Thermal limits for the establishment and growth of populations of the invasive apple snail *Pomacea canaliculata*. *Biol. Invasions* **2017**, *19*, 1169–1180. [CrossRef]
- 20. Wada, T.; Yoshida, K. Burrowing by the apple snail, *Pomacea canaliculata* (Lamarck); daily periodicity and factors affecting burrowing. *Kyushu Plant Prot. Res.* 2000, *46*, 88–93. [CrossRef]
- 21. Estebenet, A.; Cazzaniga, N. Growth and demography of *Pomacea canaliculata* (Gastropoda: Ampullariidae) under laboratory conditions. *Malacol. Rev.* **1992**, *25*, 1–12.
- 22. Martin, P.R.; Estebenet, A.L. Interpopulation variation in life-history traits of *Pomacea canaliculata* (Gastropoda: Ampullariidae) in southwestern Buenos Aires Province, Argentina. *Malacologia* **2002**, *44*, 153–163.
- 23. Chaichana, R.; Sumpan, T. The potential ecological impact of the exotic snail *Pomacea canaliculata* on the Thai native snail Pila scutata. *Scienceasia* **2014**, *40*, 11–15. [CrossRef]
- 24. Chaichana, R.; Sumpan, T. Environmental tolerance of invasive golden apple snails (*Pomacea canaliculata* (Lamarck, 1822)) and Thai native apple snails (Pila scutata, (Mousson, 1848). *Trop. Ecol.* **2015**, *56*, 347–355.
- 25. Morrison, W.E.; Hay, M.E. Feeding and growth of native, invasive and non-invasive alien apple snails (Ampullariidae) in the United States: Invasives eat more and grow more. *Biol. Invasions* **2011**, *13*, 945–955. [CrossRef]
- Pradabphetrat, P.; Aroonsrimorakot, S.; Fureder, L.; Tosh, C.; Piyapong, C. A Comparison of feeding behaviour and preferences of native and non-native invasive apple snail in Thailand. *CMU Intellect. Repos.* 2018, 45, 2294–2302.
- 27. Seuffert, M.E.; Martín, P.R. Distribution of the apple snail *Pomacea canaliculata* in Pampean streams (Argentina) at different spatial scales. *Limnologica* **2013**, *43*, 91–99. [CrossRef]

- 28. Tiecher, M.J.; Burela, S.; Martín, P.R. Life cycle of the South American apple snail Asolene platae (Maton, 1811) (Caenogas-tropoda: Ampullariidae) under laboratory conditions. *J. Molluscan Stud.* **2016**, *82*, 432–439. [CrossRef]
- 29. Gurovich, F.M.; Burela, S.; Martin, P.R. Life cycle of *Pomacea* americanista, a poorly known apple snail endemic to the Iguazu and Alto Parana Rivers, southern South America. *J. Molluscan Stud.* **2018**, *84*, 62–68. [CrossRef]
- Hayes, K.A.; Joshi, R.C.; Thiengo, S.C.; Cowie, R.H. Out of South America: Multiple origins of non-native apple snails in Asia. Divers. Distrib. 2008, 14, 701–712. [CrossRef]
- 31. Rawlings, T.A.; Hayes, K.A.; Cowie, R.H.; Collins, T.M. The identity, distribution, and impacts of non-native apple snails in the continental United States. *BMC Evol. Biol.* 2007, *7*, 97. [CrossRef]
- Matsukura, K.; Okuda, M.; Kubota, K.; Wada, T. Genetic divergence of the genus *Pomacea* (Gastropoda: Ampullariidae) distributed in Japan, and a simple molecular method to distinguish *P. canaliculata* and *P. insularum. Appl. Entomol. Zool.* 2008, 43, 535–540. [CrossRef]
- 33. Seuffert, M.E.; Martin, P.R. Juvenile growth and survival of the apple snail *Pomacea canaliculata* (Caenogastropoda: Ampul-lariidae) reared at different constant temperatures. *Springerplus* **2013**, *2*, 312. [CrossRef]
- Latip, S.N.H.; Clement, M.U. The effects of different water temperatures on survival and growth rate of juvenile invasive apple snail, *Pomacea canaliculata* (Lamarck, 1822) under controlled environment. *IOP Conf. Ser. Earth Environ. Sci.* 2021, 685, 012021. [CrossRef]
- Estebenet, A.L.; Martín, P.R.; Burela, S. Conchological variation in *Pomacea canaliculata* and other South American *Ampullariidae* (Caenogastropoda, Architaenioglossa). *Biocell* 2006, 30, 329–335.
