

Diet of *Hydromedusa tectifera* (Testudines-Chelidae) in a mountain stream of Córdoba province, Argentina

Marcelo F. Bonino¹, Julián N. Lescano¹, José G. Haro², Gerardo C. Leynaud^{1,*}

Abstract. The diet of *Hydromedusa tectifera* occurring in two mountain streams in the province of Córdoba is described through a comparative analysis of 154 individuals. Turtles were manually captured between August 2005 and August 2006 from streams at the localities of Tanti and Flor Serrana. Before being released, turtles were stomach-flushed, and sex and carapace length were recorded. The stomach contents were observed under stereomicroscope; prey items were identified and classified according to size and volume. The importance of the different items was quantified using the Index of Relative Importance (IRI). Similarity in the diet between sexes and among size classes and seasons of an annual cycle was evaluated using the simplified Morisita index. Trophic breadth was estimated with the Shannon diversity index. Detrended Correspondence Analysis (DCA) was used to evaluate differences in the diet between categories (sex, size classes). Forty-seven food items belonging to the following taxa were identified: leeches, annelids, gastropods, arachnids, insects, and fishes. According to the IRI value, the most important items in the diet of *H. tectifera* were larvae of Trichoptera (IRI = 33.5), fishes (IRI = 30), and naiads of Odonata (IRI = 25.2). The relative importance of the items varied with size of turtles but not with sex. Size of prey consumed increased with increasing turtle size. A greater trophic breadth was observed in smaller individuals.

Keywords: Argentina, feeding, freshwater turtles, *Hydromedusa tectifera*.

Introduction

Turtles are an ecologically and morphologically diverse group, a characteristic that is reflected in their variety of feeding habits. Indeed, some turtle species are exclusively herbivorous (i.e. *Gopherus polyphemus*, *Homopus signatus signatus*), whereas others are exclusively carnivorous (i.e. *Chelodina expansa*, *C. longicollis*, *Chelus fimbriatus*, *Hydromedusa maximiliani*, *Pseudemys umbrina*); there are also species that can be omnivorous (i.e. *Carettochelys insculpta*, *Phrynops geoffroanus*) (Georges, Norris and Wensing, 1986; Allanson and Georges, 1999; Zug, Vitt and Caldwell, 2001; Mushinsky, Stilson and McCoy, 2003; Souza, 2004; Loehr, 2006).

The diet of freshwater carnivorous turtles includes insects (and their aquatic larvae), annelids, gastropods, fishes, amphibians, and even carrion (Georges, 1982; Georges, Norris and Wensing, 1986; Souza and Abe, 1995, 1997a, 1998; Allanson and Georges, 1999; Cooley et al., 2003; Aguirre León and Aquino Cruz, 2004; Souza, 2004). Some turtle species consume food according to its local availability, and are therefore regarded as opportunist; other species behave as selective and specialized predators, using resources disproportionately according to availability (Georges, Norris and Wensing, 1986; Tucker, Fitzsimmons and Gibbons, 1995; Souza and Abe, 2000; Souza, 2004). In addition, there are often ontogenetic (Tucker, Fitzsimmons and Gibbons, 1995; Souza, 2004) and seasonal (Souza and Abe, 1997b) differences in diet composition among turtles of a single species.

The ecology of Neotropical freshwater turtles, including the feeding habits of some species, has been increasingly studied since the past decade (Souza, 2004). Little is known, however, about the natural history of *H. tec-*

1 - Centro de Zoología Aplicada. Facultad de Ciencias Exactas, Físicas y Naturales (Universidad Nacional de Córdoba), Rondeau 798, Casilla de Correo 122, Córdoba (5000), Argentina

2 - Museo de Zoología de la Facultad de Ciencias Exactas, Físicas y Naturales (Universidad Nacional de Córdoba), Velez Sarfield 299, Córdoba (5000), Argentina

* Corresponding author;

e-mail: gleynaud@efn.uncor.edu

tifera, and information on its diet is largely anecdotal.

