PEDAL SURFACE COLLECTING AS AN ALTERNATIVE FEEDING MECHANISM OF THE INVASIVE APPLE SNAIL *POMACEA CANALICULATA* (CAENOGASTROPODA: AMPULLARIIDAE)

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ABSTRACT

Apple snails are freshwater gastropods with highly diverse feeding mechanisms (shredding, scraping and collecting) to exploit diverse food sources. *Pomacea canaliculata* is listed among the world's 100 worst invaders, mainly due to its effects on aquatic crops and submersed macrophytes through shredding, its main feeding mechanism. In one of the alternative mechanisms, the snails obtain material from the water surface through a funnel formed by the anterior part of the foot, here termed pedal surface collecting (PSC). Our aims were to study the potential trophic spectrum of PSC and the effects of snail size and sex, density of food particles and particle size on efficiency of this feeding mechanism under laboratory conditions. We also explored occurrence and daily fluctuations in the field. *Pomacea canaliculata* snails were able to capture different food types irrespective of their physical nature (liquid, organic particles and biofilms) and size, although not all of them could be ingested. PSC was performed only when food was available on the surface by snails from the whole size range tested (3–52.8 mm shell length), although it was less frequent in snails <10 mm. The amount of food captured by unit mass decreased with animal size, but is partially compensated by a corresponding increase in frequency and duration of PSC. The specific capture rate increased, and the time spent forming pedal funnels decreased, with food density, but no effects of particle size were observed. In the field, PSC was observed only occasionally during the day, but showed a marked increase after sunset, and was observed even when submerged macrophytes and associated periphyton were abundant. The wide trophic spectrum, the high and adaptable capture rates and the wide size tolerance likely allow *P. canaliculata* to take advantage of highly variable and unpredictable food resources present on the water surface, thereby contributing to the invasion success of the species.

INTRODUCTION

Apple snails (Ampullariidae) are freshwater gastropods that mostly inhabit lentic or slow-running watercourses in tropical to warm temperate regions and display highly diverse feeding modes that allow them to exploit a great diversity of food sources (e.g. Andrews, 1965; Cazzaniga & Estebenet, 1984; Aditya & Raut, 2001; Kwong, Chan & Qiu, 2009, Kwong *et al.*, 2010). The feeding habits of some invasive apple snails can provoke marked changes in wetlands and cause major economic losses in aquatic agricultural systems (Cowie, 2002; Carlsson, Brönmark & Hanson, 2004; Joshi & Sebastian, 2006). According to the classification of functional feeding groups of aquatic invertebrates by Cummins & Klug (1979), apple snails feed by shredding (obtaining pieces of submersed materials, mainly with the jaws), scraping (obtaining material adhering to submersed surfaces, mainly with the radula) and collecting (obtaining material from the water surface with the foot). All three mechanisms can be used by the same individual in rapid succession to obtain vegetal, animal or microbial materials.

Shredding is the best-studied mechanism in ampullariids, particularly when feeding on macrophytes, aquatic crops (e.g. Cowie, 2002; Morrison & Hay, 2011b) and animal material (e.g. Demian & Lutfy, 1966; Cazzaniga & Estebenet, 1984; Aditya & Raut, 2001). In spite of the wide dietary spectrum, feeding rates on different macrophytes are highly variable (Morrison & Hay, 2011b) and some even appear to be totally unpalatable (Estebenet, 1995; Lach *et al.*, 2000; Howells, 2002). Apple snails can deplete the palatable aquatic vegetation (e.g. Horne, Arsuffi & Neck, 1992; Carlsson *et al.*, 2004; Pointier & David, 2004), favour the dominance of unpalatable species (Qiu & Kwong 2009; Tamburi & Martín, 2009a) or induce the expression of chemical defences (Morrison & Hay,

2011a). In these three situations, the lack of palatable macrophytes may promote the use of resources that require alternative feeding mechanisms, including surface collecting.

When collecting food from the water surface, the posterior part of the foot remains attached to a submerged substrate and its anterior part forms a funnel that attracts and captures material by ciliary action (Johnson, 1952; Cheesman, 1956; McClary, 1964; Cazzaniga & Estebenet, 1984). The captured material is bound with pedal mucus, collected at the base of the funnel and ingested using the jaws and radula. Johnson (1952) first described this mechanism and named it 'ciliary feeding' because of its apparent resemblance to ciliary feeding in the Viviparidae, although the latter use the ctenidium as a filter to collect material suspended in the water (Hockelmann & Pusch, 2000). Declerk (1995) used 'ciliary feeding' for gastropods, including ampullariids, that use pedal cilia and mucus to capture food particles suspended in the water column (seston). However, the inclusion of ampullariids in this category is misleading, as they capture what is usually termed neuston (i.e. organisms resting or swimming on the water surface; Allaby, 1998) and associated remains of terrestrial and aquatic organisms, rather than seston. To be consistent with the classification of Cummins & Klug (1979), we prefer the term 'pedal surface collecting' (PSC), which alludes to the particular site where food is collected and the specific organ used.

PSC has been considered characteristic of ampullariids and is very rare among freshwater gastropods (McClary, 1964; Dillon, 2000). Only McClary (1964) has studied it experimentally and quantitatively, using artificial food particles in the laboratory. Ontogenetic and sexual variation in PSC might be expected in ampullariids as feeding rates on macrophytes are dependent on snail size (Hannifa 1982; Carlsson & Brönmark, 2006; Burlakova et al., 2009) and sex (Tamburi & Martín, 2009b).

Pomacea canaliculata (Lamarck, 1822) occurs in lakes, ponds and streams in southern South America (Martín, Estebenet & Cazzaniga, 2001; Hayes et al., 2008). This species and congeners have been introduced in Asia, North America and the Pacific islands (Cowie, 2002; Rawlings et al., 2007; Hayes et al., 2008; Lv et al., 2012). Pomacea canaliculata is the only freshwater snail listed among the 100 worst invaders worldwide (Lowe et al., 2000). The present contribution reports laboratory experiments on the potential trophic spectrum available to P. canaliculata via PSC and the effects of snail size and sex, density of food particles and particle size. We also report on the occurrence and daily fluctuations of this feeding mechanism in the field.

