

Primary Research Paper

Factors affecting the distribution and abundance of the commensal *Temnocephala iheringi* (Platyhelminthes: Temnocephalidae) among the southernmost populations of the apple snail *Pomacea canaliculata* (Mollusca: Ampullariidae)

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Abstract

Temnocephala iheringi is the most common temnocephalan inhabiting the mantle cavity of the apple snail *Pomacea canaliculata*, a freshwater neotropical gastropod that has become a serious rice pest in Southeastern Asia. *T. iheringi* has been recorded from Mato Grosso (Brazil) to water bodies associated with the Río de la Plata river (Argentina). During an extensive survey in the southern limit of the native area of *P. canaliculata* the presence of *T. iheringi* eggs was recorded in several apple snail populations, extending the known distribution of the commensal more than 400 km southwards. The aim of this study was to understand the factors affecting the distribution and abundance of *T. iheringi* among populations of *P. canaliculata*. Only 23% of the apple snail populations inhabiting streams harboured temnocephalans while the occurrence among lentic ones was 71%. *T. iheringi* was found mostly in populations of apple snails living in non-alkaline sites and where snails attaining sizes larger than 4 cm were very common. The prevalence of the temnocephalans in lentic populations was higher than 90%. The number of eggs on the shell (not including the umbilicus) ranged between 0 and 470 and was different among populations of *P. canaliculata*. The prevalence and number of eggs were lower in the lotic populations, except for a stream population immediately downstream of a lake with commensals. There was no difference between males and females of *P. canaliculata* neither in the prevalence nor in the number of eggs on the shell. The southernmost population of the world of *P. canaliculata* harbours commensals that tolerate cold winter water temperatures (4–5 °C) as well as its host. On the other hand, *T. iheringi* was found only in sites with bicarbonate concentrations lower than 6.6 meq l⁻¹, suggesting that the tolerance of the commensal is very much lower than that of the apple snail (up to 9.95 meq l⁻¹). The number of worms inside each snail or the life history variation of *P. canaliculata* could explain the influence of the size of the snails on the occurrence of *T. iheringi*. In the big-sized snails, where the number of commensals is higher, the probability of survival of at least one worm is also higher, specially during the hibernation period, when crawling and feeding are null and snails remain buried. On the other hand, *P. canaliculata* snails from lentic populations are generally bigger and mostly iteroparous, while those inhabiting streams are smaller and semelparous. In these populations the snails have access to mate only with snails of their same cohort, while in iteroparous populations they can copulate with individuals of other cohorts, allowing the inter-generation transmission of worms and the long term persistence of the population of commensals.

Introduction

Pomacea canaliculata (Lamarck, 1822), the southernmost apple snail of the world, is a freshwater prosobranch gastropod with a basically tropical and subtropical natural distribution, including the Amazonas and the Plata basins (Cowie, 2002). In the last two decades it has invaded most South-eastern Asian countries, becoming a serious rice pest (Wada, 1997). During an extensive survey in the southern limit of its native area (Martín et al., 2001), we observed that many populations of *P. canaliculata* harboured temnocephalan worms.

The Temnocephalidae are commensal turbellarians from New Guinea, New Zealand, Australia, Madagascar, Central and South America. Nineteen species of *Temnocephala* have been reported in the Neotropical region, mostly associated with crustaceans as hosts, and ten of these have been found in Argentina. Only three species (*Temnocephala iheringi* Haswell, 1893, *Temnocephala rochensis* Ponce de León, 1979 and *Temnocephala haswelli* Ponce de León, 1989) are associated with freshwater snails belonging to the family Ampullariidae and only *T. iheringi* has been reported from Argentina, mostly on *Pomacea canaliculata*. These species live in a closer relationship with their host than most other *Temnocephala* spp., because they occupy the mantle cavity of the snails which they leave only to lay the egg capsules on the shell (Damborenea & Cannon, 2001).