The South American chelid genus *Hydromedusa* is represented by two species: *H. maximiliani* and *H. tectifera*, the latter being the least studied (Souza, 2004; Souza and Martins, 2006; Kurzmann Fagundes and Bager, 2007). *H. tectifera* is defined as a zoophagous species, feeding on fishes, insects, anuran adults and larvae, and snails (Cabrera, 1998).

H. tectifera is distributed in the east and southeast of Brazil, Paraguay (Paraná River basin), and throughout most of Uruguay. In Argentina, *H. tectifera* is found in the upper Paraná River basin, its tributaries in Misiones, the Paraná delta, the Uruguay River basin, and the rivers and streams of the province of Buenos Aires that flow into the La Plata River basin (Cabrera, 1998). In the province of Córdoba, an isolated population of *H. tectifera* inhabits mountain rivers and streams in the south of the Punilla department (Cabrera, Haro and Monguillot, 1986; Cabrera, 1998). Information about the reproduction and size of these mountain populations of *H. tectifera* has been reported by Lescano, Bonino and Leynaud (2007, 2008).

In the study of isolated populations, population dynamics, recruitment rate, and food availability are especially important (Andrén and Nilson, 1983; Forsman, 1991; Dodd, Franz and Smith, 1994; Pearson, Shine and How, 2002). If resources are limited and subsequently reduced through habitat modification, then reproductive output may decrease, growth rate of juveniles or adult's condition may be affected, mortality may rise, and population may decline (Allanson and Georges, 1999). Hence, knowing the trophic ecology of these currently isolated populations of *H. tectifera* may become very useful, since natural environments in the Córdoba mountain area are seriously threatened by urban expansion and consequent deforestation (Gavier and Bucher, 2004).

Documenting research on a particular study related to the natural history of the turtles in

general is very important, because it may allow for extrapolations and generalizations to other areas, and could be useful to implement reliable conservation strategies for the preservation of turtle biodiversity that can work at a large scale (Luiselli, Akani and Politano, 2006). The aims of this study are: (a) to describe the diet of *H. tectifera* occurring in a mountain environment of the province of Córdoba and quantify the relative importance of the different prey items; (b) to determine if feeding habits vary with sex, body size, and seasons of an annual cycle.

Materials and methods

Study site

Fieldwork was carried out in a stretch of Toro Muerto and Tanti streams, in a mountain area of Córdoba province, Argentina, at 800 m a.s.l. (Toro Muerto: 31°23'12.94''S; 64°36'08.56''W; Tanti: 31°21'21.41''S; 64°34'01.73''W). Both streams flow irregularly over granitic rock and their mean depth is 70-100 cm. The physiognomy of the surrounding vegetation is that of sierras secondary forest and thorny shrublands, typical of the Chaco region (Cabrera, 1976; Luti et al., 1979). Annual rainfall is 800 mm and is mainly concentrated in spring and summer. Mean minimum temperature is 9.8°C and mean maximum temperature is 21.5°C, with peak values in summer that may exceed 38°C and frosts in winter. Climatic information was extracted from a global database, comprising the period 1961-1990. This database was downloaded from the Intergovernmental Panel on Climate Change Data Distribution Centre (http://ipcc-ddc.cru.uea.ac.uk/cru_data/datadownload).

Diet analysis

From August 2005 to August 2006 weekly samplings were conducted alternatively at both sites, totalling 24 sampling dates at each stream. Individuals were observed after sunset through visual encounter surveys because *H. tectifera* is a species of nocturnal habits (Cabrera, 1998). Data were recorded for all turtles captured. Carapace length (straight line) was measured to the nearest 0.1 cm with Vernier calipers. Sex was determined according to secondary sex characters (males have concave plastrons and longer tails; Cabrera, 1998). Stomach contents were removed by stomach flushing (Legler, 1977) and individuals were released at the capture site. Stomach contents were fixed, maintained in 10% formaldehyde, and analyzed under stereomicroscope. Diet items were identified using keys of Needham and Needham (1978), Rodríguez Capítulo (1992), and Lopretto and Tell (1995) to the lowest possible taxonomic level. The results are expressed in three ways: (1) number of prey of each species or taxonomic level reached; (2) frequency of occurrence of each component (F_o), defined as the percentage of turtles in which a given food item was

present; (3) percentage of volume (V_i), defined as the percentage of volume of an item relative to the total food volume. Volume of each prey item was calculated by water displacement, using graduated cylinders to the nearest 0.1 ml. Foods displacing < 0.1 ml were recorded as "trace".