MATERIAL AND METHODS

Origin of individuals and rearing conditions

Adult snails were hand-collected in Guaminí Stream ($37°$ $02'$ $59''$ S, $62°$ $25'$ $26''$ W) in the Encadenadas del Oeste basin (Buenos Aires province, Argentina). Hatchlings were obtained from egg masses laid by these snails in the laboratory. They were reared in collective aquaria in a rearing room at $25 \pm 2°$C, under a photoperiod of 12 h light/12 h dark, with $CaCO_3$-saturated tap water, and fed on fresh lettuce. Aquaria were cleaned and the water changed once a week.

Food spectrum under laboratory conditions

To evaluate the trophic spectrum available through PSC, different items of diverse origin were offered to the snails (see Results, Table 1). These items were chosen as representative of food types that are typically abundant on the surface of water bodies from Encadenadas del Oeste basin. Some were obtained from natural environments in southern Buenos Aires province, while others were chosen as surrogates of trophic resources that are potentially available in aquatic environments (e.g. cockroaches as remnants of large insects or their exuviae, commonly found floating in ponds). We also tested the capture and ingestion of organic films on the water surface, including

Table 1. Capture and ingestion by pedal surface collecting of different materials supplied to *Pomacea canaliculata*. Each item was provided in a different aquarium.

Material type	Item	Scientific name	Description	Origin	Capture	Ingestion
	PVC	Polyvinyl chloride	Scraps, 0.5–2.0 mm	C	0	0
Inedible	Tracing paper		Squares, <0.5 mm	C	+	+
	Aluminium foil		Squares, <0.5 mm	C	0	0
	Natural biofilm		Mucilaginous layer, 1–5 mm thick	L	++	++
Films	Vegetable oil		Drops <3 mm thick	C	+[1]	+
	Mineral oil		Drops <3 mm thick	C	+[1]	+
Inflorescences	Pampas grass	*Cortaderia selloana*	Rachis pieces with seeds and flowers, 10–20 mm	N	++	++
	Bulrush	*Typha* sp.	Flowers, seeds,10–15 mm	N	++	++
	White poplar	*Populus alba*	Leathery bracts, 4–6 mm	N	++	−
			Cottony seeds, 2–5 mm	N	++	++
Pollen	Ash	*Fraxinus* sp.	Spheroidal grains, 18–25 μ	N	++	++
Seeds	Poppy	*Papaver rhoeas*	Reniform seeds, <1 mm	C	++	++
Petals	Chinese wisteria	*Wisteria sinensis*	Dry, 10–20 mm	G	++	++
	Fat duckweed	*Lemna gibba*	Alive, 3–5 mm	N	++	++
Floating plants	Duckweed	*Wolffia columbiana*	Alive, <1.5 mm	N	++	++
	Water fern	*Azolla filiculoides*	Alive, 5–15 mm	N	++	++
Insect remains	Cockroaches	*Blatella germanica*	Exuviae, nymphs, 10–20 mm	L	++	++
			Oothecae, dead adults, 5–10 mm	L	++	−
Whole insects	Leafcutter ants	*Acromyrmex striatus*	Dead worker ants, 3–5 mm	N	+	0
	Aphid	*Aphis nerii*	Alive wingless females, 2–3 mm	G	+	+
Bird feathers	Pigeon	*Columba livia*	Down feathers, 20–50 mm	N	0	−

C, commercial; N, natural environment; G, urban garden; L, laboratory; +, moderate; ++, intense; 0, no attempts; −, failed attempts; [1], without forming a mass.
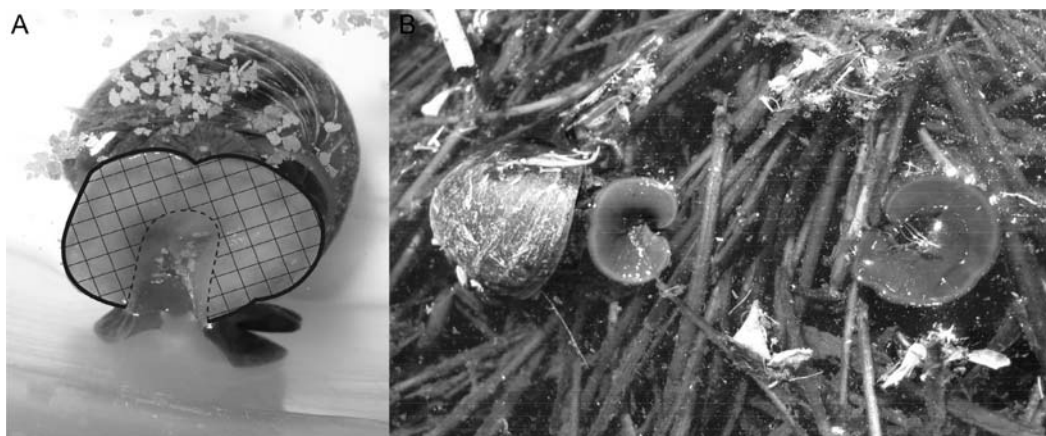
Figure 1. A. *Pomacea canaliculata* performing pedal surface collecting (PSC) in a laboratory trial; the thick black line indicates the perimeter of the pedal funnel (PFP) and the crossed zone its area (PFA). **B**. Two *P. canaliculata* performing PSC in the Pigüé-Venado channel.

biofilms (composed mostly of bacteria, ciliates and rotifers, developed naturally in aquaria used to stock *P. canaliculata*) and vegetable oil. Additionally, we tested inedible materials (PVC, tracing paper, aluminium foil) and mineral oil.

Qualitative observations were carried out in 24-l glass aquaria (20 wide, 40 long, 30 cm deep) at 25°C under natural illumination complemented with artificial light. Each food item was tested separately. Ten snails randomly chosen from a laboratory stock [shell length (SL) 10–50 mm, measured from the apex to the farthest point of the aperture] were placed in a clean aquarium with tap water. When the snails became active (i.e. foot in full contact with the bottom), each item was scattered or poured gently onto the surface and its capture by PSC and subsequent ingestion were recorded for the next 2 h. Sufficient quantities of each item were provided to ensure even distribution on the water surface.

Effect of snail size and sex, food density and particle size under laboratory conditions

To quantify the parameters of PSC and the effects of snail size and sex, food density and food particle size, we performed three experiments using isolated snails. TetraFin[®] fish food flakes, dried at 70°C for 48 h, were used as floating particulate material. Observations were carried out in circular plastic aquaria (depth 5 cm; water surface area 962 cm^2), with tap water at 22–25°C, under natural illumination complemented with artificial light. Each aquarium was surrounded by an acetate film cylinder (35 cm high) to minimize drafts that might generate movement of the particles on the water surface.