Although many aspects of the biology of temnocephalans have been studied, the knowledge of their interactions with their hosts is still fragmentary (Jones & Lester, 1993; Jennings, 1997). Most studies have focused on the intrapopulation level and almost nothing is known about the factors regulating the distribution and abundance of these commensal worms at higher levels (i.e. among the populations of their hosts). The aim of this study was to understand the factors affecting the distribution of *Temnocephala iheringi* in the southernmost populations of *P. canaliculata*, where this commensal worm has not been recorded previously.

Study area

The sampling region extended from 36° S to 39° S in southern Buenos Aires province. This range

covers the southern limit of the distribution area of *Pomacea canaliculata* and includes the southern part of the Pampas and the only two mountainous areas in the province (Ventania and Tandilia mountains (Fig. 1)). The climate of the region is temperate, with a marked humidity gradient from the NE (mean annual rainfall 900 mm) to the SW (600 mm). The whole region lies within the 14 and 16 °C annual mean isotherms. Rivers and streams have scant and very variable water flow, with a pluvial hydrological regime (Grondona, 1975).

Materials and methods

The sampling scheme included all the main drainage basins and many isolated streams and lakes. Seventy-six sites were visited in February and March 1998 (late summer) (Martín et al., 2001). Two people searched for living apple snails among the submerged vegetation, under stones, or buried in the substrate; all snails larger than 2 cm were collected.

At every site the specific richness of snails and aquatic macrophytes (submerged, floating or emergent) were recorded. Other 16 environmental variables were recorded. Conductivity (mS cm^{-1}) and pH were determined *in situ* with a multimeter (Horiba U-10). Total and volatile suspended matter (g l^{-1}) were determined according to American Public Health Association (1981) methods. The concentrations (meq l^{-1}) of Na^+ , Ca^{++} , Mg^{++} , K^+ and SO_4^- were measured with an inductively coupled plasma emission spectrometer (Shimadzu ICPS 1000-III), and Cl^- , CO_3^- and HCO_3^- were measured by titration. Surface water velocity (m s^{-1}) was measured at different points within each site. The dominant substrate was characterised on an arbitrary scale: 1 (sapropel, mud), 2 (sand) and 3 (pebbles, boulders, limestone). The trophic resource availability was coded as 1 (low), 2 (medium) and 3 (high), through a visual estimation of the abundance of macrophytes, microphytes, riparian vegetation and their debris.

The collected snails were killed by immersion in 70 °C water and stored at -20 °C. Forty snails from each site were selected for further analysis (except for the sites LA, TA, AC and QG, where the numbers were 12, 30, 8 and 22, respectively)

and sexed on the basis of shell shape (Estebenet, 1998) and the presence of penis sheath or albumen gland (Andrews, 1964). Soft parts of snails were carefully extracted from the shell with forceps. Bodies and shells were dried and bodies were incinerated for later analysis which will be published elsewhere. Shell length (from the apex to the basal extreme of the aperture) was measured and the number of growth marks recorded. The presence of temnocephalan eggs on the shell was registered and the prevalence of temnocephalans in each population was estimated on this basis. Non-hatched eggs and hatched ones with an intact hatching border were counted on the shell of ten snails (except for AC), excluding only those located inside the umbilicus. Two sites (LL and PP) were revisited to collect snails from which eggs and adult worms were extracted for further examination in the laboratory (*in vivo* or after fixation with 70% ethanol). Voucher specimens of these populations (worms and eggs) have been deposited in the Invertebrate Collection of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN-In 36210 and MACN-In 36211).

To characterise the populations of *Pomacea canaliculata* five variables were calculated: relative density (estimated by reference to searching time), mean shell length, percentage of snails larger than 4 cm, mean shell length of the five largest snails, and percentage of snails with two or more growth marks.

The variables used to characterise each site and each population were standardised and examined by stepwise discriminant analysis (SDA) to find linear combinations of variables maximising distances between sites with and without temnocephalans. Group sizes were used to determine group membership probabilities.