The data obtained was used to describe the diet of *H. tectifera*. Subsequent analyses compared the diet (a) between adult males and females, considering adults as those individuals whose carapace length was equal to or greater than that of the smallest-sized individual showing secondary sexual characters (≤ 130 mm, Lescano, Bonino and Leynaud, 2008); (b) among size classes; for this purpose, individuals were assigned to one of three classes: <130 mm (class 1) (all turtles considered subadults were included, because secondary sex characters were not evident in individuals smaller than 130 mm); 130-199 mm (class 2), >199 mm (class 3). Size classes were defined following the criterion that each class should include a 70-mm interval, considering that size of sampled individuals ranged between 60 mm and 270 mm of carapace length; (c) between the warm and wet season (October-March) and the cold and dry season (April-September).

Data analyses

Differences in diet composition between sexes and among size classes were evaluated with the Detrended Correspondence Analysis (DCA; McGarigal, Cushman and Stafford, 2000; McCune and Grace, 2002), using PC-ORD version 4.0 (McCune and Mefford, 1999). Results were plotted in an ordination diagram (which summarizes the data in a two-dimension graph), where the distance between the represented scores is inversely proportional to the similarity between the entities represented. Thus, turtles with greater similarity in the use of food items will be closer to one another in ordination space and also closer to the item most represented in the diet. Only the most important diet components were considered for this analysis, including items with Index of Relative Importance (IRI) values higher than 15, because rare items probably appear randomly and do not represent true differences between the entities to be compared (Gido and Matthews, 2000).

The importance of each food item in the diet was quantified separately for sex, size class, and season by IRI, integrating frequency of occurrence and volume:

$$IRI = 100(F_o \cdot V_i) / \sum (F_o \cdot V_i)$$

in which values near 0 indicate low importance and values near 100, high importance (Bjorndal et al., 1997). Similarity or niche overlap between males and females, and among sizes class, was measured by the Simplified Morisita Index (CH):

$$CH = 2 \sum P_{ij} \cdot P_{ik} / \sum P_{ij}^2 + \sum P_{ik}^2,$$

where j and k are categories to be compared, and P_{ij} , P_{ik} is the proportion represented by item i in such categories; values near 0 indicate low similarity and values near 1, high similarity (Krebs, 1999). Diversity in the diet was estimated

using the Shannon diversity index (Krebs, 1999):

$$H' = \sum -p_j \log p_j,$$

where p_j stands for the percentage of prey items of a given taxon relative to the total number of prey items found. Thus, the lowest H' value corresponds to the category with the most specialized food habits. Significant differences between H' of the different categories were evaluated with the t test.

With the aim of evaluating a possible relationship between size of turtles and size of prey captured, a regression analysis was performed with these variables, considering maximum carapace length of each turtle as the independent variable and the length of the biggest prey consumed by each turtle as the dependent variable.

Results

Stomach contents of 154 individuals of *H. tectifera* (59 males, 43 females, and 52 subadults) were obtained. Size of individuals ranged between 60-270 mm: size class 1 comprised 50 individuals (<130 mm); size class 2, 53 individuals (130-199 mm); and size class 3, 51 individuals (>199 mm). 81 individuals were captured in the warm season (October-March) and 73 individuals in the cold season (April-September).

Diet composition

A total of 47 items of diverse taxa were identified in the diet of *H. tectifera*: insects (item present in 45% of turtles), gastropods (45%), fishes (40%), leeches (8%), arachnids (3%), amphipods (2%), and annelids (1%) (table 1). The most important items in the diet of *H. tectifera* were trichoptera larvae (IRI = 33.5), fishes (IRI = 30), and naiads of Odonata (IRI = 25.2); the remaining items had IRI values lower than 10 (fig. 1).