In each trial, one snail was placed in the centre of an aquarium and a measured quantity of food was scattered on the water surface after it became active; four aquaria were observed simultaneously. The SL (mm) and live weight (LW, g) were recorded. Snails of <30 mm SL were considered sexually undifferentiated and those of >30 mm SL were sexed by the shape of the operculum (Estebenet, Martín & Burela, 2006). Snails were starved for 24 h prior to the trial and were used only once in each experiment.

Observation periods began with the activation of each snail. During the 2 h of observation, the time spent performing PSC was recorded, as well as the number of pedal funnels formed; they were considered finished when the snail commenced another activity (e.g. ingestion of the mucous ball, crawling, etc.). The rate of pedal funnel formation (PFR, funnel snail^{-1} h^{-1}) was calculated based on the number of funnels divided by the total time the snail was active during the observation period. At least one funnel for each snail was photographed from above. The perimeter of the pedal funnel (PFP, cm) and its horizontal area in contact with air (PFA, cm^2) were measured from the photographs (Fig. 1A), using the image analysis software SigmaScan Pro[®].

Following each observation period, the remains of food captured but not ingested (abandoned mucous balls) and faeces were collected with a plastic Pasteur pipette. The water in each aquarium then was filtered with a pre-weighed paper filter to retain any non-captured food. The filter was dried at 70°C for 48 h and weighed; the total amount of food captured (TFC, g) was estimated as the difference between the ration provided and the non-captured food. Specific capture rate (SCR, g g^{-1} min^{-1}) was estimated as the food captured (TFC, g) divided by the time performing PSC (in min) and the LW. The percentage of time performing PSC (TPSC, %) relative to the total active time was also calculated. The number of snails in the statistical analyses of these variables varied as the number of active snails and the number of activities performed varied among experiments.

In all trials, some food flakes sank to the bottom partly due to snail activity. In the experiment dealing with different densities, it was evident that the amount of food on the bottom differed among treatments. The amount of sunken food was estimated by recovering it in a series of eight trials in which feeding on the bottom was impeded by a horizontal plastic grid. The percentage of sunken food was estimated as 7.5 ± 3.4% (mean ± SD) and the amount of food captured by PSC corrected accordingly.

To assess sexual and ontogenetic variations in PSC, snails of different sexes (58 undifferentiated, 29 males and 29 females) and sizes (2.7–52.8 mm SL) were used. In each aquarium, 0.5 g of food of the same particle size (<1 mm) was distributed (food density: 0.52 mg cm^2). A simple allometry model relative to SL (mm) ($Y = a \cdot SL^b$) was adjusted by a least-squares regression analysis of the variables, which were transformed logarithmically to linearize the relationship ($\log_{10} Y = \log_{10} a + b \cdot \log_{10} SL$). Differences between males and females in the slope (b) and the intercept ($\log_{10} a$) were analysed by one-way ANCOVAs.

To determine the effect of food density on PSC, four treatments of increasing food density (0, 0.26, 0.52 and 1.04 mg cm^{-2}) were performed. Each treatment was replicated 12 times using sexually differentiated snails (SL 25–35 mm). Food particle size was <1 mm. SCR was $\log_{10}$-transformed after the rejection of homoscedasticity (Levene's test, $P < 0.006$). The data were analysed by one-way ANOVAs.

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To assess any effect of particle size relative to snail size on PSC, 0.25 g of food of four different particle sizes ($<$1, 1–3.5, 3.5–10 and 10–15 mm, fractionated with sieves) were provided to snails of two different sizes (20–25 and 30–40 mm SL); each combination was replicated five times. The data were analysed by two-way ANOVAs, using particle size and snail size as main factors. After the rejection of homoscedasticity (Levene's test, $P < 0.037$), TPSC was $\log_{10}$-transformed.

Occurrence and daily fluctuations in the field

Observations were performed in an excavated channel (6 wide, 1 m deep) with a muddy bottom that links Pigüé and Venado Streams (37° 09′ 59″ S, 62° 40′ 28″ W, Encadenadas del Oeste basin). The fairly transparent water and gently sloping bank facilitate observation without disturbing snail activities. Water flow was heavily impeded by dense mats of *Potamogeton* sp.; isolated patches of floating duckweed, *Wolffia columbiana*, were present among them.

PSC was recorded for 27 h on 18–19 March 2011, with nine observation periods of 1 every 3 h. Air and water temperature were recorded every 5 min with two Hobo® dataloggers located 5 above and 15 cm below the surface. To quantify PSC, 10 floating quadrats (96 × 48 cm) were deployed along 30 m of the channel and anchored at 10–40 cm from the shore. Each quadrat was a plastic grid of 32 squares (12 × 12 cm). The availability of macroscopic particulate material on the surface of each quadrat (percentage of squares containing floating macroscopic material other than *Potamogeton* sp. leaves and stems) was estimated at the beginning of the first observation period.

Observations started 1 h after the deployment of quadrats. During each observation period, the water surface in each quadrat was scanned by two operators for 1 min and 45 s; the inspection of the 10 quadrats was repeated three times in each observation period. In each quadrat, the number of pedal funnels was recorded; the snails performing PSC were assigned to different SL classes (15–25, 25–35, 35–45 and 45–55 mm) by observing them through a transparent visor with four concentric circumferences of increasing diameter (1, 2, 3 and 4 cm). A dim LED flashlight, which caused no reaction in the snails, was used for nocturnal observations. At the end of the observation period, the snails within each quadrat were collected in an upstream direction to minimize disturbance; the size of each snail was estimated as above.

The intensity of PSC during each observation period was estimated as the average number of pedal funnels observed in each of the three series in a given quadrat divided by the number of snails collected within that quadrat. The size frequency distributions of the snails performing PSC during each observation period and those collected in the quadrats were compared using χ^2 tests. The intensity of PSC in each quadrat was correlated with the availability of macroscopic particulate material and the mean intensity during each observation period was correlated with mean air and water temperatures.

RESULTS

During laboratory observations, PSC was performed typically using the walls of the aquarium as a substrate, in which case the lateral edges of the foot were not in contact with each other. In a few cases, the snails performed PSC while floating with both edges of the foot in close contact and the funnel was conical.