Results

Pomacea canaliculata was recorded in 25 out of the 76 sites surveyed, though adult snails were collected only at 20 sites. Temnocephalan eggs were recorded only at eight sites (Fig. 1). Most of the eggs were hatched and distributed over the last part of the sutural line and inside the umbilicus. The egg capsules were shiny, dark brown to

cinnamon, ellipsoidal (major axis (mean \pm SD) = $415 \pm 44 \mu\text{m}$, minor axis = $187 \pm 19 \mu\text{m}$, $n = 26$), with a short stalk (length = $67 \pm 34 \mu\text{m}$, width = $46 \pm 13 \mu\text{m}$) and slender apical mucron ($81 \pm 4 \mu\text{m}$). The hatching line was circular and located in the apical third of the capsule and it was not evident in the unhatched eggs.

The body of adult worms was whitish with two red coloured eyes; body length without tentacles of the 17 largest worms of each population was $3.26 \pm 0.68 \text{ mm}$ (mean \pm SD) and $2.97 \pm 0.70 \text{ mm}$ for LL and PP; body width was 2.07 ± 0.47 and $1.77 \pm 0.49 \text{ mm}$, respectively. The sucker disc was circular ($915 \pm 175 \mu\text{m}$ and $776 \pm 190 \mu\text{m}$ in diameter for LL and PP, respectively). The cirrus, bearing strong apical spines, was short and conical, measuring $171 \pm 23 \mu\text{m} \times 101 \pm 14 \mu\text{m}$ (length \times width) in LL and $191 \pm 22 \times 110 \pm 13 \mu\text{m}$ in PP.

Thirteen out of the 20 water bodies where *P. canaliculata* was collected were streams and in only three (23%) of these the apple snails harboured temnocephalans. The remaining seven water bodies were reservoirs or permanent lakes, in five (71%) of which the commensals were present.

The concentration of bicarbonate as opposed to the percentage of snails larger than 4 cm discriminate significantly between the populations of *P. canaliculata* with and without temnocephalans (Wilk's $\lambda = 0.397$, $p < 0.001$; standardised discriminant coefficients: -0.895 for HCO_3^- and 0.843 for the percentage larger than 4 cm). The commensals were found mostly in populations of apple snails living in non-alkaline sites and where snails attaining sizes larger than 4 cm at the end of the summer were very frequent (Fig. 2). The overall percentage of cases correctly classified was 90%, since only two lotic apple snail populations with temnocephalans were misclassified (CH and LA, Fig. 1).

Except for HCO_3^- concentration, the physicochemical variables showed no significant differences between sites inhabited or not by the commensal worm (Table 1). On the other hand, the apple snail density was significantly lower, and the means of variables related to their body size higher, in the populations with temnocephalans. The substrate, the trophic resource