Variations in the diet between sexes

No noticeable differences in diet composition between sexes were recorded. The DCA revealed that along the two axes there is no differential segregation of the points representing males and females relative to the prey items consumed (fig. 2). The most important items in the diet of males were trichoptera larvae and

Table 1. Composition and frequency of occurrence (%) of prey items found in the stomachs ($n = 154$) of *Hydromedusa tectifera* collected from Toro Muerto and Tanti streams, Córdoba, between August 2005 and August 2006.

Prey Item	F _o (%)	Prey Item	F _o (%)
<i>Hirudinea</i> spp.	(8)	Order Coleoptera	(8)
<i>Oligochaeta</i> spp.	(1)	Fam. Hydrophilidae	
Mollusca		<i>Berosus</i> sp.	(1)
Gastropoda	(45)	spp. indet.	(6)
spp. indet.	(44)	Order Trichoptera	(73)
Fam. Ampullaridae		spp. indet.	(3)
<i>Pomacea</i> sp.	(5)	Fam. Helicopsychidae	
ARTHROPODA		<i>Helicopsiche</i> sp.	(56)
Arácnida		<i>Smicridea</i> sp.	(10)
Order Araneae	(3)	Fam. Leptoceridae (spp.)	(7)
Fam. Lycosidae (spp.)	(<1)	Order Lepidoptera	
Fam. Anyphaenidae (spp.)	(<1)	Fam. Pyralidae (spp.)	(3)
Fam. Tetragnathidae (spp.)	(1)	Order Hymenoptera (spp.)	(1)
Fam. Indeterminada (spp.)	(<1)	Order Diptera	(22)
Malacostraca		Fam. Simuliidae (spp.)	(7)
Order Amphipoda		Fam. Chironomidae (spp.)	(2)
Fam. Hyalellidae		VERTEBRATA	
<i>Hyalella</i> sp.	(2)	Pisces	(40)
Insecta		Order Siluriformes	
Order Ephemeroptera	(45)	Fam. Loricariidae	
Fam. Caenidae (spp.)	(23)	<i>Rineloricaria catamarcensis</i>	(3)
Fam. Baetidae (spp.)	(31)	<i>Hypostomus</i> sp.	(9)
Fam. Leptohypidae (spp.)	(4)	Order Characiformes	
Order Odonata	(68)	Fam. Characidae	
Subord. Zygoptera	(52)	<i>Astyanax</i> sp.	(5)
Fam. Coenagrionidae (spp.)	(43)	Order Cyprinodontiformes	
Fam. Protoneuridae (spp.)	(16)	Fam. Anablepidae	
Fam. Calopterygidae (spp.)	(10)	<i>Jenynsia multidentata</i>	(26)
Subord. Anisoptera	(34)	Order Perciformes	
Fam. Aeshnidae (spp.)	(27)	Fam. Cichlidae	
Fam. Libellulidae (spp.)	(10)	<i>Cichlasoma facetum</i>	(3)
Fam. Corduliidae (spp.)	(3)		
Order Orthoptera			
Fam. Acridiidae (spp.)	(2)		
Order Hemiptera	(21)		
Fam. Belostomatidae (spp.)	(11)		
Fam. Naucoridae (spp.)	(8)		

fishes (IRI: 38.3 and 38, respectively). In females, fishes and trichopter larvae had the highest IRI values (40.8 and 34.1, respectively) (table 2).

Trophic niche overlap between males and females was confirmed by a high value of Morisita simplified index ($CH = 0.98$). Diet composition of males ($H' = 1.15$), however, was significantly more diverse than that of females ($H' = 1.04$) ($t = 2.53$; $P < 0.01$).

