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Diet variation of the South American snake-necked turtle (*Hydromedusa tectifera*) from two different urban neighboring streams

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Abstract. Dietary studies provide data about the biology of species such as food specialization, spatial and temporal feeding variation, and adaptations to different habitat characteristics. We analyzed the diet of the South American snake-necked turtle *Hydromedusa tectifera* using complementary techniques (stomach flushing and feces collection) from two urban watercourses in La Plata city (Buenos Aires, Argentina), one more natural and other more polluted. The Index of Relative Importance (IRI) was calculated to assess the contribution of each prey to the diet, and the Index of Electivity (E) to evaluate food selection. In general, *H. tectifera* displayed a generalist carnivorous habit with clear adaptations to variations in the environments in which this species lives. The diet composition showed marked differences between the two streams: in the more impacted watercourse, amphipods, aquatic coleopterans, and water bugs of the family Belostomatidae were the main items, while in the less anthropogenically disturbed one, aquatic snails dominated the turtles' diet. Our results highlight the importance of combining stomach flushing and fecal collection techniques to achieve a better trophic characterization and to avoid biased conclusions.

Key words: Argentine snake-necked turtle, diet composition, prey selection, urban environment, feces, stomach flushing.

Introduction

Dietary studies supply important data on the biology, physiology, and natural history of a species, as well as information regarding local restrictions such as prey availability or intra- and inter- specific interactions (Ottonello et al. 2017). Moreover, knowledge about what an animal eats and what its feeding preferences are is a useful tool for environmental management and conservation programs.

Globally, most lotic and lentic ecosystems have been highly affected by urbanization since they were usually chosen for human settlements (Bodie 2001). In this context, understanding how habitat transformations shape the ecological niche dimension of species becomes crucial to mitigate impacts, promote restoration actions and generate long-term conservation programs on freshwater ecosystems (Bodie 2001, Spinks et al. 2003).

Feeding habits of urban freshwater turtle populations have been assessed for several species around the world (Souza & Abe 2000, Wilson & Lawler 2008, Wilhelm & Plummer 2012, Stephens & Ryan 2019). In some cases (e.g., *Phrynops geoffroanus*), variations in feeding habits between individuals from urban and non-urban sites have been reported (Ferronato et al. 2013).

The exclusively aquatic medium size South American snake-necked turtle *Hydromedusa tectifera* Cope, 1870 is distributed from southern Brazil and southeastern Paraguay to northeastern and central Argentina and almost all of Uruguay (Sánchez et al. 2019). It inhabits highly diverse environments like ponds, lagoons, rivers, and streams. Some of these habitats are located in urban areas affected by different sources of pollution such as industrial discharges, sewage and toxins from farming activity. Previous works on the diet of *H. tectifera* demonstrated that this species is generalist, zoophagous and preys on a wide variety of invertebrates and vertebrates, mainly aquatic arthropods, mollusks, fish and even carrion (Bonino et al. 2009, Alcalde et al. 2010). It has probably a reduced home-range evidenced by the high number of recaptures obtained in one or two period studies (Lescano et al. 2008, Semeñiuk et al. 2019).

The present study compares diet composition and prey selection of *H. tectifera* in two neighboring urban streams with contrasting habitat characteristics. The research was designed to test the hypothesis that feeding habits of turtles from both streams reflect the differences observed in the environmental characteristics of their respective habitats. We expected that a more diverse diet would be observed in the less anthropogenically modified stream than in the more impacted stream.

Materials and methods

Field work was carried out in two urban streams, Rodríguez and Carnaval (La Plata city, in northeastern Buenos Aires province, Argentina; Fig. 1). The study area was located in the southern limit of the AMBA (Área Metropolitana de Buenos Aires), the most populated region of the country, with a population of about 14 million people (37% of the Argentinian population) and a density of 1140 people/km^2 (INDEC, 2010).

Both streams are tributaries of the Río de la Plata River and part of the southernmost core of the distribution of *H. tectifera* (Sánchez et al. 2019). These Pampean streams share characteristics typical of most of the watercourses of the region: high turbidity, low basin slope and low-water depths periodically interrupted by flooding due to heavy rains.

Both streams receive untreated domestic water discharges and solid garbage (e.g., bottles, plastics, food remains) from the neighboring houses in the section they cross the city. Overall, the housing density was higher around Rodríguez than in Carnaval (Fig. 1). The Rodríguez stream also receives industrial effluents without appropriate treatment (a meat processing plant and a pork farm) and untreated sewage from the Grand Bell neighborhood.

Due to the high density of housing and the above-mentioned water discharges, Rodríguez has a permanent flow of water even during drought periods (summer). On the contrary, the headwaters and part of the middle section of Carnaval can dry up since its flow depends mainly on underground water which is sometimes overexploited (Rodrigues Capítulo L. et al. 2020).

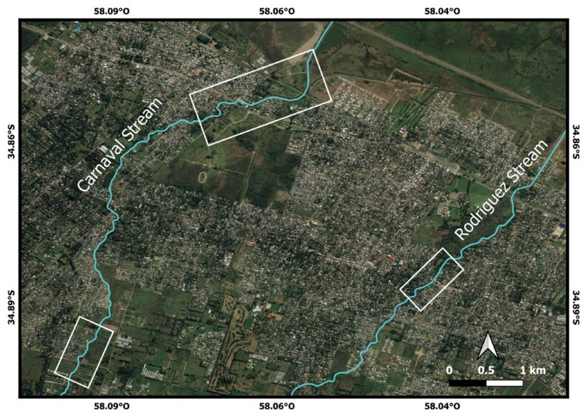

Figure 1. The Rodríguez and Carnaval streams in La Plata city (Buenos Aires province, Argentina), indicating the location of the sampling areas.

