

Effects of food availability on reproductive output, offspring quality and reproductive efficiency in the apple snail *Pomacea canaliculata*

Nicolás E. Tamburi · Pablo R. Martín

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Abstract Phenotypic plasticity in life history traits favors the establishment of invaders and may magnify their ecological impacts. *Pomacea canaliculata*, the only freshwater snail listed among the 100 worst invaders worldwide, is able to complete its life cycle within a wide range of conditions, a capacity attributed to its life history plasticity. Using snails from their native range in Argentina we investigated the changes in fecundity, egg mass traits, offspring quality, and efficiency of food conversion into eggs in response to different levels of food availability throughout different life stages. Pre-maturity mortality was not affected by chronic reductions of up to 80% in food availability. Females fed ad libitum demonstrated no significant reproductive output differences when mated with males raised at different food availability levels. For females, the number and total weight of eggs and the size of egg masses decreased at high levels of food deprivation. Their efficiency of conversion into eggs of the food ingested during the reproductive period increased with deprivation, as did the survival time of their offspring. In contrast, the egg mass laying rate and the individual egg weight did not differ under different food availability regimes. Reductions in

food availability have been suggested as a control method but our results indicate that fecundity would be lessened only at deprivation levels higher than 50% and would be partially compensated by an increase in hatchling survival.

Keywords Wetlands · Paddy fields · Plasticity · Life history · Maternal effects · Efficiencies

Introduction

Pomacea canaliculata (Lamarck 1822) is a freshwater snail native to southern South America. It has invaded Asia, North America and some Pacific islands (Cowie 2002; Rawlings et al. 2007; Hayes et al. 2008) during the last three decades. This species is the only freshwater snail listed among the 100 worst invaders worldwide (Lowe et al. 2000), although some of the impacts may be attributable to *Pomacea insularum* (Rawlings et al. 2007; Hayes et al. 2008). It causes global economic losses of several billion dollars to aquatic crops such as rice and taro (Joshi and Sebastian 2006). The natural wetlands invaded by *P. canaliculata* suffer major ecosystem level changes due to the eradication of submerged aquatic vegetation and the subsequent increase in water turbidity (Carlsson et al. 2004). Due to the spread of *P. canaliculata*, a significant vector

N. E. Tamburi · P. R. Martín (✉)
Laboratorio de Ecología, Departamento de Biología,
Bioquímica y Farmacia, Universidad Nacional del Sur,
San Juan 670, 8000 Bahía Blanca, Argentina
e-mail: pmartin@criba.edu.ar

of the lung-worm *Angiostrongylus cantonensis* in China, eosinophilic meningitis is becoming an emergent parasitic disease (Lv et al. 2009). The list of countries invaded by *P. canaliculata* and other apple snails is still growing, including recent introductions to Chile (Letelier and Soto-Acuña 2008; Jackson and Jackson 2009) and Spain (López et al. 2010), the first record from Europe.

Most negative effects of *P. canaliculata* stem from its wide macrophytophagous habit that distinguishes it from many other freshwater snails, it being also able to obtain food by scraping, ciliary feeding and predation or necrophagy (Cazzaniga and Estebenet 1984; Wood et al. 2006; Kwong et al. 2009). Their flexible mechanisms of food gathering and ability to exploit diverse food resources is reflected in their capability of growing and maturing in a wide range of trophic situations (Estoy et al. 2002a; Tamburi and Martín 2009a, b).

Pomacea canaliculata shows a high degree of plasticity in various life history traits (Estebenet and Martín 2002). It displays different reproductive patterns depending on the temperature regime to which it is exposed; under a constant temperature of 25°C it is semelparous (one reproductive period per lifetime) whereas under the fluctuating temperatures occurring at its southernmost limit of distribution (monthly means ranging from 7 to 24°C), the populations are iteroparous (multiple reproductive periods per lifetime) (Estebenet and Cazzaniga 1992; Estebenet and Martín 2002; Seuffert et al. 2010).

Additionally, both the identity and the quantity of the plants consumed affect various life history parameters. For instance, despite their wide trophic spectrum, when limited to mono-specific diets, growth rates, survivorship and fecundity are strongly dependent on plant identity (Estebenet 1995; Lach et al. 2000; Qiu and Kwong 2009). Food availability also affects the age and size at maturity (in females and males respectively; Estoy et al. 2002a; Tamburi and Martín 2009a) and the total number of eggs produced by mature females (Estoy et al. 2002b).