Although we did not record substantial differences in the composition of diet among males

and females, during the warm season in particular, some differences in the order of importance of the more relevant preys were detected: the most important items in the diet of males during the warm season were Trichoptera and Odonata, with IRI values of 51.1 and 26.5, respectively, whereas the highest IRI values in females corresponded to fishes and Trichoptera (32.2 and 27, respectively); in addition, IRI of gastropods in the diet of females was 19.8, whereas in males this value was below 5. By contrast, dur-

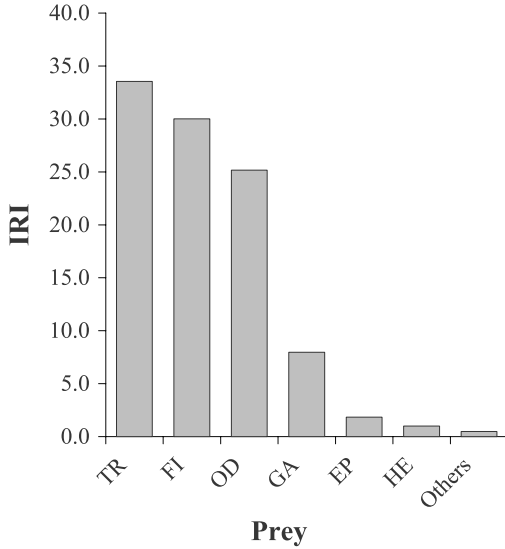


Figure 1. Index of relative importance (IRI) of prey items consumed by *Hydromedusa tectifera* from Aug. 2005–Aug. 2006. TR: *Trichoptera*; FI: *Fishes*; OD: *Odonata*; GA: *Gastropoda*; EP: *Ephemeroptera*; HE: *Hemiptera*; Others: *Hirudinea*, *Oligochaeta*, *Amphipoda*, *Araneae*, *Orthoptera*, *Coleoptera*, *Lepidoptera*, and *Diptera*.

ing the cold season differences in the diet between males and females were minimal.

Size-class variations in the diet

The DCA revealed high variability in prey items consumed among turtles of different size classes. In the ordination space, a differential clustering of points representing turtles of different size was observed. Thus, the point group associated with the variables *Ephemeroptera* and *Odonata* included mainly turtles of size class 1 (small individuals), the group associated with *Trichoptera* was composed of size class 2 turtles (medium-sized individuals), and the group associated with *Fishes* included turtles of size class 3 (the largest individuals) (fig. 3).

F_0 and V_i values differed among size classes (table 2), in agreement with IRI values of the different prey items, which also differed considerably. The main prey item in the diet of size class 1 turtles was *Odonata* (IRI: 63.3), followed by *Trichoptera* and *Ephemeroptera* (IRI: 14 and 13.5, respectively). The most important

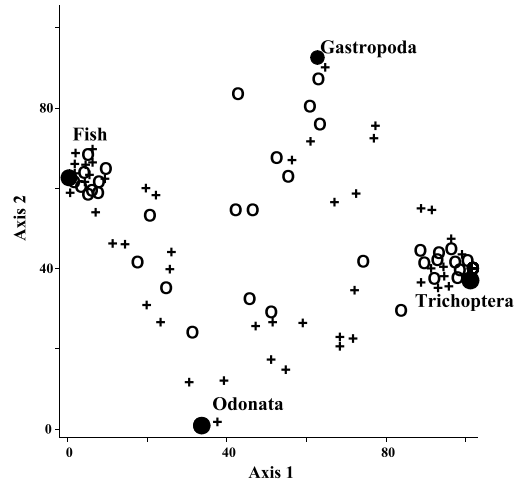


Figure 2. Ordination (Detrended Correspondence Analysis) of *Hydromedusa tectifera* males and females, considering the most important prey items. Crosses, males; empty circles, females; solid circles, item prey. Along the two axes there is no differential segregation of the points representing males and females relative to the prey items consumed. Eigenvalue: Axis 1 = 0.77; Axis 2 = 0.21.

prey items in size class 2 turtles were larvae of *Trichoptera* (IRI: 55), followed by naiads of *Odonata* and fishes (IRI: 23 and 15.2, respectively). Fishes were the item with the highest IRI value (60.3) in size class 3, followed by larvae of *Trichoptera* (IRI: 22.6); the remaining prey items were below 10 (table 2). The regression between carapace length of turtles and length of the biggest prey consumed by each turtle yielded a significant positive relationship ($r^2 = 0.24$; $P < 0.01$; fig. 4).