Food spectrum under laboratory conditions

Once the snails became active, they crawled up to the water surface within a few minutes and started PSC. The snails were able to capture most of the materials provided (Table 1); the capture of ants, aphids, oils and tracing paper was less intense than that of the other food types. The captured material (including natural biofilms) formed a mass with abundant mucus within the funnel, except in the case of oils, in which part of the collected oil was lost when the snail put its mouth in the funnel and tried to ingest it. No attempts to capture pigeon feathers, PVC and aluminium foil with pedal funnels were observed; the snails repeatedly attempted to ingest the feathers directly from the surface but ignored the other two materials.

Commonly, when the snails reached the water surface and made direct contact with the floating material, they ingested it directly without forming a pedal funnel. Not all the food types captured by PSC were ingested. The bracts of *P. alba* and the cockroach oothecae and adults were repeatedly attacked with the radula and jaws, but the snails were not able to ingest them and abandoned the mucous balls, forming a new funnel a few minutes later. No attempts to ingest the few captured ants were observed. No harmful effects or deaths were observed in the snails in the week after the trials.

Effect of snail size and sex, food density and particle size under laboratory conditions

Pedal funnel formation was observed in 94% of snails $>$10 mm SL, but only in 36% of the smaller snails (Fig. 2). Surface scraping (crawling upside-down on the water surface and ingesting food directly from it) was observed only in snails smaller than 20 mm, in which 21% of snails alternated this mechanism with PSC. Twenty per cent of snails $<$10 mm only fed by surface scraping. In trials with small snails, SCRs included food captured both by pedal funnel and by surface scraping; however, the rates attained by snails performing PSC only were not significantly different from those attained by surface scraping with or without the use of pedal funnels (Kruskal–Wallis test, $H = 2.392$; $P > 0.302$). Therefore, we incorporated the time spent on surface scraping in our estimation of SCRs.

All PSC variables showed a significant relationship with SL (Table 2). Total food captured (TFC), percentage of time performing PSC (TPSC) and pedal funnel rate (PFR) all increased with SL, although at a lower rate than expected under isometric growth ($b = 1$). The perimeter (PFP) and area (PFA) of the pedal funnels both grew with negative allometry, with the slopes ($b = 0.916$, $b = 1.732$) significantly lower than expected under simple scaling ($b = 1$, $b = 2$, respectively). The SCR showed a steeper decrease relative to SL ($b = -2.443$) than expected by
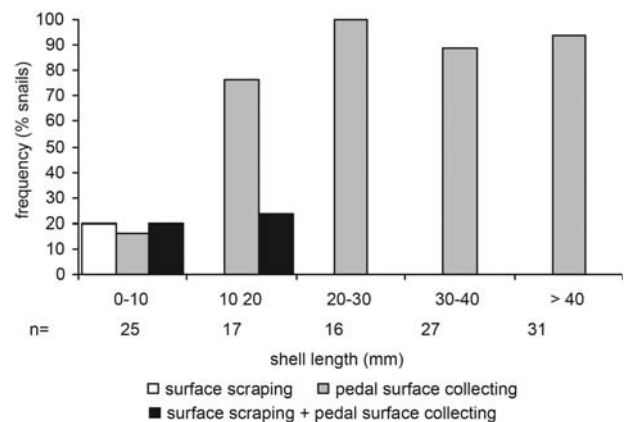

Figure 2. Frequencies of *Pomacea canaliculata* of different sizes that performed surface scraping, pedal surface collecting and a combination of both activities under laboratory conditions.

Table 2. Parameters of the relationship between shell length (SL) and the variables of pedal surface collecting by *Pomacea canaliculata*.

Variable	log a (95% CI)	b (95% CI)	Adjusted mean	n	R^2	P
PFR (funnel. snail^{-1} h^{-1})	−0.112 (−0.499; 0.275)	0.316 (0.049; 0.583)	2.134	93	0.057	0.021
TPSC (%)	0.261 (−0.131; −0.652)	0.568 (0.298; 0.839)	11.326	93	0.161	0.001
PFP (cm)	−0.707 (−0.806; −0.608)	0.916 (0.847; 0.985)	3.732	92	0.887	0.001
PFA (cm^2)	−2.599 (−2.830; −2.368)	1.732 (1.572; 1.891)	0.660	92	0.838	0.001
TFC (g)	−1.293 (−1.414; −1.173)	0.456 (0.373; 0.539)	0.221	92	0.570	0.001
SCR (g g^{-1} min^{-1})	0.957 (0.627; 1.287)	−2.443 (−2.670; −2.215)	0.004	92	0.835	0.001

All the variables were log$_{10}$-transformed; adjusted means were calculated back-transforming the values obtained with the allometric equations for a snail of average size (SL: 24.9 mm). Only snails that performed pedal surface collecting were included in these analyses.

Abbreviations: PFR, pedal funnel rate; TPSC, time performing pedal surface collecting; PFP, pedal funnel perimeter; PFA, pedal funnel area; TFC, total amount of food captured; SCR, specific capture rate.
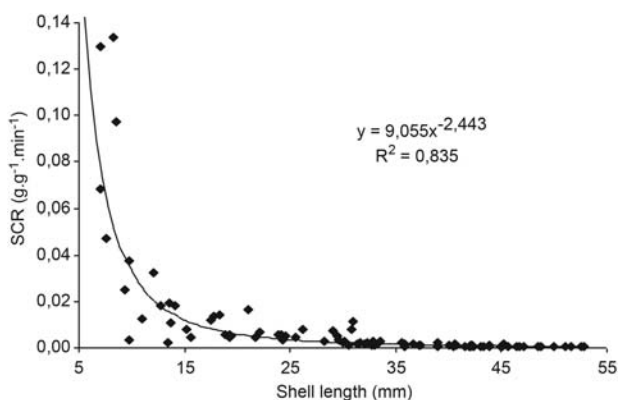

Figure 3. Scatter-plot of the specific capture rate (SCR) by pedal surface collecting relative to shell length (SL) in *Pomacea canaliculata* under laboratory conditions.

allometry models ($b = -1$) (Fig. 3). No sexual differences were found for any of the variables ($P > 0.10$ in all cases).

In the food density trials, on average 75% of the snails formed funnels in the three treatments with food, while none formed funnels in the treatment without food. For the three food treatments (Table 3), food density negatively influenced TPSC and positively influenced TFC and SCR.

PSC was performed in all combinations of particle and snail size. None of the variables was affected by the size of food particles (Table 4). The effect of snail size was non-significant only for the PFR. The interaction between food size and snail size was significant only for SCR, but when SCR was analysed separately for small and large snails, no significant effect of particle size was found (one-way ANOVAs: $F_{2,5} = 3.939$, $P > 0.094$ and $F_{3,10} = 0.433$, $P > 0.734$, respectively).