In general, colonizers of new areas are expected to have low genetic variability due to founder effects, and this may impede them from becoming established as successful invaders (Guo 2006). Phenotypic plasticity is itself an adaptive trait (Caswell 1983; Gotthard and Nylin 1995; Whitman and Agrawal 2009), which is selectively favored by environmental

variability, therefore increasing environmental tolerance (Seigel and Ford 2001; Chevin et al. 2010). Phenotypic plasticity in behavioral and life history traits can help increase their success as invaders of new environments and magnify their ecological effects (e.g. Hänfling and Kollmann 2002; Wilson et al. 2009; Valiente et al. 2010).

For freshwater mollusks, fecundity (eggs per female per year) is the primary predictor of successful establishment and of the potential to generate detrimental economic and ecological consequences in invaded areas (Keller et al. 2007). *Pomacea canaliculata* females deposit egg masses above the water line, each containing 100–300 eggs (Estebenet and Cazzaniga 1993; Albrecht et al. 1996; Estoy et al. 2002b; Martín and Estebenet 2002). The high fecundity of *P. canaliculata* females coupled with their sperm storage capabilities (Estebenet and Martín 2002; Burela and Martín 2011) may enable colonizers to overcome low density or Allee effects, considered a cause for invasion failure (Jerde et al. 2009). In this context, we investigated the reproductive response to food availability in *P. canaliculata*, specifically its effects on reproductive output, offspring quality and efficiency of food conversion to reproductive products, to identify the key factors of its life history strategy that contribute to its invasiveness.

Materials and methods

The general setting of the experiment has been described in previous works, where the chronic effects of food availability on age and size at maturity (Tamburi and Martín 2009a) and on growth rates (Tamburi and Martín 2009b) were reported. Snails were reared individually under seven food availability treatments from an age of 3 weeks up to 1 month after maturation. Maturity was tested with an independent set of mature consort snails (fed ad libitum) that were allowed to copulate with experimental ones once a week. The experiment was ended after 70 weeks, when 96% of the snails were already mature.

To focus on phenotypic plasticity and to minimize the interaction between genotype and environment (food availability) the experimental snails used in the study were full-siblings. They came from a single egg mass laid by a laboratory female that had been

coupled during all her life with the same male (both obtained from egg masses from the Curamalal Grande stream, Southern Pampas, Buenos Aires Province, Argentina). Snails were reared in a rearing chamber at $25 \pm 3^\circ\text{C}$ and a 14:10 h (light:dark) photoperiod. During all the experiments tap water saturated with Ca CO_3 was used and the snails were fed only on fresh lettuce. All the hatchlings from the egg mass were reared in a 20 l collective aquarium for 3 weeks until they reached a size (shell length: $4.96 \text{ mm} \pm 0.056$, mean \pm SE, $n = 25$) that allowed manipulation without damage. After this initial period, 72 hatchlings were randomly selected and thereafter reared in isolation under seven levels of relative food availability (FA%) in 3 l aquaria. As snails were sexed a posteriori it was not possible to achieve a total balance of the experimental design. The final number of males in each FA% level was five while for females it varied from three to six.

The daily amount of drained fresh lettuce ingestion by a snail of a given size (FA100%, g) was calculated using an empirical equation with shell length (SL) as the predictive variable (i.e.: $\text{FA100\%} = 0.0033 \cdot \text{SL}^{1.9322}$, Tamburi and Martín, 2009b). The other levels of relative food availability were calculated accordingly (FA%: 87, 73, 60, 47, 33 and 20%); for instance, the initial daily rations for the different treatments were 0.084, 0.0728, 0.0616, 0.0504, 0.0392, 0.028 and 0.0168 g respectively.

Once a week the water was changed, aquaria were cleaned of feces and debris, and their position in the rearing chamber was changed randomly. The shell length of each snail was measured using a micrometric lens (up to the 6th week) or with calipers thereafter. Males were identified, typically at shell length of 15 mm, by the observation of the testicle through the translucent shell (Takeda 1999) and of the humping of the operculum (Estebenet et al. 2006); in all cases the sex was confirmed later by their reproductive behavior (Tamburi and Martín 2009a). The weekly amount of lettuce for each FA% level was calculated according to the mean shell length of all snails assigned to it. The live weight (LW, g) of each snail was obtained every 4 weeks using an analytical scale (± 0.1 mg).