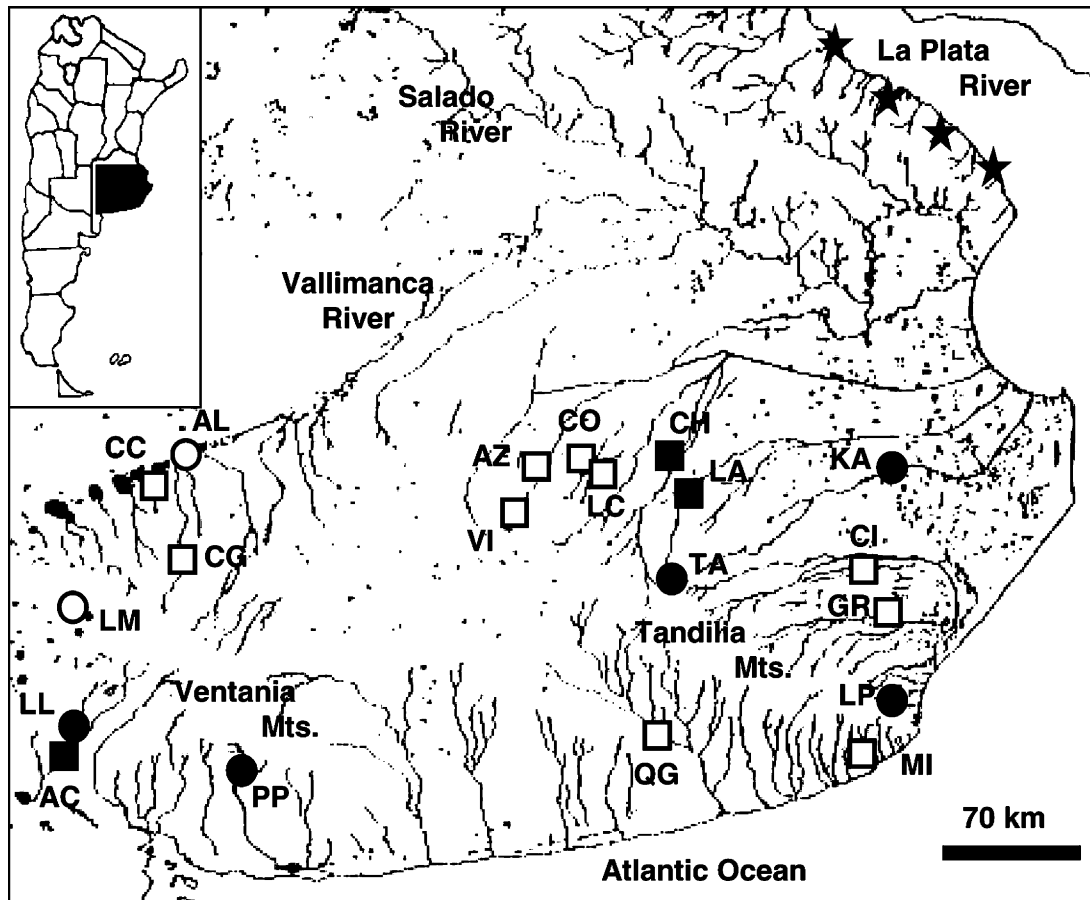


Figure 1. Map of a sector of Buenos Aires province showing the study zone (inset: political map of Argentina). Squares and circles locate lotic and lentic sites inhabited by *Pomacea canaliculata*, respectively. Filled and empty symbols indicate sites inhabited and non-inhabited by *Temnocephala iheringi*, respectively. Stars locate the previous records of *T. iheringi* (Damborenea, 1992). Abbreviations: CC: Cochicó stream at national route RN 33, AL: Alsina lake at RN 33, CG: Curamalal stream at provincial route RP 85, LM: La Manuela pond, 18 km west of Villa Castelar town, AZ: Azul stream at Azul city, CO: Cortaderas stream, at RP 60, VI: Videla stream at RN 3, LC: La Corina stream at RP 60, CH: Chapaleofú stream at RP60, LA: Langueyú stream at RP60, TA: El Fuerte reservoir at Tandil city, KA: Kakel Huincul lake, at RN 2, CI: Chico stream at RN 2, GR: Grande stream at RN 2, LL: Los Chilenos lake at Club de Pesca Tornquist, AC: Chasicó stream 3 km downstream of LL, PP: Paso de las Piedras reservoir at RP 51, QG: Quequén river at RP 85, LP: de los Padres lake at RP 226, MI: El Durazno stream at Miramar town.

availability, the richness of snails and of macrophytes were not different between the two groups of populations.

The prevalence of the temnocephalans in most populations of *P. canaliculata* was higher than 90%, except for the two lotic populations misclassified in the SDA, where prevalences were lower than 60% (Fig. 2). In the three populations with prevalences lower than 100%, the prevalences among males and females were 100 ($n\sigma$: 16) and 85.7 ($n\text{♀}$: 14) for TA, 40 ($n\sigma$: 5) and 83.3

($n\text{♀}$: 6) for LA and 43.8 ($n\sigma$: 20) and 22.7 ($n\text{♀}$: 19) for CH.