- Ichinose, K.; Tochihara, M. Increased per-capita investment in egg production by female apple snails in the presence of pred-atory common carp. *Behaviour* 2003, 140, 935–945. [CrossRef]
- Albrecht, E.; Carreño, N.; Castro-Vazquez, A. A quantitative study of copulation and spawning in the South American ap-ple-snail, Pomacea canaliculata (Prosobranchia). Veliger 1996, 39, 142–147.
- Kuznetsova, A.; Brockhoff, P.B.; Christensen, R.H.B. ImerTest Package: Tests in linear mixed effects models. J. Stat. Softw. 2017, 82, 1–26. [CrossRef]
- 39. Wickham, H. Elegant Graphics for Data Analysis; Springer: New York, NY, USA, 2016.
- 40. Rypel, A.L. Do invasive freshwater fish species grow better when they are invasive? Oikos 2014, 123, 279–289. [CrossRef]
- 41. Arendt, J.D. Adaptive Intrinsic Growth Rates: An Integration Across Taxa. Q. Rev. Biol. 1997, 72, 149–177. [CrossRef]
- 42. Werner, C.; Zumkier, U.; Beyschlag, W.; Máguas, C. High competitiveness of a resource demanding invasive acacia under low resource supply. *Plant Ecol.* **2010**, *206*, 83–96. [CrossRef]
- Funk, J.L.; Vitousek, P.M. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 2007, 446, 1079–1081. [CrossRef] [PubMed]
- 44. Raghu, S.; Anderson, R.C.; Daehler, C.C.; Davis, A.S.; Wiedenmann, R.N.; Simberloff, D.; Mack, R.N. Adding biofuels to the invasive species fire? *Science* 2006, 313, 1742. [CrossRef] [PubMed]
- 45. Graebner, R.C.; Callaway, R.M.; Montesinos, D. Invasive species grows faster, competes better, and shows greater evolution toward increased seed size and growth than exotic non-invasive congeners. *Plant Ecol.* **2012**, *213*, 545–553. [CrossRef]
- Hierro, J.L.; Eren, O.; Villarreal, D.; Chiuffo, M.C. Non-native conditions favor non-native populations of invasive plant: Demographic consequences of seed size variation? *Oikos* 2013, 122, 583–590. [CrossRef]
- Blossey, B.; Notzold, R. Evolution of Increased Competitive Ability in Invasive Nonindigenous Plants: A Hypothesis. *J. Ecol.* 1995, *83*, 887–889. [CrossRef]
- 48. Vila, M.; Gomez, A.; Maron, J. Are alien plants more competitive than their native conspecifics? A test using *Hypedeum per-foratum* L. *Oecologia* **2005**, *145*, 175. [CrossRef]
- 49. Willis, A.J.; Thomas, M.B.; Lawton, J.H. Is the increased vigour of invasive weeds explained by a trade-off between growth and herbivore resistance? *Oecologia* **1999**, *120*, 632–640. [CrossRef]
- Bossdorf, O.; Auge, H.; Lafuma, L.; Rogers, W.E.; Siemann, E.; Prati, D. Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 2005, 144, 1–11. [CrossRef]
- Martín, P.R.; Burela, S.; Seuffert, M.E.; Tamburi, N.E.; Saveanu, L. Invasive *Pomacea* snails: Actual and potential environmental impacts and their underlying mechanisms. *CABI Rev.* 2019, 2019, 1–11. [CrossRef]
- Hayes, K.A.; Burks, R.L.; Castro-Vazquez, A.; Darby, P.C.; Heras, H.; Martín, P.R.; Qiu, J.-W.; Thiengo, S.C.; Vega, I.A.; Wada, T.; et al. Insights from an Integrated View of the Biology of Apple Snails (Caenogastropoda: Ampullariidae). *Malacologia* 2015, 58, 245–302. [CrossRef]
- 53. Guo, J.; Chen, M.; Wang, Y.; Zhang, J.E. Sex-related differences in feeding, growth and morphological characteristics of *Pomacea* canaliculata. Guangdong Agric. Sci. 2014, 41, 96–100.
- 54. Estoy, G.F.; Yusa, Y.; Wada, T.; Sakurai, H.; Tsuchida, K. Effect of food availability and age on the reproductive effort of the apple, *Pomacea canaliculata* (Gastropode: Ampullaridae). *Appl. Entomol. Zool.* **2002**, *37*, 543–550. [CrossRef]
- 55. Estebenet, A.L.; Martín, P.R. *Pomacea canaliculata* (Gastropoda: Ampullariidae): Life-history traits and their plasticity. *Biocell* 2002, 26, 83–89.