To detect the effect of food availability independently for each sex, couples of snails were arranged with an external set of consort snails (fed with lettuce ad libitum). The consort snails had hatched 3 months

before the experimental ones from egg masses from the same stream. Once they could be sexed males and females were reared separately to guarantee their virginity and identity. Consort snails were assigned randomly to experimental snails of the opposite sex. Each week after the water change the experimental snails and their assigned consorts were put together for 24 h to allow copulation. During this day no food was provided, to avoid trophic interferences between experimental and consort snails. After this period of 24 h the consort snails were removed and the experimental ones were fed their assigned weekly ration.

Once the first egg mass appeared in each aquarium of experimental and consort females, the reproductive output was quantified for 4 weeks. When an egg mass was observed attached to the aquarium walls, the contents (female, water, lettuce remains and feces) were transferred to an empty aquarium. All the egg masses (excluding the second one) were treated with bleach (sodium hypochlorite 55 g l^{-1}) to detach them from the glass and to loosen the eggs. The eggs of each egg mass were counted and the dry weights of the first nine egg masses were obtained after 48 h at 80°C .

The second egg mass of each female was incubated at room temperature in the aquarium in which it was laid (with 1 cm of water in the bottom) until hatching was completed. The number of hatchlings was counted and the number of non-hatched eggs was obtained by treating them by the same method as used for the other egg masses. Ten hatchlings from each egg mass were separated on their first day and reared in cylindrical plastic pots (diameter: 7 cm) with 200 cm^3 of tap water in a closed rearing chamber without illumination or food at $25^\circ\text{C} \pm 1$. Once a week live snails were counted and dead ones removed to preclude necrophagy.

We recorded the accumulated number of egg masses (EM) and eggs (E) laid during the first month after the first egg mass for each female (experimental or consort). The mean number of eggs per egg mass (EEM) was calculated as E/EM , and the mean weight of an individual egg (IEW; mg) was calculated as the weight of the first nine egg masses divided by the number of eggs in that mass. The total weight of eggs (TEW, g) was calculated as the product of IEW by E.

For experimental females two indices of reproductive efficiency were calculated. The efficiency of

conversion into eggs of the food ingested as immature individuals (EFI) was calculated as the ratio between TEW and the accumulated fresh weight of the lettuce consumed during the entire pre-reproductive period. The efficiency of conversion of food as mature individuals (EFM) was calculated on the basis of TEW and the accumulated lettuce consumed during the reproductive month. The egg mass viability (V) was calculated as the number of hatchlings divided by the number of eggs in the second egg mass from each experimental or consort female. The median survival time of hatchlings (ST50) was estimated by linear interpolation as the time at which half of the starving hatchlings died.

Statistical analyses were performed separately for experimental females and consort females of experimental males due to a strong interaction between sex and food availability in most analyzed variables (Tamburi and Martín 2009a, b). The effect of food availability was investigated through one-way ANOVAs when Levene's test for homogeneity of variances was not rejected (for original or transformed variables; see "Results") and by the Kruskal–Wallis test when it was rejected even after the different transformations indicated by the Box-Cox method had been applied.

Results

The growth curves of live weight (LW, g) showed a steady increase in males (Fig. 1), while in females a reduction in growth rates, and even in individual absolute weight, was observed after egg laying started (especially in females maintained at food

availability levels that resulted in higher weights). Only three out of six females from the most deprived treatment (20 FA%) showed copulatory behavior, and deposited egg masses at 50 weeks of age on average. The remaining three did not copulate or lay eggs during the entire 70 week experimental period. The mean live weight of males at the beginning of the copulatory behavior was 0.84–5.4 g and was directly related to food availability ($r = 0.97$; $P < 0.001$; $n = 7$), whereas for females it was 7.3–15.3 g without a definite pattern ($r = 0.018$; $P = 0.970$; $n = 7$).

The food availability at which experimental males were reared showed no significant effect on any of the variables related to reproductive output (Table 1) or offspring quality measured on their consort females (Table 2).