Previous investigations of the two streams revealed poorer water quality in Rodríguez, evidenced by high values of conductivity, organic matter, nutrients, and oxygen chemical demand, as well as low values of dissolved oxygen (López van Oosterom et al. 2015, Lavarías et al. 2017). Furthermore, the contamination with organic matter of Rodríguez was also evidenced by alterations of biological functions in hemipterans (Lavarías et al. 2017) and the presence of annelid families associated with organic pollution (López van Oosterom et al. 2015). Based on biotic indices of macroinvertebrate assemblages, Rodríguez was classified as heavily polluted (Bauer et al. 2002, López van Oosterom et al. 2014) and Carnaval as slightly/moderately polluted (López van Oosterom et al. 2014, Rodrigues Capítulo A. et al. 2020).

Another important difference between the streams is that Carnaval had markedly higher abundance and diversity of aquatic macrophytes compared to Rodríguez. Indeed, we identified 16 species and two genera of aquatic macrophytes for Carnaval, classified as submerged (s), floating-leaved (f) or emergent (e): *Egeria densa*, *Elodea callitrichoides*, *Stuckenia striata* (s); *Alternanthera philoxeroides*, *Hydrocleys nymphoides*, *Hydrocotyle ranunculoides*, *Lilaeopsis* spp., *Ludwigia peploides*, *Nasturtium officinale*, *Polygonum punctatum* (f); *Cyperus eragrostis*, *Eleocharis elegans*, *Iris pseudacorus*, *Ludwigia elegans*, *Sagittaria montevidensis*, *Schoenoplectus* spp., *Schoenoplectus californicus*, and *Senecio bonariensis* (e). In contrast, only five of these aquatic plant species were found in the sampled area of Rodríguez: *A. philoxeroides*, *H. ranunculoides*, *N. officinale*, *P. punctatum* (f), and *S. montevidensis* (e).

Finally, Rodríguez is periodically affected (mainly in its middle section, where sampling was carried out, Fig. 1) by dredging and channelization works to avoid floods. This leads to the destruction of the riversides and the natural riparian and aquatic vegetation. On the contrary, the headwaters and middle section of Carnaval lack this kind of disturbances.

Field work was carried out between late spring 2016 (November) and early summer 2017 (January). We went five times (November-December) to Rodríguez and eight times to Carnaval (January). Physical features (width, depth, aquatic vegetation) were different between both streams (Table 1). In Rodríguez we sampled only in a single section (300 m length) but we had to sample in two sections of Carnaval (300 m each) to get a representative sample due to lower turtle abundance in the last stream. Both sampled sections of Carnaval had visibly similar environmental features in terms of aquatic vegetation cover, macrophytes diversity and basin shape (width and depth). Thus the sample effort in Carnaval was about two times higher than in Rodríguez.

Turtles were caught using trotlines without hooks (Semeñiuk et al. 2017) and by hand. For each individual we recorded body mass, straight carapace length and sex based on dimorphic features: deep plastral concavity and longer tail in males (Cabrera 1998). For each turtle we obtained stomach content samples at the moment of capture using gastric flushing (Legler 1977). Subsequently, to collect fecal samples, turtles were taken to the laboratory and placed in individual 40 × 40 cm water buckets for 24 h. After that, water was filtered through a dense net to obtain the feces. Both fecal and stomach samples were preserved in individually labeled containers with 70% ethanol. Finally, turtles were individually marked according to Cagle (1939) before being released at the site of capture.

We chose to use both stomach flushing and feces collection because quite different results were observed using a single technique (Caputo &Vogt 2008), mainly associated with the different prey digestibility and prey size at the moment of ingestion.

Every field day we sampled turtles we also took samples of potential aquatic prey to analyze their availability in the environment (five samples from Rodríguez and eight from Carnaval). For Carnaval prey items samples were taken in both sampling sites and then they were analyzed together. Sampling of aquatic prey items was carried out by passing 30 times a dip net (circumference: 60 cm, mesh size: 2 mm) along the bottom and around the marginal aquatic vegetation.

Samples were observed under a Nikon ZMZ745T stereomicroscope. Prey items were classified to the family or order level, and in cases of particular interest, to the genus or species level (e.g., some gastropods). Each prey item was identified as larva or adult and aquatic or terrestrial. We calculated three variables for each prey category: numeric frequency (N_i, total number of items *i* for all samples), occurrence frequency (OF_i, number of turtles in which item *i* was present), and volume (V_i). The volume was calculated by applying the ellipsoid method of Dunham (1983) in the case of very small items (<0.1 ml, e.g., ostracods) or by the Archimedes method of water displacement in a graduated cylinder for larger items. For prey fragments (e.g., beetle elytra, gastropod opercula) volume was calculated using whole items of the same species with similar size to that of the fragments.