Occurrence and daily fluctuations in the field

During the field observations, most snails used *Potamogeton* leaves and stems as the foothold substrate for PSC (Fig. 1B) and in a few cases used the bottom of the channel. Most funnels were almost conical, with the lateral edges of the foot in close contact with each other. No snail was observed crawling upside-down on the water surface. Among the material gathered by pedal funnels were insect wings, duckweed, parts of flowers and stems of terrestrial plants and floating foamy scum.

During daylight hours, the intensity of PSC was low [from 0.0 to 0.014 ± 0.020 (mean ± SD) funnels per snail] but peaked rapidly after sunset to a maximum of 0.268 ± 0.082 (Fig. 4); PSC decreased through the night and dropped to zero

after sunrise. At night, PSC was observed in all quadrats, including those in which no macroscopic material was visible on the surface.

The average intensity of PSC was significantly correlated with air temperature ($r = -0.682$, $P < 0.043$, $n = 9$) but not with water temperature ($r = -0.213$, $P > 0.582$, $n = 9$). The intensity of PSC in each quadrat at the 20:30 h observation was not significantly correlated with the availability of macroscopic particulate material on the surface ($r = 0.576$, $P > 0.082$, $n = 10$).

The size–frequency distribution of snails in the quadrats (mean density: 46.4 ± 22.5 snail m^{-2}) and those performing PSC differed significantly only during nocturnal observation periods (χ^2 test, $P < 0.005$ in all three cases: 20:30, 23:30 and 02:30 h); the numbers of small snails (15–25 mm SL) and large snails (35–55 mm) performing PSC were lower and higher than expected, respectively. At 05:30 h, no significant differences were found (χ^2 test, $P > 0.189$). The diurnal frequencies were too low to test.

DISCUSSION

Our study revealed for the first time the wide spectrum of potential food resources available to *Pomacea canaliculata* through PSC. Previous reports on this species (Cazzaniga & Estebenet, 1984) and on *P. paludosa* (Say, 1829) (Johnson, 1952; McClary, 1964) described only the capture and ingestion of artificial food particles (breadcrumbs, rolled oats, pulverized fish food, etc.). Cheesman (1956) suggested that protein monolayers naturally present on the water surface were the only quantitatively important material that *P. canaliculata* could capture by this mechanism. However, in our study, *P. canaliculata* used pedal funnels to capture different items irrespective of their physical nature (liquid, organic particles and biofilms) and size, although not all of them could be ingested in spite of repeated attempts, as occurred with very large, hard particles. Leafcutter ants were the only biotic item that snails did not attempt to ingest, perhaps due to the presence of some toxic substance. PSC not only allows apple snails to capture food items occasionally present on the water surface, but also one of their basic food sources, vascular plants, either as fragments or whole floating plants. In our field observations, *P. canaliculata* did capture and ingest floating materials corresponding to those offered in the laboratory [e.g. insect wings and legs, duckweed (*Wolffia columbiana*), petals, twigs, pappus, scum, springtails (Collembola)].

In our experiments, PSC was performed by snails of the whole size range (3–52.8 mm SL), although it was quite infrequent in snails of <10 mm. Cazzaniga & Estebenet (1984) mentioned 8 mm as the length of the smallest snail observed using this feeding mechanism. In contrast, Cheesman (1956)

Table 3. Summary of ANOVAs results and means for the variables of pedal surface collecting by *Pomacea canaliculata* under three different surface food densities (0.26, 0.52 and 1.04 mg cm^{-2}).

Variable	Food density	P-value	Means (mg cm^{-2})		
			0.26	0.52	1.04
PFR (funnel snail^{-1} h^{-1})	$F_{2,24} = 2.129$	>0.141	2.850	2.410	1.357
TPSC (%)	$F_{2,24} = 5.415$	<0.011	21.900[a]	13.300[b]	10.857[b]
PFP (cm)	$F_{2,24} = 0.880$	>0.428	4.744	4.458	4.234
PFA (cm^2)	$F_{2,24} = 0.988$	>0.387	0.992	0.947	0.765
TFC (g)	$F_{2,24} = 70.430$	<0.001	0.125[a]	0.198[b]	0.357[c]
SCR (g g^{-1} min^{-1})	$F_{2,24} = 34.170$	<0.001	0.0007#[a]	0.0020#[b]	0.0036#[c]

SCR was log$_{10}$-transformed. Least significant differences (LSD) tests were performed when the effect of food density was significant; different letters indicate significant differences between means ($P < 0.05$).

Abbreviations: PFR, pedal funnel rate; TPSC, time performing pedal surface collecting; PFP, pedal funnel perimeter; PFA, pedal funnel area; TFC, total amount of food captured; SCR, specific capture rate; #, back-transformed means.

Table 4. Summary of two-way ANOVAs for pedal surface collecting variables of *Pomacea canaliculata*.

Variable	PS	SS	PS × SS
PFR (funnel snail^{-1} h^{-1})	$F_{3,17} = 1.072, P > 0.387$	$F_{1,17} = 0.994, P > 0.333$	$F_{3,17} = 0.488, P > 0.695$
TPSC (%)	$F_{3,17} = 1.531, P > 0.243$	$F_{1,17} = 8.886, P < 0.008$	$F_{3,17} = 0.783, P > 0.520$
PFP (cm)	$F_{3,16} = 0.990, P > 0.422$	$F_{1,16} = 5.405, P < 0.034$	$F_{2,16} = 0.770, P > 0.479$
PFA (cm^2)	$F_{3,16} = 0.525, P > 0.671$	$F_{1,16} = 14.829, P < 0.001$	$F_{2,16} = 0.780, P > 0.472$
TFC (g)	$F_{3,15} = 0.165, P > 0.918$	$F_{1,15} = 10.540, P < 0.001$	$F_{2,15} = 0.176, P > 0.840$
SCR (g g^{-1} min^{-1})	$F_{3,15} = 1.926, P > 0.169$	$F_{1,15} = 9.933, P < 0.007$	$F_{2,15} = 3.944, P < 0.042$