The number of eggs on the shell ranged between 0 and 470. The number of eggs showed no differences between males and females of *P. canaliculata* although it was significantly different among populations (two-way ANOVA; sex: $F_{1, 64} = 1.301$, $p = 0.258$; population: $F_{7, 64} = 16.654$, $p < 0.0001$; population \times sex: $F_{7, 64} = 2.765$, $p < 0.02$). The number of eggs was generally higher in the lentic populations of *T. iheringi* (Fig. 3).

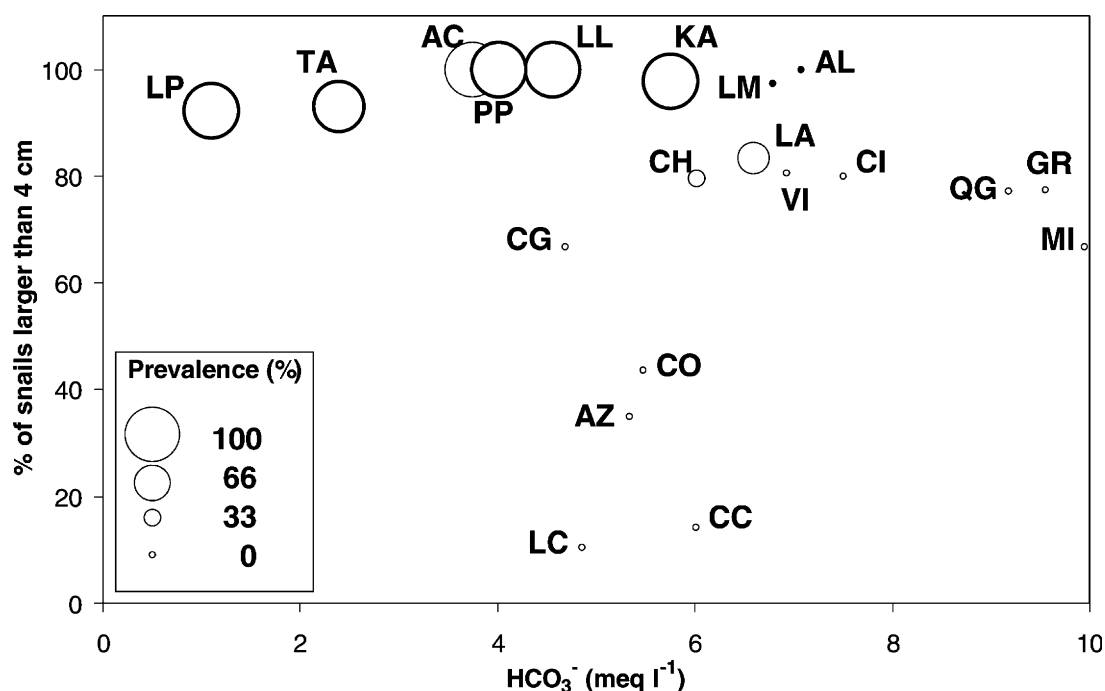


Figure 2. Scatter plot of bicarbonate concentration vs. snails larger than 4 cm for the 20 populations of *Pomacea canaliculata*. Thick and thin circles indicate lentic and lotic habitats, respectively (abbreviations as in Fig. 1).

Discussion

The cirrus of adult worms and the eggs recorded here on *P. canaliculata* fit well with those of *Temnocephala iheringi* (Moretto & Durquet, 1977; Damborenea & Cannon, 2001). The eggs of the other two species of *Temnocephala* associated with *P. canaliculata* are different in size and structure: the eggs of *T. rochensis* are quite smaller ($298 \times 71 \mu\text{m}$; Ponce de León, 1979) while those of *T. haswelli*, though of similar size ($460 \times 136 \mu\text{m}$), lack an apical mucron and have a more rounded distal extreme (Ponce de León, 1989). These two species are only known from their type localities in Uruguay and have never been recorded in apple snails from Argentina (Damborenea, 1992; Damborenea & Cannon, 2001).