The contribution of each item to the diet was evaluated by means of the Index of Relative Importance: $IRI = \%OF_i \times (\%V_i + \%N_i)$ (Pinkas 1971), where $\%OF_i$ is the percentage of turtles that consumed the item i, $\%V_i$ is the proportion between the volume of the item i and the total volume of all items, and N_i represents the proportion between the number of individuals of the item i and the total number of individuals of all items. The IRI for each stream was calculated for each technique separately (stomach flushing vs. fecal samples) before integrating both into a single analysis.

The item category with highest IRI value was used to rank the percentage values of the remaining ones. Thus, according to this ranking procedure, items were classified into four categories (based on the %IRI values): ≥75.1% = Fundamental; 75–50.1 % = Secondary; 50–25.1% = Accessory, and ≤25 % = Accidental.

Table 1. Mean and range values (in m) of width and depth and physical characteristics of sampling sites in Rodriguez and Carnaval streams.

	Rodríguez	Carnaval
Width	8.91 (8.57–9.3)	2.75 (2.0–3.5)
Depth	0.15 (0.12–0.19)	0.77 (0.75–0.80)
Aquatic vegetation cover	Low	Abundant
Substrate	Clay, mud	Clay, mud

The Ivlev index of Electivity: $E = r_i - p_i / r_i + p_i$ (Ivlev 1961) was used to evaluate prey selection by turtles, where r_i is the percentage numerical frequency of item *i* present in turtle samples (feces and stomach contents together), and p_i is the percentage numerical frequency of item *i* present in environment samples. Since prey diversity was sampled only in water, terrestrial items that fell into water and become ingested by turtles were removed from the counts and not used for this analysis, given that we lacked the environmental counterpart to calculate the index.

Furthermore, E was calculated excluding the item categories that were absent in either of the two types of samples (diet or environment) as suggested by Paloheimo (1979), to reduce biases due to item densities. Items only present in dietary samples of turtles from the Rodríguez stream were small aquatic gastropods (family Physidae), aquatic hemipterans (family Nepidae), larvae of aquatic beetles, fish remains and tadpoles. Items only present in environmental samples from the same stream were aquatic hemipterans (family Gerridae). For the Carnaval stream the single item only present in dietary samples was an aquatic hemipteran (family Nepidae) whereas items only present in environmental samples were small crustaceans (Orders Cladocera and Ostracoda), aquatic hemipterans (family Notonectidae), ephemeropteran larvae, leeches, and tadpoles. Those categories whose numerical frequency in both diet and environment samples were equal to 1 were also excluded due to their low relevance. The E-index ranges from -1 (maximum prey avoidance) to +1 (maximum prey selection). Values of 0 ± 0.20 were considered as indicators of random prey consumption.

Additionally, a series of non-parametric Mann-Whitney U-tests were performed to evaluate differences for the same pair of items (habitat-diet) that were used for the E-index. The main goal of this analysis was to compare and complement the E results and obtain statistical significance for the final results. For example, if at least one turtle of a sampled group consumed a large amount of a given item category that had a very low environmental abundance, we would surely obtain a highly positive E value (prey preference), but this would not be representative of the population mean. All analyses were carried out using the free version of the statistical software Info Stat (2018), assuming a significance value of $p<0.05$.

Results

We captured 24 turtles from Rodríguez (16 stomach samples and 21 fecal samples) and 15 turtles from Carnaval (10 stomach contents and 12 fecal samples).

We identified 26 prey categories ingested by turtles from Rodríguez and 25 consumed by turtles from Carnaval, totaling 38 prey item categories for both streams (Table 2). Feathers and chicken remains (surely ingested as carrion) were not included in the IRI analysis in reason of difficulty for calculating the original volume consumed. Vegetation was also excluded from the analyses due it is accidentally ingested by turtles when they prey upon animals that live amongst the sub-aquatic vegetation (see Alcalde et al. 2010).

In general, the diet of the turtles of Rodríguez was dominated by aquatic insects and amphipods, while that of Carnaval had a high proportion of gastropods (Fig. 2). Items of the families Hyalellidae, Hydrophilidae and Belostomatidae were the most eaten prey by turtles of Rodríguez (40%, 34% and 14%, respectively) while they represented a low percentage of consumption for turtles of Carnaval (5%, 1% and 5%, respectively; Fig. 2). The remaining items in turtle samples from Rodríguez included, although with less importance, other aquatic insects (Corixidae, Notonectidae, immature Chironomidae), terrestrial and aquatic annelids and anuran larvae. All these items (except chironomids) were absent in diet samples of turtles from Carnaval. On the contrary, more than half of the items consumed by individuals from Carnaval were snails, principally of the family Ampullariidae (47%; Fig. 2). This prey category was absent in dietary samples from Rodríguez, site that also displayed a very low numerical percentage of the remaining gastropod categories ("others", Fig. 2). Similarly, woodlice, which appeared as the second most consumed item for Carnaval (21%), were practically absent in diet samples of turtles of Rodríguez.

The IRI values were very different for turtles from both streams (Table 2). Considering both sample sources, the Fundamental prey in the diet of *H. tectifera* from Rodríguez were amphipods (100%) and aquatic coleopterans (86.88%) whereas Secondary prey were water bugs of the family Belostomatidae (55.72%). All the remaining items fell into the Accidental prey category (≤ 25%). Regarding the turtles from Carnaval, the combined IRI results showed a clear dominance of *Pomacea* snails (Fundamental prey), while the other items were within the Accidental prey category.