Abbreviations: PFR, pedal funnel rate; TPSC, time performing pedal surface collecting; PFP, pedal funnel perimeter; PFA, pedal funnel area; TFC, total amount of food captured; SCR, specific capture rate. Fixed factors: PS, particle size; SS, snail size; PS × SS (interaction). TPSC was log$_{10}$-transformed.
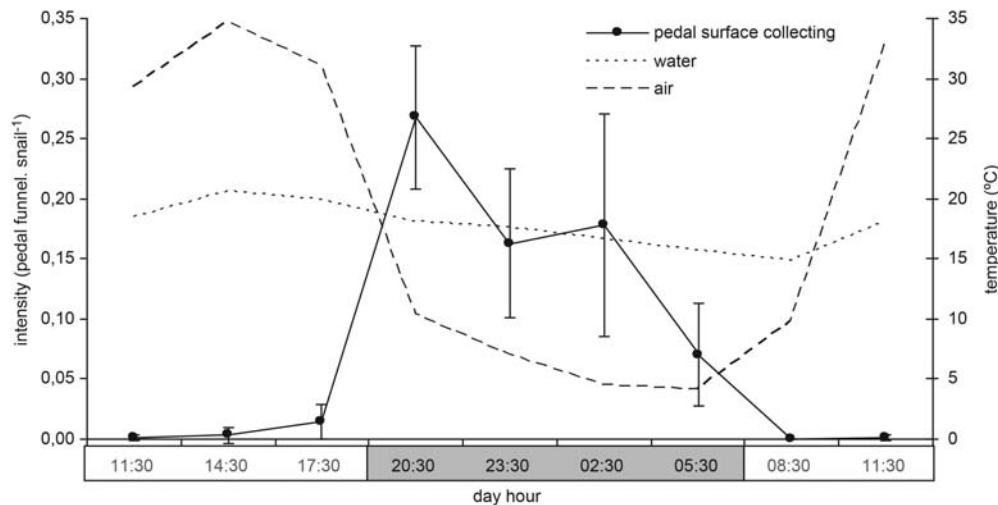
Figure 4. Temporal pattern of the intensity of pedal surface collecting (mean ± 95% CI) of *Pomacea canaliculata* in the Pigüé-Venado channel. Air and water temperatures correspond to the means during observation periods. The labels on the x-axis correspond to the mid-point of each observation period; the night hours are shaded.

commented that it was more frequent in juveniles than adults, without indicating any size. Only snails <20 mm captured and ingested food present on the water surface while crawling upside down (surface scraping). Size-dependent ecological effects are probably important in apple snails due to their large maximum sizes.

The SCR by PSC decreases strongly with size in *P. canaliculata*. This decrease is expected based on allometric considerations and also occurs in freshwater gastropods that feed on suspended material with the ctenidium (Brendelberger & Jürgens, 1993; Hockelmann & Pusch 2000). For *P. canaliculata*, this decrease may be related to the ontogenetic decrease in the specific ingestion rate (Tamburi & Martín, 2009b) and in the relative size of pedal funnels (as shown by the negative allometry of their perimeter and area). However, the increase in the time invested in PSC probably compensates for the ontogenetic decrease in SCR, although only partially, since the TFC grew with strong negative allometry ($b = 0.456$, i.e. at a lower rate than length).

Carlsson & Brönmark (2006) showed strong negative effects of the density of hatchlings on the growth of medium-sized snails of *P. canaliculata*, whereas the density of large snails only had a weak effect on hatchling growth. The higher grazing rates and food conversion efficiencies of small individuals (Tamburi & Martín, 2009b) and their higher SCR during PSC and surface scraping could partly explain this size-asymmetric intraspecific competition.

Using the equations for SCR and TPSC (Table 2), the SCR per hour can be estimated; for average snails of 12 mm and 50 mm SL, these rates were 0.0939 and 0.0065 g g^{-1} h^{-1}, respectively. These values are higher than 0.0021 and 0.0004 g g^{-1} h^{-1}, the equivalent specific ingestion rates of lettuce calculated from data of Tamburi & Martín (2009b) after correcting for the water content of lettuce (95%) and trial duration (24 h). *Pomacea canaliculata* increases the SCR according to food availability, while simultaneously reducing the time performing PSC. On the whole, the TFC in 2 h increased 2.77 times when food density increased 4-fold; McClary (1964) reported qualitatively similar results for *P. paludosa*. No effect of particle size was observed on the functional variables of PSC for both large and small snails. The high and adaptable capture rates and the wide size tolerance probably allow *Pomacea* snails to take advantage of food resources (petals, pollen, seeds, exuviae, etc.) whose availabilities on the surface of natural waterbodies are highly variable and unpredictable.

In our study, the size of the pedal funnel was not related to particle size, neither in absolute nor relative terms, contrasting with the findings of Cazzaniga & Estebenet (1984), who observed small pedal funnels when particles were small. During our field observations, most funnels were conical and smaller than those observed when an aquarium wall was used for attachment. This could be caused by the use of slender substrates in the field (leaves and stems of *Potamogeton*) as was mentioned by McClary (1964) and Cazzaniga & Estebenet (1984).

In agreement with McClary (1964), *Pomacea* snails seem to perform PSC only when food is available on the surface, since the presence of floating PVC and aluminium particles did not elicit PFR. This shows that they do not use pedal funnels to sense and search for food but that PSC is triggered by previous detection underwater. This probably minimizes the risk of detection by visual aerial predators during surfacing (Bennetts, Collopy & Rodgers, 1994) when a trophic reward is not likely.

Even if food is available at the surface, the snails seem to refrain from PSC during daylight hours, but perform it intensely after sunset. The negative relationship of PSC with air temperature does not seem to be causal as activity levels of *P. canaliculata* increase with temperature (Seuffert, Burela & Martín, 2010) within the range observed. The peak in PSC seems to be directly related to the disappearance of direct sunlight on the water surface. The decrease in intensity during the night was probably partly due to a decrease in water temperature (from 18 to 15.7°C), near to the threshold beyond which snails become increasingly inactive (Seuffert *et al.*, 2010); satiety of snails and depletion of surface material are also possible causes. Heiler *et al.* (2008) observed higher levels of activity during the first hours of darkness in *P. canaliculata* under constant temperature and suggested that this pattern evolved in order to reduce the probability of detection by specialized visual predators such as the Snail Kite. We did not observe Snail Kites during our 27-h observation period, but have observed them in summer in Pigüé Stream. Empty shells under fence poles, usually indicating Snail Kite predation, were found near the channel.