The reproductive output measured as the number of egg masses (EM), eggs (E) and eggs per egg mass

Table 1 One-way ANOVAs for the effect of food availability on reproductive output variables of *P. canaliculata*

	EM	E	EEM	IEW	TEW
<i>Male</i>					
$F_{6;27}$	0.528	0.345	0.561	6.69*	1.435
P	0.78	0.91	0.757	0.35	0.238
<i>Female</i>					
$F_{6;21}$	1.11	4.96	3.88	1.467	2.84
P	0.388	0.0026	0.0092	0.237	0.035

EM, log-transformed Number of egg masses, E number of eggs, EEM number of eggs per egg mass, IEW weight of an individual egg, TEW total weight of eggs

* Analyzed with Kruskal–Wallis test (χ^2_6)

Fig. 1 Growth curves for mean live weight of *P. canaliculata* reared over a range of food availabilities; **a** males, **b** females. Black diamonds indicate the first copulation at each FA% level. Curves extend to 1 month after the first egg mass was laid

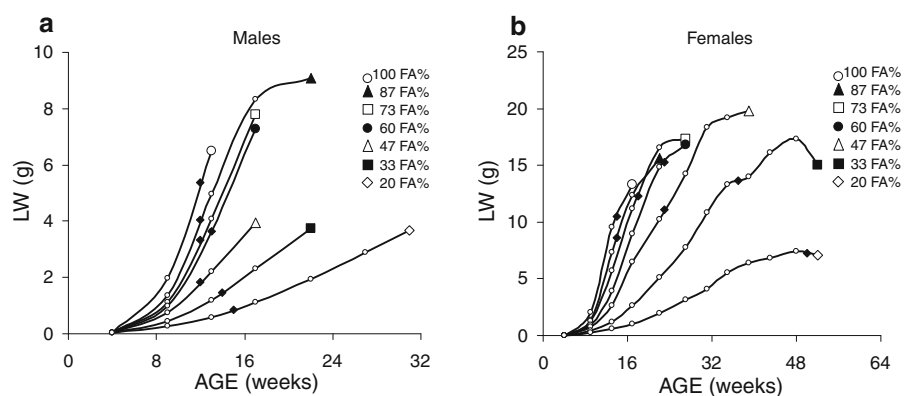


Table 2 One-way ANOVAs for the effect of food availability on offspring quality variables of *P. canaliculata*

	V%	ST50%
<i>Male</i>		
<i>df</i>	6;26	6;21
<i>F</i>	1.295	0.776
<i>P</i>	0.294	0.597
<i>Female</i>		
<i>df</i>	6;23	6;19
<i>F</i>	0.817	3.45
<i>P</i>	0.568	0.0178

Egg mass viability (V%); median survival time of hatchlings (ST50%)

(EEM) showed a decreasing trend with the decreasing food availability to which the experimental females were exposed, especially for levels lower than 60% (Fig. 2). However, only E and EEM were significantly different among treatments (Table 1). The weight of an individual egg (IEW) showed no significant variation across the food availability range tested, whereas the total weight of eggs (TEW) showed a significant effect, with a maximum value at 73% of food availability. Egg numbers showed the greatest effect of food availability with variation between FA% levels being 4.96 times higher than levels within. The values of the reproductive output variables of experimental females in the lower FA% levels were generally lower than those of consort females (fed ad libitum) (Fig. 2).

The quality of the experimental females' offspring (Table 2), measured as the viability of their egg masses, was not altered by food availability, and was in all cases similar to that of consort females (68.5 vs. 65.5%, respectively), with a grand mean of 67%. The median survival time of starving hatchlings from experimental females (Table 2; Fig. 3), increased significantly as food availability decreased (from 22 to 43 days on average compared to 26 days for experimental males' offspring). The maximum individual survival times recorded for the offspring of consort and experimental females were 63 and 80 days, respectively.