These IRI results were quite different when feces and stomach flushing samples were analyzed separately (Table 2), especially for Rodríguez. The stomach flushing IRI determined the amphipods as the only Fundamental prey, whereas the fecal samples IRI showed aquatic coleopterans (Hydrophilidae) and water bugs (Belostomatidae) as Fundamental and Secondary items, respectively. Regarding Carnaval, woodlice (suborder Oniscidea) and aquatic snails of the genus *Pomacea* were the Fundamental prey for stomach contents (100% and 84.61%, respectively). The *Pomacea* snails were the single Fundamental prey category item according to the feces IRI.

In regard to the results of the index of electivity (E), aquatic coleopterans of the family Hydrophilidae (0.95) and water bugs of the family Corixidae (0.83) were the prey item categories for the turtles of Rodríguez with the highest positive values, near maximum electivity (Fig. 3). Conversely, the item with the lowest E value for the same stream were immature midges of the family Chironomidae (-0.88). The randomly ingested prey items were amphipods of the family Hyalellidae (0.02) and immature midges of the family Culicidae (0.14). For Carnaval, the electivity values indicated that the most preferred prey were aquatic gastropods of the family Ampullariidae (genus *Pomacea*, 0.90), and water bugs of the family Belostomatidae (0.95), while the least preferred items were small fishes (-0.88) and small water gastropods of the families Cochliopidae (-0.77) and Physidae (-0.73). Prey items with E values closest to zero were water snails of the family Viviparidae (genus *Sinotaia*, -0.05) and Odonata naiads (-0.14), indicating they were neither selected nor rejected by turtles. The most abundant prey items on the environmental samples of Rodriguez were amphipods (Family Hyalellidae) and immature midges (Family Chironimidae), while those of Carnaval were amphipods (Family Hyalellidae), water gastropods of the family Cochliopidae and fishes (Fig. 4).

It is worth noting that, among those prey items that were present in only one type of sample (diet or habitat), the anuran larvae appeared in turtles of Rodríguez but were absent in environmental samples, and vice versa in Carnaval. So, we think that the sampling methods we used for trapping such mobile prey (the same as for aquatic insects) would not have been a limitation.

Regarding the paired comparisons of the complementary Mann-Whitney U-test, all the items with a positive E value from both streams had no significant differences between presence of a given item in the diet of turtles and in the

Table 2. Percentages of numeric frequency (N), occurrence frequency (OF), volume (V), and IRI values of each prey item in the diet of *Hydromedusa tectifera* discriminating by type of sample (Feces and Stomach contents) and stream. Fundamental and secondary prey items are in bold. Items shared by turtles from both streams are highlighted in gray. References: Undet. = undetermined.