As far as we know, there are no previous reports of PSC in the field, for it has only been reported in *Pomacea* under laboratory conditions (Johnson, 1952; Cheesman, 1956; McClary, 1964; Cazzaniga & Estebenet, 1984). Only Louda & McKaye (1982) observed a "feeding posture" in *Lanistes nyassanus* (Montfort, 1810) from Lake Malawi similar to that of *Pomacea* during PSC. The lack of field reports may be due to its mainly nocturnal occurrence.

In the present study, as well as in other field sampling, we observed a high frequency of PSC even when abundant underwater food sources (e.g. *Potamogeton* sp.) were present (Fig. 1B). *Pomacea canaliculata* exhibited a low preference for *Potamogeton striatus* and growth rates were low when feeding on it (Estebenet, 1995). This evidence highlights the importance of PSC as an alternative or complementary feeding mechanism. Perhaps this and other alternative feeding mechanisms explain the persistence of high densities of *P. canaliculata* in wetlands where this species has eliminated the cover of submerged and floating aquatic plants (Carlsson *et al.*, 2004). This suggests a capacity to resist self-induced catastrophic ecosystem changes and thereby impede the recovery of aquatic vegetation in invaded wetlands.

Apple snails are regarded mainly as phytophagous shredders and scrapers (Dillon, 2000; Cowie, 2002; Merritt *et al.*, 2002) but, surprisingly enough, there are few direct studies on their natural diet (e.g. Madsen, 1992; Kwong *et al.*, 2010). Future studies will probably reveal a high diversity in the use of trophic resources, even for well-known species of *Pomacea*. For instance, *P. glauca* (Linnaeus, 1758) was classified as a detritivore, with >90% of its diet constituted by allochthonous detritus (leaves, fruits and drifting particulate matter) (Coat *et al.*, 2009). On the other hand, *P. patula* (Baker, 1922) bioaccumulates toxins produced by filamentous planktonic cyanobacteria (Berry & Lind, 2010), which indicates their use as a trophic resource. The alternative feeding mechanisms of *Pomacea* must be considered when interpreting indirect evidence about their use of trophic resources (Coat *et al.*, 2009) or the pathways of bioaccumulation of toxins (Berry & Lind, 2010), pesticides (Coat *et al.*, 2011) and heavy metals (Deng *et al.*, 2008).

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REFERENCES

ADITYA, G. & RAUT, S.K. 2001. Food of the snail, *Pomacea bridgesi*, introduced in India. *Current Science*, **80**: 919–921.

ALLABY, M. 1998. *A dictionary of ecology*. Edn 2. Oxford University Press, New York, USA.

ANDREWS, E.B. 1965. The functional anatomy of the gut of the prosobranch gastropod *Pomacea canaliculata* and some other pilids. *Proceedings of the Malacological Society of London*, **145**: 19–36.

BENNETTS, R.E., COLLOPY, M.W. & RODGERS, J.A. 1994. The snail kite in the Florida Everglades: a food specialist in a changing environment. In: *Everglades: the ecosystem and its restoration* (S.M. Davis & J.C. Ogden, eds), pp. 507–532. St Lucie Press, Delray Beach, FL.

BERRY, J.P. & LIND, O. 2010. First evidence of "paralytic shellfish toxins" and cylindrospermopsin in a Mexican freshwater system, Lago Catemaco, and apparent bioaccumulation of the toxins in "tegogolo" snails (*Pomacea patula catemacensis*). *Toxicon*, **55**: 930–938.

BRENDELBERGER, H. & JÜRGENS, S. 1993. Suspension feeding in *Bithynia tentaculata* (Prosobranchia, Bithyniidae), as affected by body size, food and temperature. *Oecologia*, **94**: 36–42.

BURLAKOVA, L.E., KARATAYEV, A.Y., PADILLA, D.K., CARTWRIGHT, L.D. & HOLLAS, D.N. 2009. Wetland restoration and invasive species: apple snail (*Pomacea insularum*) feeding on native and invasive aquatic plants. *Restoration Ecology*, **17**: 433–440.

CARLSSON, N.O.L. & BRÖNMARK, C. 2006. Size-dependent effects of an invasive herbivorous snail (*Pomacea canaliculata*) on macrophytes and periphyton in Asian wetlands. *Freshwater Biology*, **51**: 695–704.

CARLSSON, N.O.L., BRÖNMARK, C. & HANSON, L.A. 2004. Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. *Ecology*, **85**: 1575–1580.

CAZZANIGA, N.J. & ESTEBENET, A.L. 1984. Revisión y notas sobre los hábitos alimentarios de los Ampullariidae (Gastropoda). *Historia Natural*, **4**: 213–224.

CHEESMAN, D.F. 1956. The snail's foot as a Langmuir trough. *Nature*, **178**: 987–988.

COAT, S., MONTI, D., BOUCHON, C. & LEPOINT, G. 2009. Trophic relationships in a tropical stream food web assessed by stable isotope analysis. *Freshwater Biology*, **54**: 1028–1041.

COAT, S., MONTI, D., LEGENDRE, P., BOUCHON, C., MASSAT, F. & LEPOINT, G. 2011. Organochlorine pollution in tropical rivers (Guadeloupe): role of ecological factors in food web bioaccumulation. *Environmental Pollution*, **159**: 1692–1701.

COWIE, R.H. 2002. Apple snails (Ampullariidae) as agricultural pests: their biology, impacts and management. In: *Molluscs as crop pests* (G.M. Barker, ed.), pp. 145–192. CABI Publishing, Wallingford.

CUMMINS, K.W. & KLUG, M.J. 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics*, **10**: 147–172.

DECLERK, C. 1995. The evolution of suspension feeding in gastropods. *Biological Reviews*, **70**: 549–569.

DEMIAN, E.S. & LUTFY, R.G. 1966. Factors affecting the predation of *Marisa cornuarietis* on *Bulinus (B). truncatus*, *Biomphalaria alexandrina* and *Lymnaea caillaudi*. *Oikos*, **17**: 212–230.

DENG, P.Y., SHU, W.S., LAN, C.Y. & LIU, W. 2008. Metal contamination in the sediment, pondweed, and snails of a stream receiving effluent from a lead/zinc mine in Southern China. *Bulletin of Environmental Contamination and Toxicology*, **81**: 69–74.

DILLON, R.T. 2000. *The ecology of freshwater molluscs*. Cambridge University Press, Cambridge.

ESTEBENET, A.L. 1995. Food and feeding in *Pomacea canaliculata* (Gastropoda: Ampullariidae). *Veliger*, **38**: 277–283.