The efficiency of conversion into eggs of food ingested by immature snails (EFI) showed a decreasing trend with food availability, but it was not significant (Table 3; Fig. 4). The reproductive efficiency

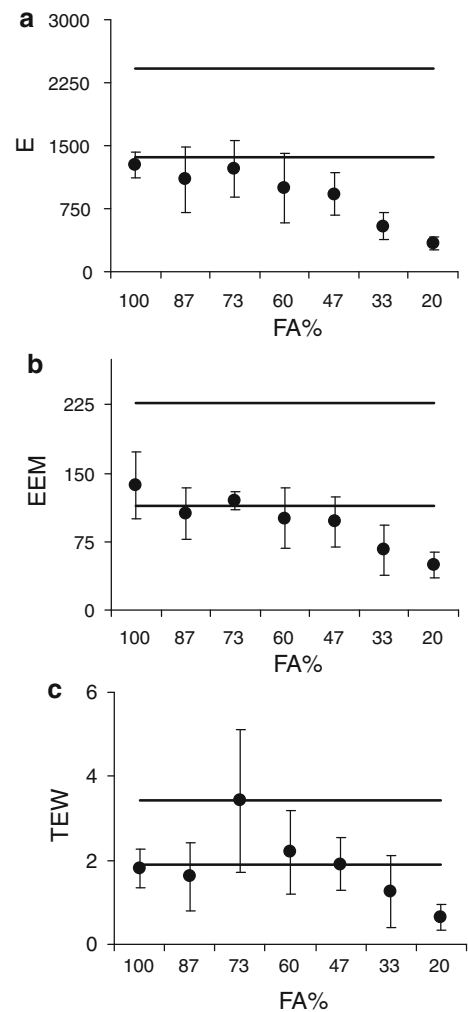


Fig. 2 Effect of food availability on reproductive output variables of *P. canaliculata* during the first reproductive month; **a** number of eggs (*E*), **b** mean number of eggs per egg mass (*EEM*), **c** total weight of eggs (*TEW*). Error bars are mean \pm SD for experimental females. Continuous lines are total mean \pm SD for consort females

calculated for the mature individuals (EFM) showed a significant increase with the decrease of food availability. The variation between FA% levels for EFI and EFM was 2.22 and 5.41 times higher than the intra-level variation, respectively.

Discussion

The increase in live weight of *P. canaliculata* females slowed when reproductive activity began, while

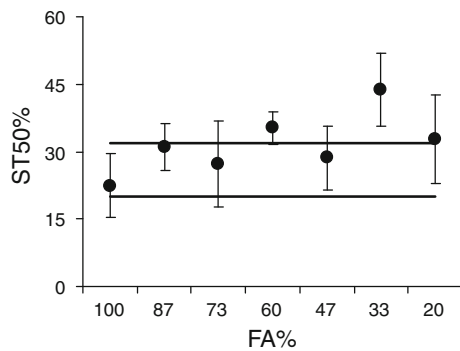


Fig. 3 Effect of food availability on median survival time of hatchlings (ST50%) of *P. canaliculata*. Error bars are mean \pm SD for hatchlings from experimental females. Continuous lines are total mean \pm SD for hatchlings from consort females

Table 3 One-way ANOVAs for the effect of food availability on the efficiency of conversion into eggs of the food ingested as immature (EFI) or as mature individuals (EFM, log-transformed) of *P. canaliculata*

	EFI	EFM
<i>Female</i>		
$F_{6;21}$	2.217	5.41
P	0.082	0.0016

males showed no change in growth pattern. There was no mortality during the study. The food availability to which males were exposed had no effect on the variables analyzed in their female consorts. In the case of experimental females the number and total weight of eggs and the size of egg masses showed a

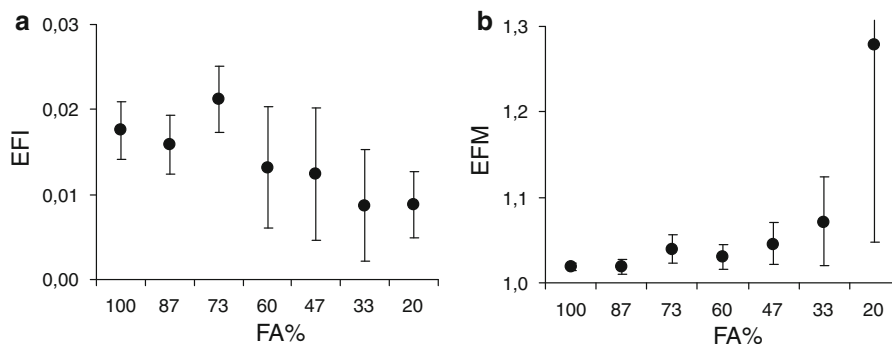


Fig. 4 Effect of food availability on the efficiency of food conversion into eggs for experimental females of *P. canaliculata*; **a** relative to food ingested during the pre-reproductive period (EFI), **b** relative to food ingested during the

decrease at high levels of food deprivation; on the other hand their efficiency of conversion of the food ingested during the reproductive period into eggs and the survival time of their offspring increased with food deprivation.