Prey items categories				**Feces**				**Stomach contents**				Total IRI
				N	OF	V	IRI	N	OF	V	IRI	
Rodríguez stream												
Annelida	Hirudinea			0.11	4.76	0.01	0.01	1.03	31.25	0.09	0.23	0.28
	Terrestrial oligochaeta			0.11	4.76	0.23	0.01	1.61	25.00	3.88	0.90	0.98
Mollusca	Gastropoda	Physidae		-	-	-	-	0.11	6.25	0.08	0.01	0.01
		Cochliopidae		0.21	9.52	0.01	0.02	0.23	12.50	0.01	0.02	0.07
		Planorbidae		0.426	19.05	0.59	0.17	0.46	25.00	0.29	0.12	0.40
Arthropoda	Acari	Arrenuridae		0.11	4.76	0.00	0.00	-	-	-	-	0.00
	Crustacea	Amphipoda	Hyalellidae	0.11	4.76	0.19	0.01	**83.22**	**87.50**	**90.91**	**100**	**100**
		Isopoda	Oniscidea	0.11	4.76	0.06	0.01	0.11	6.25	0.04	0.01	0.02
	Hexapoda	Odonata	Zygoptera (naiads)	-	-	-	-	0.11	6.25	0.00	0.00	0.00
		Hemiptera	Belostomatidae	**25.35**	**100**	**44.95**	**63.36**	**1.15**	**37.50**	**3.25**	**1.08**	**55.72**
			Corixidae	4.15	33.33	1.00	1.55	2.76	25.00	0.17	0.48	3.08
			Nepidae	0.21	4.76	0.70	0.04					0.03
			Notonectidae	0.96	19.05	0.27	0.21	0.11	6.25	0.02	0.01	0.26
		Coleoptera	Hydrophilidae	**65.18**	**95.24**	**51.31**	**100**	**1.26**	**31.25**	**0.79**	**0.42**	**86.88**
			Curculionidae	0.32	14.29	0.03	0.04	-	-	-	-	0.04
			Undet. larvae	0.11	4.76	0.00	0.00	-	-	-	-	0.00
			Undet. terrestrial adults	0.21	9.52	0.53	0.06	-	-	-	-	0.05
		Hymenoptera	Formicidae	0.43	14.29	0.07	0.06	-	-	-	-	0.06
			Undet. family	0.11	4.76	0.00	0.00	-	-	-	-	0.00
		Diptera	Culicidae (pupae)	0.53	4.76	0.00	0.02	0.11	6.25	0.00	0.00	0.08
			Chironomidae (immature states)	1.17	19.05	0.04	0.21	5.86	43.75	0.12	1.72	2.43
			Muscidae	-	-	-	-	0.11	6.25	0.00	0.00	0.00
			Undet. pupae	0.11	4.76	0.01	0.00	0.11	6.25	0.17	0.01	0.03
Vertebrata	Pisces, undet. Family			-	4.76	-	-	-	-	-	-	-
	Anura (undet. tadpoles)			-	-	-	-	1.61	6.25	0.17	0.07	0.07
	Feathers			1.00	4.76	-	-	-	-	-	-	-
Carnaval stream												
Mollusca	Gastropoda	Physidae		0.76	8.33	0.00	0.17	-	-	-	-	0.08
		Cochliopidae		3.05	25.00	0.00	2.00	-	-	-	-	0.99
		Ampullariidae (genus *Pomacea*)		**62.60**	**25.00**	**90.07**	**100.00**	**25.00**	**10.00**	**96.48**	**84.61**	**100.00**
		Viviparidae (*Sinotaia quadrata*)		9.92	25.00	8.47	12.05	-	-	-	-	6.65
		Planorbidae		1.53	16.67	0.01	0.67	4.55	10.00	0.25	3.34	1.01
		Ancylidae		0.76	8.33	0.00	0.17	-	-	-	-	0.08
Arthropoda	Araneae, undet. Family			-	-	-	-	1.14	10.00	0.00	0.79	0.08
	Crustacea	Amphipoda	Hyalellidae	-	-	-	-	11.36	20.00	0.13	16.01	1.65
		Isopoda	Oniscidea	3.82	25.00	0.05	2.53	**46.59**	**30.00**	**1.27**	**100**	15.35
	Insecta	Collembola		-	-	-	-	1.14	10.00	0.00	0.79	0.08
		Zygentoma		-	-	-	-	1.14	10.00	0.00	0.79	0.08
		Odonata	Anisoptera (naiads)	3.82	16.67	0.21	1.76	1.14	10.00	0.36	1.04	1.61
			Undet. naiads	0.76	8.33	0.00	0.17	-	-	-	-	0.08
		Phasmida		-	-	-	-	1.14	10.00	0.51	1.15	0.10
		Hemiptera	Belostomatidae	7.63	50.00	1.05	11.37	2.27	20.00	0.83	4.32	6.98
			Nepidae	0.76	8.33	0.04	0.18	-	-	-	-	0.09
		Coleoptera	Hydrophilidae	0.76	8.33	0.01	0.17	1.14	10.00	0.04	0.82	0.17
			Coccinelidae	0.76	8.33	0.00	0.17	-	-	-	-	0.08
			Undet. terrestrial adults	0.76	8.33	0.00	0.17	-	-	-	-	0.08
		Hymenoptera	Formicidae	-	-	-	-	1.14	10.00	0.00	0.79	0.08
		Lepidoptera (larvae)		0.76	8.33	0.00	0.17	-	-	-	-	0.08
		Diptera	Chironomidae (larvae)	-	-	-	-	1.14	10.00	0.00	0.79	0.08
			Syrphidae (larvae)	1.53	8.33	0.06	0.35	-	-	-	-	0.17
Vertebrata	Pisces, undet. Family			-	-	-	-	1.14	10.00	0.13	0.88	0.09
	Chicken remains, feathers			1.53	16.67	-	-	1.14	10.00	-	-	-

environmental samples. On the contrary, almost all the items that had negative E values showed significant differences between the dietary and environmental samples, except for aquatic gastropods of the family Planorbidae from Carnaval (two-tailed p = 0.28). Most of the prey items categorized as randomly consumed according to the E-index, presented statistically significant differences between consumed vs. habitat values, except for the hydrophilid coleopterans (p = 0.12) and viviparid gastropods (p = 0.35) from Carnaval.

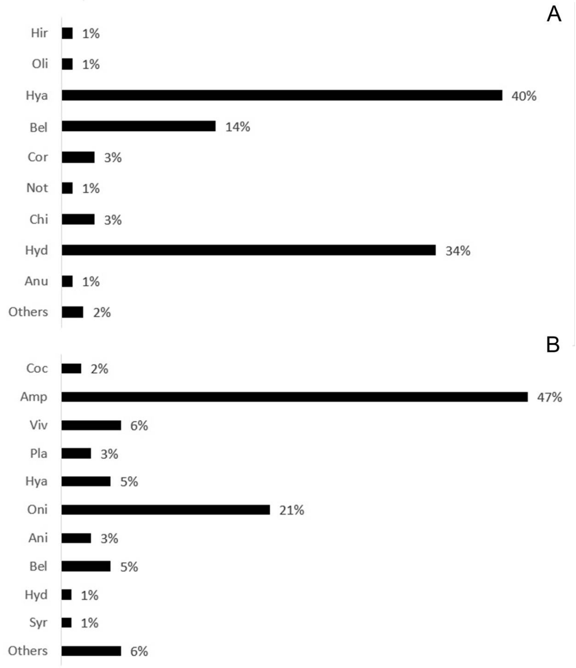

Figure 2. Percentage numeric frequency (%N) of each prey item categories consumed by *Hydromedusa tectifera* from (A) Rodríguez and (B) Carnaval streams. Amp= Ampullariidae; Ani= Anisoptera; Anu= Anura; Bel= Belostomatidae; Chi= Chironomidae; Coc= Cochliopidae; Cor= Corixidae; Hir= Hirudinea; Hya= Hyalellidae; Hyd= Hydrophilidae; Not= Notonectidae; Oli= Oligochaeta; Oni= Oniscidea; Pla= Planorbidae; Viv= Viviparidae; Syr= Syrphidae; Others: prey items categories <1%.