The lowest value of trophic niche overlap (CH) was found between classes 1 and 3 (0.23), a value considerably lower than the upper limit on tolerable niche overlap (< 0.4), indicating a significant resource partitioning between those classes. CH values between classes 1 and 2, and between classes 2 and 3 were 0.56 and 0.59, respectively.

Class 1 had the highest diet diversity ($H' = 1.31$) and was significantly different from classes 2 ($H' = 1.09$) and 3 ($H' = 1.05$) ($t = 6.738$, $P < 0.01$ and $t = 7.006$, $P < 0.01$); classes 2 and 3 were not significantly different.

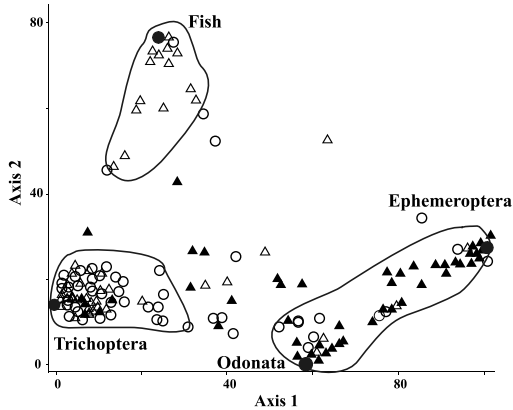


Figure 3. Ordination (Detrended Correspondence Analysis) of individuals of *Hydromedusa tectifera* of the different size classes, considering the most important prey items. Solid triangles, small turtles (class 1: <130 mm); empty circles, medium-sized turtles (class 2: 130-199 mm); empty triangles, big turtles (class 3: >199 mm); solid circles item prey. Eigenvalue: Axis 1 = 0.86; Axis 2 = 0.3.

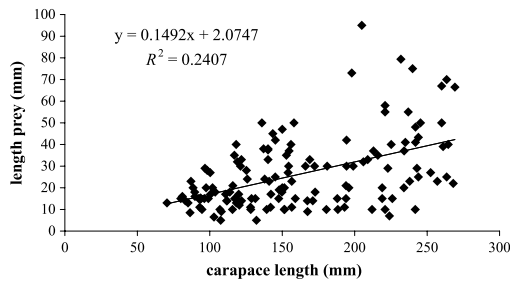


Figure 4. Regression analyses between prey length and carapace length of *Hydromedusa tectifera*.

Table 3. Values of Simplified Morisita Index (CH) for size classes of *Hydromedusa tectifera* in relation to feeding resources consumed in the warm and cold seasons.

Size Class (mm)	Warm Season			Cold Season		
	<130	130-199	>199	<130	130-199	>199
<130	-	0.78	0.45	-	0.25	0.04
130-199	-	-	0.60	-	-	0.58
>199	-	-	-	-	-	-

Differences in the diet among size classes of turtles were present throughout the year, although they were greatest in the warm season (October-March). This was evident in CH values, which were lower in all categories in those months than in the cold season (table 3).

Discussion

Diet composition

The diet of *H. tectifera* individuals inhabiting the streams studied was mainly composed of aquatic macroinvertebrates and fishes; this finding is consistent with previous records on the diet of other freshwater turtle species (Georges, 1982; Souza and Abe, 1995, 1998; Allanson and Georges, 1999; Souza and Abe, 2000; Cooley et al., 2003; Souza, 2004). According to Pritchard (1984) the evolution of long necks in various chelid species is related to the capture of agile prey, including fishes, just as we see in the result of this work.