The natural distribution of *Pomacea* spp. is basically tropical and subtropical and *T. iheringi* has been recorded from Mato Grosso (Brazil) to water bodies associated with the Río de la Plata river (Argentina) (Fig. 1; Damborenea, 1996; Damborenea & Cannon, 2001). The present records extend the known distribution of this species more than 400 km southwards. Most of the new

localities belong to the Centro-Este basin (Torensani et al., 1994), a flood-prone and profusely channelled plain where *P. canaliculata* occurs naturally (Martín et al., 2001). On the other hand, the three populations of *T. iheringi* located in the southern slope of the Ventania Mountains correspond to water bodies where *P. canaliculata* has been introduced in the last decades (Martín et al., 2001). One of these populations (PP, Paso de las Piedras reservoir) is the southernmost record for *P. canaliculata*, indicating that the commensal can tolerate cold winter water temperatures ($4\text{--}5^\circ\text{C}$) as well as its host.

Southern Pampas is a semiarid region with a poorly integrated and developed drainage system resulting in a difficult dispersal of aquatic animals. The lack of specific phases able to resist aerial transport renders difficult the dispersal of temnocephalans among different basins. The transmission or colonization from other apple snail species is impossible, since *P. canaliculata* is the only ampullarid present in the study area. The only other habitual hosts of *Temnocephala* spp. inhabiting this area are the occasionally present shrimps *Palaemonetes argentinus* Nobili,

Table 1. Mean and extreme values of selected physico-chemical variables and *Pomacea canaliculata* population' variables for the sites where the temnocephalan eggs were present (P) or absent (A)

Variables	Eggs	Mean	Minimum	Maximum
CO ₃ ⁼ (meq l ⁻¹)	A	0.27	0.00	1.25
	P	0.28	0.00	1.43
HCO ₃ ⁻ (meq l ⁻¹) **	A	6.95	4.69	9.95
	P	4.27	1.10	6.60
Cl ⁻ (meq l ⁻¹)	A	3.10	0.68	9.96
	P	2.60	1.01	6.20
SO ₄ ⁼ (meq l ⁻¹)	A	2.06	0.13	15.31
	P	0.38	0.11	0.79
Na ⁺ (meq l ⁻¹)	A	7.73	1.19	19.84
	P	4.99	1.09	11.43
Ca ⁺⁺ (meq l ⁻¹)	A	1.60	0.53	3.50
	P	1.56	0.38	3.69
Mg ⁺⁺ (meq l ⁻¹)	A	1.60	0.83	2.81
	P	1.41	0.78	2.47
K ⁺ (meq l ⁻¹)	A	0.28	0.17	0.40
	P	0.25	0.11	0.60
Conductivity (mS cm ⁻¹)	A	1.25	0.46	2.89
	P	0.88	0.39	1.71
pH	A	8.18	7.36	9.42
	P	8.67	8.17	9.90
Total suspended matter (g l ⁻¹)	A	0.03	0.00	0.08
	P	0.02	0.00	0.09
Volatile suspended matter (g l ⁻¹)	A	0.01	0.01	0.04
	P	0.02	0.01	0.03
Water velocity (m s ⁻¹)	A	0.14	0.00	0.63
	P	0.08	0.00	0.60
Substrate type	A	1.62	1	2.5
	P	1.31	1	2
Trophic resource availability	A	2.17	1	3
	P	2.19	1	3
Macrophyte richness	A	4.09	0	8
	P	4.87	2	7
Other snails richness	A	1.58	0	4
	P	1.25	0	3
Density (snail min ⁻¹)*	A	3.87	0.43	13.30
	P	0.54	0.09	0.98
Mean shell length (cm)*	A	4.42	3.38	6.07
	P	5.36	4.64	6.57
Snails with two or more growth marks (%)	A	65.50	17.50	95.55
	P	68.35	46.15	100
Snails larger than 4 cm (%)*	A	62.46	10.53	100
	P	93.28	79.50	100
Mean shell length of the five largest snails (cm)*	A	5.40	4.09	7.28
	P	6.41	5.39	7.76

Variables marked with asterisk differed between P and A sites (*: $p < 0.05$, **: $p < 0.01$, t -test, d.f.: 18).