Discussion

The studied *H. tectifera* from two neighboring and contrasting urban streams has a carnivorous generalist diet with highly similar amounts of item categories consumed by these turtles. Therefore, this rejected our hypothesis of a more diverse diet in the population inhabiting the stream with better habitat conditions. Nevertheless, prey item composition was markedly different in the two streams.

Turtles of both streams shared 39% of the consumed items (Table 2); the rest of the items established a clear difference in consumption by turtles. The diet of turtles from the more disturbed Rodríguez stream was mainly based on amphipods, aquatic coleopterans, and water bugs, whereas individuals from Carnaval mainly fed on aquatic gastropods.

The items most consumed by the turtles of Rodríguez were insects moderately resistant to water pollution: water bugs of the family Belostomatidae and aquatic coleopterans of the family Hydrophilidae (Rodrigues Capítulo et al. 2004). Although these items were not abundant in the habitat samples from Rodríguez, they were positively selected by turtles, as is expressed by the E index results (Fig. 3). These items were almost absent in the habitat samples from Carnaval.

Turtles from Carnaval mostly consumed aquatic snails of the family Ampullariidae (particularly *Pomacea canaliculata*), unlike those from Rodríguez (Fig. 2). Environmental abundance of this species (and of other snails) seems to explain the differences of this prey item between the diet of the turtles from both stream: this gastropod was present in all environmental samples from Carnaval, but it was never found in those from Rodriguez (Fig. 4), indicating either absence or extremely low abundance. Diversity and abundance of macrophytes appear as the environmental feature probably related to the variations in presence and abundance of *Pomacea* snails between both studied streams. Gastropods use macrophytes as substrate for oviposition and to grasp and feed on the epiphytic algae that grow on the surface of these plants (Brönmark 1989). The abundance of gastropods (and of macrophytes) was greater in Carnaval than in Rodríguez (Fig. 4) and this fact may surely explain the differences found for *Pomacea* snails in the diet of turtles from both streams.

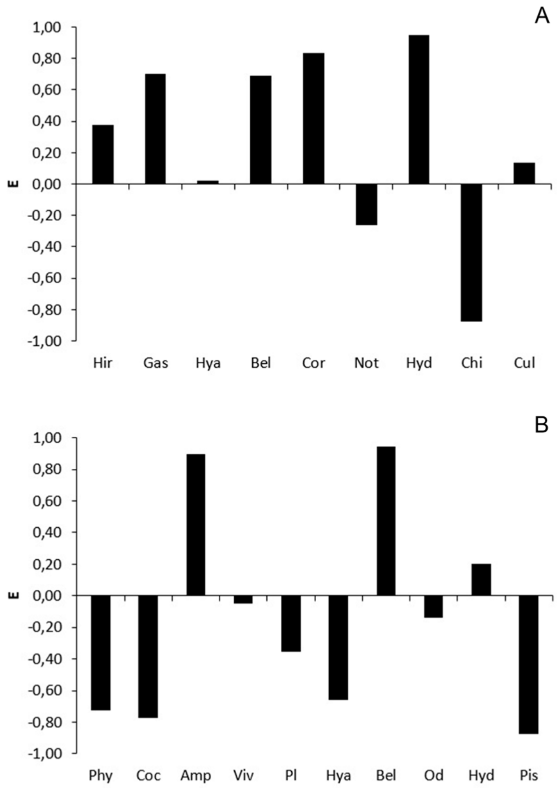

Figure 3. Index of electivity values (E) for each prey item consumed by *Hydromedusa tectifera* from Rodríguez (A) and Carnaval (B) streams. Amp= Ampullariidae; Bel= Belostomatidae; Chi= Chironomidae (immature stages); Coc= Cochliopidae; Cor= Corixidae; Cul= Culicidae (immature stages); Gas= Gastropoda (families Planorbidae and Cochliopidae); Hir= Hirudinea; Hya= Hyalellidae; Hyd= Hydrophilidae; Not= Notonectidae; Od= Odonata (naiads); Phy= Physidae; Pis= Pisces; Pl=Planorbidae; Viv= Viviparidae.

Other contrasting result between both water courses was the differential consumption of amphipods (family Hyalellidae): although this item was abundant in the environmental samples of both streams, it was scarcely consumed by turtles of Carnaval, unlike those of Rodríguez (Fig. 4). Hyalellids can live associated with submerged and floating macrophytes, as gastropods, and in the benthos (Casset et al. 2001). Likely, these small preys were more difficult to be found by turtles when they are among dense plant communities (as in the case of Carnaval) than on bare bottom without (or with low abundance of) vegetation, as in Rodríguez.