According to the relative importance of the different prey items observed, larvae of Trichoptera, fishes, and naiads of Odonata can be regarded essential components of the diet of *H. tectifera* in the streams studied. Considering prey diversity in the diet of this species, which includes benthic forms (e.g. larvae of Trichoptera and Diptera), forms that live on aquatic vegetation (such as naiads of Zygoptera), and nectonic forms (e.g. fishes), *H. tectifera* can be regarded a species of high dietary plasticity, because it uses resources from different microhabitats within the stream.

Variations in the diet between sexes

Similarity in diet composition of males and females of freshwater turtles has been largely documented. Several works conducted on species of the family Chelidae reported that sex is not a determining factor in feeding (Georges, 1982; Souza and Abe, 1998, 2000), except in species with strong sexual dimorphism relative to size (Slatkin, 1984; Shine, 1989; Camilleri and Shine, 1990; Tucker, Fitzsimmons and Gibbons, 1995; Lindeman, 2006). The sexual dimorphism observed in *H. tectifera* is not closely related to size of individuals (Cabrera, 1998), and should not therefore be the reason for strong variations in the diet. Some differences in consumption of certain food items by males and females were detected between the warm and

cold seasons. Assuming that food items are equally available to both sexes, in the warm season males showed higher preference for larvae of Trichoptera than females, whereas the latter showed higher preference for fishes and gastropods than males. By contrast, minimum differences between males and females were observed during the cold season. Accordingly, Ramo (1982) and Balensiefer and Vogt (2006) stated that the influence of sex on the diet might be related to differences in physiological requirements between sexes; for example, a greater consumption of shelled-mollusks and fishes by females observed at certain times of the year in this work would be due to a higher demand for calcium during egg formation.

Variations in the diet among size classes

Our results show that *H. tectifera* exploits food resources differentially depending on body size. Furthermore, the greatest diversity in the diet of small turtles indicates that these are more generalist than bigger turtles. These findings are consistent with data reported for other Neotropical turtles, such as *Phrynops geoffroanus* and *Hydromedusa maximiliani* (Souza and Abe, 1998, 2000). Our results indicate that bigger turtles tend to consume bigger prey. The positive relationship between size of prey and size of predator has been reported in works on the diet of freshwater turtles (Georges, 1982; Tucker, Fitzsimmons and Gibbons, 1995; and Souza and Abe, 1998). Georges (1982) stated that variations in the diet relative to turtle size can be explained mostly in terms of energy efficiency and by the fact that as individuals grow in size and strength, bigger prey are more easily available to them. When turtles grow, the energy they obtain from consuming small prey may not compensate for the energetic cost of prey capture; therefore, predated on small prey would be energetically inefficient for big-sized turtles. Accordingly, small turtles consume small food items as a consequence of necessity, whereas large turtles prefer to ingest larger items and consume small items when encountered by

chance. This turtle size-related variation in feeding habits explains the high variability in the size of prey consumed by larger turtles (fig. 4). The great availability of larvae of Trichoptera in environments of this type may be a factor determining the strong presence of this item in the diet of small and middle-sized turtles, and even in larger ones (table 2), although it is a relatively small item; it should be noted that because of its abundance, larvae of Trichoptera are as very important components in trophic chains in rivers and streams (Lopretto and Tell, 1995).

Final considerations

Previous works conducted by this research group indicate that *H. tectifera* has high density and biomass values in the study area (Lescano Bonino and Leynaud, 2008). The plasticity shown in their feeding habits agrees with these results because probably this flexible behaviour allows the species to find and use resources efficiently, which is reflected in the high biomass values recorded. Hence, *H. tectifera* might be an adaptable species able to profit from different resources in several ways in order to survive in diverse habitats. The high prey diversity found in the stomach contents showed that *H. tectifera* exploits numerous food resources and might be considered an opportunistic predator; although some preferences in the diet have also been reported. Animals that are opportunistic in their use of available foods are likely to be less vulnerable to habitat modification than those with specialized dietary requirements. Therefore, taking this fact into account as well as the data on structure and density of the species in the area, the species would not be under immediate pressure, because it is locally abundant (even in highly modified by humans, pers. obs.), and its feeding plasticity would confer it certain degree of tolerance to possible changes in these aquatic systems.

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