Mortality was not affected by food availability, even in the case of females under the most severe deprivation, in which the pre-reproductive period extended from 13 to 50 weeks (relative to those better fed; Tamburi and Martín 2009a). Similarly, there was no correlation between food availability and mortality for *P. canaliculata* in Japan (Estoy et al. 2002a, b). Our results confirm that these apple snails are able to survive in good condition to complete their life cycle under a very wide range of food availability.

Recent theoretical models of *P. canaliculata* invasions indicate that the survival probability of a fertilized female is a key factor to invasion success (Jerde et al. 2009). In this species, males can mate with several females (Burela and Martín 2009), the age at which males mature is not affected by food availability (Estoy et al. 2002a; Tamburi and Martín 2009a) nor are the fecundity and the quality of the offspring of their mates. Male size is strongly reduced as deprivation increases (Tamburi and Martín 2009a) but size has no effect on their mating or reproductive success (Estoy et al. 2002a). These results indicate that in most circumstances the availability of fertile males is not a limitation for the successful establishment or persistence of populations of this apple snail. So, the diverse consequences of food availability on population growth and spread probably arise only

reproductive period (EFM). Error bars are mean \pm SD. The mean values of EFM were back-transformed using anti-logarithms to show the variable in the original scale

from the response of females' reproductive output and quality of offspring.

The number of eggs per egg mass decreased as food availability decreased while the number of egg masses was not significantly reduced. This lack of response to deprivation could be related to the adoption of a strategy that spreads the risk of a potential loss of a big egg mass among several smaller ones. Such losses may result from changes in water level that lead either to submersion or to hatchlings falling beyond the water's edge (Turner 1998; Pizani et al. 2005; Horn et al. 2008).

Egg size is a highly conservative trait, usually less variable than offspring number (Stearns 1992). Our results show no change in individual egg weight with decreasing food availability. As food deprivation increases the female strategy seems to be to sacrifice the number of eggs instead of their size. Due to mechanical constraints of the female reproductive tract, the constancy in egg size may be related to the small variation in female size at maturity (Tamburi and Martín 2009a), or to stabilizing selection on the surface-to-volume ratio of these aerial cleidoic eggs that are fully exposed to weather conditions (Pizani et al. 2005).

The viability of eggs may change the importance of fecundity's role in invasiveness in *Pomacea canaliculata* (Barnes et al. 2008; Burks et al. 2010) but it was not affected by maternal food deprivation in our study. The average value (67%) reported herein falls into the lower extreme of the range reported for *P. canaliculata*. (e.g. 68%, Terra and Schäfer 1999, 77%, Pizani et al. 2005; 86%, Estebenet and Cazzaniga 1993).

Survival times of several weeks have been reported for starving adult and juvenile *P. canaliculata* (Estebenet and Martín 2002; Seuffert and Martín 2010), but no data were available hitherto for hatchlings, which depend only on the perivitelline egg reserves stored in their mid-gut gland (Heras et al. 1998; Koch et al. 2009). Hatchlings showed a high resistance to starvation, with median survival times longer than 3 weeks and individual maximum values of up to 80 days, a capacity probably relevant to their establishment in habitats in which food availability is low or highly variable. Moreover, survival time of hatchlings under starvation increased with the level of food deprivation of their mothers.

Maternal effects such as this may be mediated cytoplasmically by the egg cell (e.g. yolk quality, hormones, mRNAs; Mousseau and Fox 1998) or by the external reserves provided by the mother. *Pomacea canaliculata* females lay fewer eggs when they are exposed to very low food availability, but as the weight of individual eggs did not change, an effect of the amount of reserves can be ruled out. Consequently, a plausible explanation is that the composition and quality of the biochemically complex perivitelline reserves of each egg (Heras et al. 2007) changed to increase the chances of the hatchlings surviving under conditions similar to those to which their mothers had been exposed. Food related maternal effects may result in better fed females producing offspring of higher quality by virtue of their own somatic condition (e.g. van der Sman et al. 2009); or alternatively, less well fed females produce offspring better fitted to cope with a poor environment, despite their lower somatic condition (Plaistow et al. 2004). This last type of maternal effect is considered adaptive transgenerational plasticity (Plaistow et al. 2004) and in the case of *P. canaliculata* may serve to compensate for the diminished number of eggs at very low food availability.