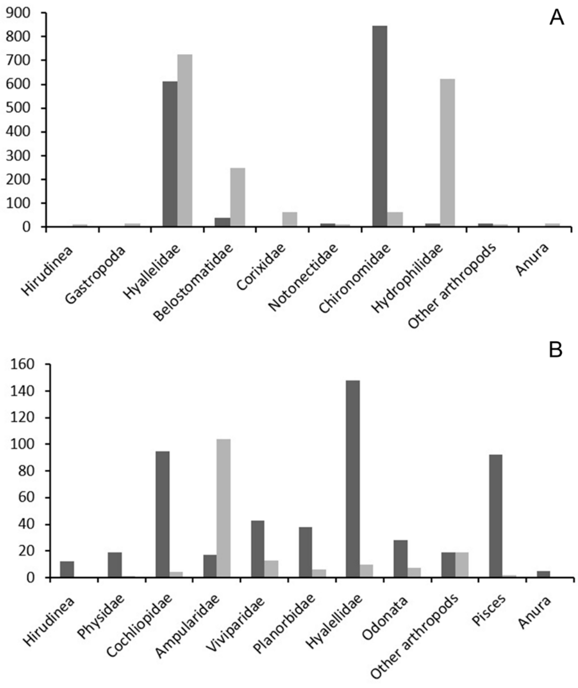

Figure 4. Numeric frequency (n) of prey items present in the diet of *Hydromedusa tectifera* (gray columns) and habitat samples (dark columns) from the Rodríguez (A) and Carnaval (B) streams. In (A) Gastropoda: Planorbidae and Cochliopidae; Other arthropods: Acari, Collembola, Odonata, Gerridae, Nepidae, Culicidae; in (B) Other arthropods: Acari, Ostracoda, Cladocera, Ephemeroptera, Phasmida, Belostomatidae, Nepidae, Notonectidae, Hydrophilidae, undetermined coleopterans, Chironomidae and Syrphidae. Note different Y-axes.

Mollusk ingestion by generalist freshwater turtles has been reported for several species (e.g., Lindeman 2006, Works & Olson 2018). For the case of *H. tectifera*, Gallardo (1956) mentioned the presence of a large amount of opercula of *Pomacea* in the feces of an individual that was in captivity for a brief period. Stomach flushing-based studies of the feeding habits of the species detected a very low or no contribution of *Pomacea* snails to the diet (Bonino et al. 2009, Alcalde et al. 2010), despite their presence in the habitat. In the present study, fecal samples revealed a high ingestion of *Pomacea* snails by turtles from Carnaval (e.g., one individual yielded 65 *Pomacea* opercula), but no consumption by turtles from Rodríguez. Hence, *Pomacea* snails appear as an important food item for *H. tectifera* but its consumption probably depends on its abundance.

The greater frequency of *Pomacea* opercula in feces than in stomach samples resembles the case of palm seeds in the diet of *Rhinemys rufipes* described by Lima et al. (1997), since these authors could not dislodge palm seeds from stomachs with the flushing technique. Thus, we agree with Caputo & Vogt (2008) that the use of both sampling techniques yields better results in the study of turtles' diet than either one of them, avoiding both underestimation and overvaluation of certain prey categories. With respect to the ingestion mechanism of *Pomacea* snails displayed by *H. tectifera*, Gallardo (1956) observed that a captive individual of the species ingested snails by suction of their soft body parts (and the attached opercula) but discarding the shell. This was verified in fecal and stomach samples in which only whole *Pomacea* opercula were found, without shell pieces. Bonino et al. (2009) obtained *Pomacea* remains but without specifying if they were very small specimens or shell fragments and opercula of larger snails. Similarly, predation of *Pomacea* snails by *Pelusios sinensis* and *Trachemys scripta* was revealed by stomach dissections (Works & Olson 2018) without details about the way the turtles ingested the snails.

Our study demonstrated that molluscivory by turtles of Carnaval also included five small-shelled native snails and the exotic gastropod *Sinotaia quadrata*, totaling six species of aquatic gastropods. This number is higher than those reported for this species: two for Buñirigo (Alcalde et al. 2010), Toro Muerto and Tanti streams (Bonino et al. 2009), and three for Rodríguez stream (this work).

The non-native aquatic snail *Sinotaia quadrata* was recently reported from the sampling area of Carnaval (Ferreira et al. 2017). *H. tectifera* seems to ingest these snails using the same mechanism it uses to prey on *Pomacea* snails. The samples revealed that *Sinotaia* snails were consumed less than the native *Pomacea* snails, in a 1:8 proportion (104 *Pomacea vs.* 13 *S. quadrata*) and were eaten randomly according to the E-index values. Further studies would be interesting for evaluating the impact of predation by *H. tectifera* on this alien snail population.

In general, our results coincide and complement previous studies carried out in other populations of the species (Bonino et al. 2009, Alcalde et al. 2010). Comparing the sum of items eaten by *H. tectifera* with the above mentioned feeding studies, using the same prey item categories (at family and order levels) used by Alcalde et al. (2010), the following results were obtained: turtles consumed 25 items in the Toro Muerto and Tanti streams (Córdoba province, Argentina: Bonino et al. 2009; for the comparison we considered Trichoptera and Ephemeroptera as order levels and Odonata as suborder level); 29 items in the Buñirigo stream (Buenos Aires province, Argentina: Alcalde et al. 2010), and 26 and 25 items in the Rodríguez and Carnaval streams respectively, in the present study. These data show a similar amount of prey item categories, regardless of the features of the streams where the species lives.