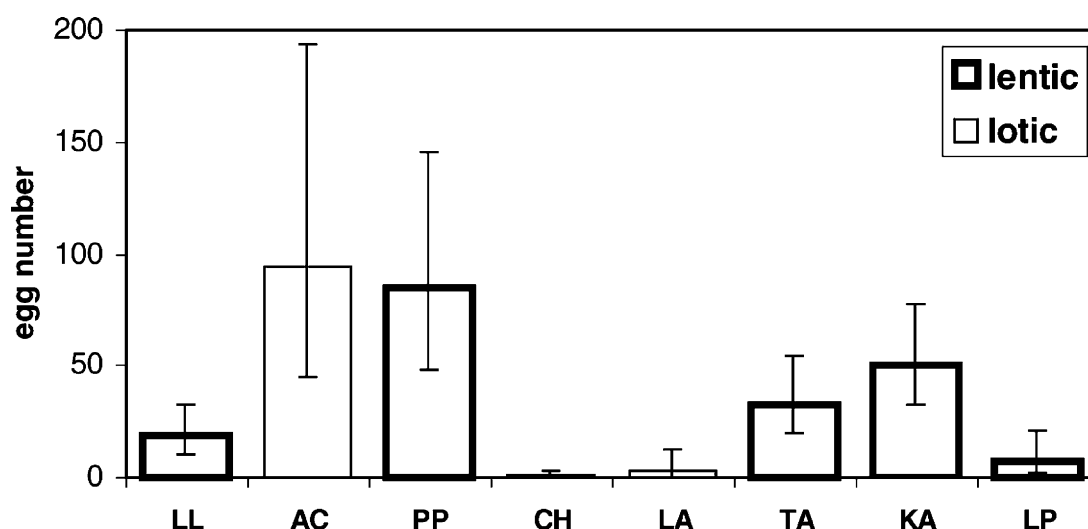


Figure 3. Number of eggs per shell from *Temnocephala iheringi* (mean \pm 95% CI) on *Pomacea canaliculata* snails (males and females pooled) inhabiting lotic and lentic waterbodies (abbreviations as in Fig. 1).

1901 and the more frequent water bugs *Belostoma* spp. Apart from anthropic dispersal, accidental transport by flying water bugs is probably the only way of colonization of new drainage basins or isolated waterbodies (Vianna & de Melo, 2002). However, *T. iheringi* has been reported only from ampullarid snails and the principal way of dispersal is probably by drifting individuals of *P. canaliculata*.

Five out of the seven lentic populations of *P. canaliculata* harboured temnocephalans while only in three out of thirteen lotic populations the commensals were present and two of them (AC and LA) were located downstream of lakes with worms. In the Río de la Plata basin *T. iheringi* has been recorded both in lentic and lotic water bodies (Damborenea, 1996; Moretto & Durquet, 1977; Damborenea & Cannon, 2001; Moretto, 2001), but a higher frequency of occurrence on lentic sites had not been acknowledged previously.

Temnocephalans were found mostly in populations of *P. canaliculata* living in non-alkaline sites where big snails were very frequent. In Southern Buenos Aires province water bodies not habitable by snails are characterised by high alkalinity among other factors (Martín et al., 2001). Within the range of bicarbonate concentrations of sites inhabited by *P. canaliculata* (1.10 to 9.95 meq l^{-1}), *T. iheringi* was found only in

sites with bicarbonate concentrations lower than 6.6 meq l^{-1} , indicating that the tolerance of the commensal to this factor is very much lower than that of the apple snail. Little is known world-wide about the physicochemical factors affecting the distribution and abundance of temnocephalans, but most species of *Temnocephala* in South America inhabit lakes and rivers in glacier regions or rivers running across tropical forests, aquatic systems characterised by more acidic waters.