- Burela, S.; Martín, P.R. Nuptial Feeding In the Freshwater Snail *Pomacea canaliculata* (Gastropoda: Ampullariidae). *Malacologia* 2007, 49, 465–470. [CrossRef]

- 57. Yusa, Y. Inheritance of colour polymorphism and the pattern of sperm competition in the apple snail *Pomacea canaliculata* (gastropoda: Ampullariidae). *J. Molluscan Stud.* **2004**, *70*, 43–48. [CrossRef]
- Tamburi, N.E.; Martín, P.R. Reaction norms of size and age at maturity of *Pomacea canaliculata* (Gastropoda: Ampullariidae) under a gradient of food deprivation. *J. Molluscan Stud.* 2009, 75, 19–26. [CrossRef]
- 59. Tamburi, N.E.; Martín, P.R. Effects of food availability on reproductive output, offspring quality and reproductive efficiency in the apple snail *Pomacea canaliculata*. *Biol. Invasions* **2011**, *13*, 2351–2360. [CrossRef]
- Wu, P.; Ren, Q.; Wang, W.; Ma, Z.; Zhang, R. A bet-hedging strategy rather than just a classic fast life-history strategy exhibited by invasive fall armyworm. *Entomol. Gen.* 2021, *41*, 337–344. [CrossRef]
- 61. Dobson, F.S. A lifestyle view of life-history evolution. Proc. Natl. Acad. Sci. USA 2007, 104, 17565–17566. [CrossRef]
- 62. Liang, K.; Zhang, J.; Song, C.; Luo, M.; Zhao, B.; Quan, G.; An, M. Integrated Management to Control Golden Apple Snails (*Pomacea canaliculata*) in Direct Seeding Rice Fields: An Approach Combining Water Management and Rice-Duck Farming. *Agroecol. Sustain. Food Syst.* **2014**, *38*, 264–282. [CrossRef]
- 63. Sin, T.S. Evaluation of different species of fish for biological control of golden apple snail *Pomacea canaliculata* (Lamarck) in rice. *Crop. Prot.* **2006**, *25*, 1004–1012. [CrossRef]
- 64. Stuart, A.M.; Palenzuela, A.N.; Bernal, C.C.; Ramal, A.F.; Horgan, F.G. Effects of fertiliser applications on survival and re-cruitment of the apple snail, *Pomacea canaliculata* (Lamarck). *Crop Prot.* **2014**, *64*, 78–87. [CrossRef]
- 65. Davis, H.G. r-Selected Traits in an Invasive Population. Evol. Ecol. 2005, 19, 255–274. [CrossRef]
- 66. Cowie, R.H. *Apple snails (Ampullariidae) as agricultural pests: Their biology, impacts and management;* CABI Publishing: New York, NY, USA, 2002; pp. 145–192. [CrossRef]
- 67. Joshi, R.C. Problems with the Management of the Golden Apple Snail Pomacea canaliculata: An Important Exotic Pest of Rice in Asia; Springer: Berlin/Heidelberg, Germany, 2007; pp. 257–264.
- 68. Hu, Y.; Mu, X.; Luo, D.; Xu, M.; Yang, Y.; Gu, D.; Luo, J.; Zhang, J. Genetic variability of the invasive snail *Pomacea canaliculata* in South China based on mitochondrial 16S rDNA sequences. *Biochem. Syst. Ecol.* **2014**, *57*, 203–209. [CrossRef]
- 69. Tsutsui, N.D.; Suarez, A.V.; Holway, D.A.; Case, T.J. Reduced genetic variation and the success of an invasive species. *Proc. Natl. Acad. Sci. USA* **2000**, *97*, 5948–5953. [CrossRef]
- Minard, G.; Tran, F.; Van, V.; Goubert, C.; Bellet, C.; Lambert, G.; Kim, K.; Thuy, T.; Mavingui, P.; Moro, C. French invasive Asian tiger mosquito populations harbor reduced bacterial microbiota and genetic diversity compared to Vietnamese au-tochthonous relatives. *Front. Microbiol.* 2015, *6*, 970. [CrossRef] [PubMed]
- Zepeda-Paulo, F.; Ortiz-Martínez, S.; Silva, A.X.; Lavandero, B. Low bacterial community diversity in two introduced aphid pests revealed with 16S rRNA amplicon sequencing. *PeerJ* 2018, 6, e4725. [CrossRef] [PubMed]

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