Estoy et al. (2002b) found that current and weight specific reproductive effort were independent of food availability. For the snails used in the present study the efficiency of conversion of food into body biomass during the pre-reproductive phase was independent of food availability (Tamburi and Martín 2009b). The efficiency of conversion into eggs of the food ingested in the pre-reproductive period was not affected by food deprivation while the efficiency during the reproductive period increased with food deprivation. Consequently, the decline in female growth rates at maturity is probably caused in part by their high reproductive output. Given that the pre-reproductive period is extended as food deprivation increases (Tamburi and Martín 2009a), a feasible explanation is that poorly nourished females delay their maturation until they accumulate a certain amount of reserves and that after they have started egg laying the latter are used up intensively. This strategy seems adequate for an iteroparous organism in which mortality is not dependent on food availability (Stearns, 1992), as in *P. canaliculata* (Estoy et al. 2002a, b). Under

natural conditions in Southern Pampas, populations seem to be iteroparous (Estebenet and Cazzaniga 1992; Estebenet and Martín 2002; unpub. results) although under the experimental conditions of this study *P. canaliculata* behaves as a semelparous species (Estebenet and Martín 2002). Paddy field populations in temperate Japan are also semelparous (Yoshida et al. 2009), but in this case it is mostly due to the high winter mortalities which prevent most individuals from attaining a second reproductive period.

Reductions in food availability may improve control strategies in paddy fields since they would decrease population growth rate due to a decline in fecundity and an increase in generation time, while direct reductions in density alone (Estoy et al. 2002b) would be compensated by density-dependent increase in growth and fecundity (Tanaka et al. 1999). Any reduction in food availability would reduce population growth through a delay in female maturity (Estoy et al. 2002a; Tamburi and Martín 2009a). However our results indicate that a reduction in fecundity would appear only at deprivation levels higher than 50% and would be compensated partially by an increase in hatchling survival. Under extreme food deprivation (20 FA%) half of the females were not able to reach maturity in 70 weeks, indicating that, all other factors being equal, beyond this trophic deprivation threshold females would be incapable of completing their life cycle.

Cowie (2002) stressed the importance of comparative studies on the ecology of apple snails from both native and invaded ranges to detect evolutionary changes in the invaders. Hitherto, plasticity in non-native *Pomacea canaliculata* has been studied only in Japan (Estoy et al. 2002a, b) where, according to molecular genetic analyses, apple snails have been introduced from the Río de la Plata basin near Buenos Aires (Hayes et al. 2008). The response of reproductive and life history traits to food availability for *P. canaliculata* from Japan (Estoy et al. 2002a, b) and from Southern Pampas (Tamburi and Martín 2009a; this study) show strikingly similar patterns: male size and female age at maturity, fecundity and egg mass size are plastic while male age and female size at maturity, egg mass laying rate and egg size are canalized. This similarity supports the hypothesis (Tamburi and Martín 2009a) that phenotypic plasticity in reproductive and life history traits is not a

derived trait unique to Japanese populations of *P. canaliculata*.

The variety and flexibility of the feeding mechanisms of *P. canaliculata* and its wide dietary spectrum probably indicate an evolutionary history coping with trophic resources that are both variable and unpredictable, in part due to its own depletory activities (Tamburi and Martín 2009a). Plasticity in some traits can be viewed just as a mechanism to preserve other traits from change, and whether a given trait is canalized or plastic depends of the life history strategy of the species (Whitman and Agrawal 2009). *Pomacea canaliculata* females probably do not risk dying by depletion of somatic reserves, at the expense of a very much delayed maturity and a relatively minor reduction in numerical fecundity in the poorest habitats. The size of the eggs and their high viability are conserved, and moreover the hatchlings' survival increases with the increase in the level of food deprivation of their mothers.

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