The prevalence and abundance of *T. iheringi* within a *P. canaliculata* population increase with size (Damborenea, 1996), presumably because of longer exposure times to infestation or more time for population increase in big sized snails. In Southern Buenos Aires province the snails remain buried with their opercula totally closed during the six coldest months, crawling and feeding been null during this period (Estebenet & Martín, 2002, unpublished data), so the worms remain concealed within the snail with no renewal of food and water (Damborenea, 1996). Under these conditions, and assuming that the main mortality factors are density-independent, the probability of survival of at least one worm is directly related to the number of worms present at the beginning of the hibernation period. At the interpopulation level, this size dependent abundance interacts with an important body size variation among *P. canaliculata* populations

(Martín & Estebenet, 2002), probably resulting in different probabilities of commensal persistence.

On the other hand, the occurrence of *T. iheringi* would be related to the life history pattern of *P. canaliculata*. The transmission of worms between hosts occurs mostly during copulation (Damborenea, 1996), since the intercourses last several hours (Andrews, 1964; Albrecht et al., 1996) and other prolonged contacts are rare. Among populations of *P. canaliculata* in Southern Pampas, big maximum sizes are associated to higher frequencies of snails reproducing more than once in a lifetime (iteroparity) (Martín & Estebenet, 2002). In semelparous populations the snails have access to mate only with snails of their same cohort while in the iteroparous populations snails can also copulate with individuals of other cohorts, allowing the transmission of worms from one cohort to the following ones and hence the long term persistence of the population of commensals. *P. canaliculata* snails from lentic populations are generally bigger than those from lotic ones (Cazzaniga, 1987; Estebenet & Martín, 2003) and this could explain the higher frequency of occurrence of *T. iheringi* in lakes.

Two of the three lotic populations of *P. canaliculata* with commensals (AC and LA) were located downstream of lentic populations with temnocephalans and probably receive drifting snails from these sources. The site at Chasicó stream (AC) was located only 3 km downstream from the outlet of Los Chilenos lake (LL) and the low density of snails and their eggs observed there indicate that it was a sink population. The site at Langueyú stream (LA) was located 40 km downstream of El Fuerte reservoir (TA) and together with Chapaleofú stream (CH), which has no lentic population source, showed the lowest prevalences and egg numbers of commensals. According to the SDA these two lotic snail populations were more similar to the populations where the commensals were absent than to those with worms. The low abundances of worms evidenced by the low prevalences and egg numbers suggest that these populations are at high risk of local extinction, although in the case of Langueyú stream recolonization is more probable than in Chapaleofú stream.

Although *P. canaliculata* shows sexual differences in many bio-ecological traits as growth, survival, age at maturity, shell shape and size, etc.

(Estebenet & Martín, 2002; Estoy et al., 2002), no differences between the populations of *T. iheringi* hosted in males and females has been detected in this and other studies (Damborenea, 1996, 1998). Probably the sexual transmission of worms blurs the differences provoked by the different conditions or resources provided by each sex.

As most studies have been concentrated on demography and interactions between hosts and commensals (Jones & Lester, 1993; Damborenea, 1998), no attention has been paid to those host populations without temnocephalans. However, these populations provide valuable comparative information to understand the factors affecting the occurrence of temnocephalans among populations of their hosts. Apart from the fact that the presence of a suitable host is an essential condition, our study indicates that physicochemical water factors and population dynamics of the host are of capital importance in determining the persistence of the commensal populations. Dispersal mechanisms also emerge as relevant to the maintenance of commensal populations under conditions otherwise promoting local extinction.

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