Although with different IRI values, only four of these item categories were consumed by turtles from the five streams: amphipods (family Hyalellidae), water bugs (family Belostomatidae), aquatic coleopterans (family Hydrophilidae) and immature midges (family Chironomidae). Except for the last item, the rest had high IRI values in turtles from Rodríguez (Fundamental or Secondary categories), but they fell into Accidental prey category on turtles from the other streams. Hence, data also support a broad and versatile trophic niche that allows *H. tectifera* to exploit a variety of prey, even those that appear occasionally, such as carrion and certain terrestrial invertebrates.

Feeding habits were studied for approximately half of the other 21 Neotropical chelids species. Most of them exhibited a generalist carnivorous diet with particularities related to habitat; a few are omnivorous (mainly the genus *Mesoclemmys*) and one is piscivorous, *Chelus fimbriata* (Fachin Teran et al. 1995, Richard 1999, Caputo & Vogt 2008, Brasil et al. 2011, Böhm 2013, Ferronato et al. 2013, Brito et al. 2016, Alves Pereira et al. 2018). The sister species *Hydromedusa maximiliani* has a broad diet based on aquatic insects, crustaceans, small vertebrates (anurans) and carrion (Souza & Abe 1998, Novelli et al. 2013), with preference on trichopteran larvae, immature chironomids, and amphipods of the genus *Hyalella*. This last prey item was the main prey consumed by juveniles of *H. maximiliani* (Souza & Abe 1998), contrary to *H. tectifera* that consumed this item regardless of the size class of the individuals. Variations similar to those found here in the diet of *H. tectifera* from two streams with different urban impacts were reported for *Phrynops geoffroanus*. Its diet was extensively investigated in habitats of diverse environmental quality: turtles in protected areas and undisturbed water courses fed primarily on fish, aquatic insects, and plant material (Fachin Teran et al. 1995, de Sousa Ribeiro et al. 2017), while immature chironomid midges were the bulk of the diet of those inhabiting urban polluted rivers (Souza & Abe 2000, Martins et al. 2010, Alves Pereira et al. 2018). This item was also the most important prey for a wild population of *Phrynops hilarii* from a polluted stream of Argentina (Alcalde et al. 2010). Assmann et al. (2013) also found contrasting results among populations of *Acanthochelys spixii* inhabiting lagoons with different trophic quality: plecopterans, trichopterans and crustaceans were abundant in the diet of turtles of oligotrophic habitats, unlike those of waters with abundant organic matter which consumed mainly mollusks, fish, annelids, and terrestrial insects of the order Orthoptera.

The environmental availability of prey is generally not included in dietary studies of turtles (Georges et al. 1986, Moll 1990, Spencer et al. 1998, Ottonello et al. 2017, Petrov et al. 2018). The only antecedent of studies of prey preferences of *H. tectifera* applying the E-index of Ivlev (1961) is that of Alcalde et al. (2010) in the polluted Buñirigo stream. Prey electivity of the population from this stream differed from the values reported in our study and was even reversed in the case of particular items. Immature chironomid midges were positively selected by turtles from Buñirigo but avoided by those from Rodríguez (this item was absent in our habitat samples from Carnaval; Fig. 3). The fact that *H. tectifera* from the polluted Buñirgo stream consumed large numbers of immature chironomid midges agrees with studies on species of *Phrynops* that also inhabit highly polluted waters (Souza & Abe 2000, Alcalde et al. 2010). Although chironomid environmental abundance was significant in the polluted Rodríguez stream, turtles did not consume them in large quantities. Barrera-Oro and Casaux (1990) mentioned several variables that could determine the reason(s) for a prey to be selected by a consumer: prey size, mobility, mode of fixing to substrate, activity, digestibility, and camouflage. Although we cannot be sure on which of these factors the preference of the turtles may be based, in our case study, it seems likely that large visible items (e.g., water bugs of the family Belostomatidae), and less motile items (e.g., *Pomacea* snails) are preferred over very small and less visible prey (e.g., immature chironomid midges) regardless of their motility.

The complementary non-parametric paired comparisons not always corroborated the results obtained with the E-index. Each prey category that was preferred applying the E-index showed no significant differences between consumed and available prey. Thus, these results do not provide complete certainty that turtles do indeed select these items. Conversely, almost all items that were avoided according to the E-index showed significant U-test p values. This is the case of items from both streams that were highly abundant in environmental samples but were quite scarce in stomach and feces samples (e.g., immature chironomid midges from Rodríguez: n = 842 in habitat samples vs. n = 62 in turtle samples, Fig. 4A). These congruent results strongly suggest that turtles did not prefer this type of item despite its high environmental abundance. Therefore, we may argue that the E-index produces somewhat biased electivity values for some prey over others since it depends on the abundance of environmental items (see critiques made by Strauss 1979 and Kholer 1982). Hence, we suggest the use of the E-index as a first indicative approach that should be complemented using paired comparison tests to assess statistical significance and consequently, provide more reliable results.

To sum up, *H. tectifera* has a versatile diet that seems to be highly influenced by the type of prey and its abundance and diversity in the habitat. Moreover, this work is an example of how the combined use of more than one technique (fecal and stomach sampling) and analyses (E-index and U-test multiple comparisons) for dietary studies is helpful to obtain more complete and reliable results.

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