ESTEBENET, A.L., MARTÍN, P.R. & BURELA, S. 2006. Conchological variation in *Pomacea canaliculata* and other South American Ampullariidae (Caenogastropoda, Architaenioglossa). *Biocell*, **30**: 329–335.

HANNIFA, M.A. 1982. Effects of feeding level and body size on food utilization of the fresh water snail *Pila globosa*. *Hydrobiologia*, **97**: 141–149.

HAYES, K.A., JOSHI, R.C., THIENGO, S.C. & COWIE, R.H. 2008. Out of South America: multiple origins of non-native apple snails in Asia. *Diversity and Distributions*, **14**: 701–712.

HEILER, K.C.M., VON OHEIMB, P.V., EKSCHMITT, K. & ALBRECHT, C. 2008. Studies on the temperature dependence of activity and on the diurnal activity rhythm of the invasive *Pomacea canaliculata*. *Mollusca*, **26**: 73–81.

HOCKELMANN, C. & PUSCH, M. 2000. The respiration and filter-feeding rates of the snail *Viviparus viviparus* (Gastropoda) under simulated stream conditions. *Archiv für Hydrobiologie*, **149**: 553–568.

HORNE, F.R., ARSUFFI, T.L. & NECK, R.W. 1992. Recent introduction and potential botanical impact of the Giant Rams-Horn snail, *Marisa cornuarietis* (Pilidae), in the Comal Spring ecosystem of central Texas. *Southwestern Naturalist*, **37**: 194–214.

HOWELLS, R.G. 2002. Comparative feeding of two species of apple snails (*Pomacea*). *Ellipsaria*, **4**: 14–16.

JOHNSON, B.M. 1952. Ciliary feeding in *Pomacea paludosa*. *Nautilus*, **66**: 1–5.

R.C. JOSHI & L.D. SEBASTIAN eds. 2006. *Global advances in ecology and management of golden apple snails*. Philippine Rice Research Institute, Nueva Ecija.

KWONG, K., CHAN, R.K.Y. & QIU, J.W. 2009. The potential of the invasive snail *Pomacea canaliculata* as a predator of various life-stages of five species of freshwater snails. *Malacologia*, **51**: 343–356.

KWONG, K.L., DUDGEON, D., WONG, P.K. & QIU, J.W. 2010. Secondary production and diet of an invasive snail in freshwater wetlands: implications for resource utilization and competition. *Biological Invasions*, **12**: 1153–1164.

LACH, L., BRITTON, D.K., RUNDELL, R.J. & COWIE, R.H. 2000. Food preference and reproductive plasticity in an invasive freshwater snail. *Biological Invasions*, **2**: 279–288.

LOUDA, S.M. & MCKAYE, K.R. 1982. Diurnal movements in populations of the prosobranch *Lanistes nyassanus* at Cape Maclear, Lake Malawi, Africa. *Malacologia*, **23**: 13–21.

LOWE, S., BROWNE, M., BOUDJELAS, S. & DE POORTER, M. 2000. 100 of the world's worst invasive alien species. The Invasive Species Specialist Group, IUCN, Auckland.

LV, S., ZHANG, Y., LIU, H.-X., HU, L., LIU, Q., WEI, F.-R., GUO, Y.-H., STEINMANN, P., HU, W., ZHOU, X.-N. & UTZINGER, J. 2012. Phylogenetic evidence for multiple and secondary introductions of invasive snails: *Pomacea* species in the People's Republic of China. *Diversity and Distributions*, doi:10.1111/j.1472–4642.2012.00924.x.

MADSEN, H. 1992. Food selection by the freshwater snails in the Gezira irrigation canals, Sudan. *Hydrobiologia*, **228**: 203–217.

MARTÍN, P.R., ESTEBENET, A.L. & CAZZANIGA, N.J. 2001. Factors affecting the distribution of *Pomacea canaliculata* (Gastropoda: Ampullariidae) along its southernmost natural limit. *Malacologia*, **43**: 13–23.

McCLARY, A. 1964. Surface inspiration and ciliary feeding in *Pomacea paludosa* (Prosobranchia: Mesogastropoda: Ampullariidae). *Malacologia*, **2**: 87–104.

MERRITT, R.W., CUMMINS, K.W., BERG, M.B., NOVAK, J.A., HIGGINS, M.J., WESSELL, K.J. & LESSARD, J.L. 2002. Development and application of a macroinvertebrate functional-group approach in the bioassessment of remnant river oxbows in southwest Florida. *Journal of the North American Benthological Society*, **21**: 290–310.

MORRISON, W.E. & HAY, M.E. 2011a. Induced chemical defences in a freshwater macrophyte suppress herbivore fitness and the growth of associated microbes. *Oecologia*, **165**: 427–436.

MORRISON, W.E. & HAY, M.E. 2011b. Feeding and growth of native, invasive and non-invasive alien apple snails (Ampullariidae) in the United States: invasives eat more and grow more. *Biological Invasions*, **13**: 945–955.

POINTIER, J.P. & DAVID, P. 2004. Biological control of *Biomphalaria glabrata*, the intermediate host of schistosomes, by *Marisa cornuarietis* in ponds of Guadeloupe: long-term impact on the local snail fauna and aquatic flora. *Biological Control*, **29**: 81–89.

QIU, J.W. & KWONG, K.L. 2009. Effects of macrophytes on feeding and life-history traits of the invasive apple snail *Pomacea canaliculata*. *Freshwater Biology*, **54**: 1720–1730.

RAWLINGS, T.A., HAYES, K.A., COWIE, R.H. & COLLINS, T.M. 2007. The identity, distribution, and impacts of non-native apple snails in the continental United States. *BMC Evolutionary Biology*, **7**: 97.

SEUFFERT, M.E., BURELA, S. & MARTÍN, P.R. 2010. Influence of water temperature on the activity of the freshwater snail *Pomacea canaliculata* (Caenogastropoda: Ampullariidae) at its southernmost limit (Southern Pampas, Argentina). *Journal of Thermal Biology*, **35**: 77–84.

TAMBURI, N.E. & MARTÍN, P.R. 2009a. Reaction norms of size and age at maturity of *Pomacea canaliculata* (Gastropoda: Ampullariidae) under a gradient of food deprivation. *Journal of Molluscan Studies*, **75**: 19–26.

TAMBURI, N.E. & MARTÍN, P.R. 2009b. Feeding rates and food conversion efficiencies of the apple snail *Pomacea canaliculata* (Caenogastropoda: Ampullariidae). *Malacologia*, **51**: 221–232.