Feeding in Syntopy: Diet of *Hydromedusa tectifera* and *Phrynops hilarii* (Chelidae)

LEANDRO ALCALDE[1,2,3], NATACHA NARA DEROCCO[1], AND SERGIO DANIEL ROSSET[1,2]

[1]*Sección Herpetología, Instituto de Limnología Dr R.A. Ringuelet, CC 712, CP 1900, La Plata, Buenos Aires, Argentina*
[alcalde@ilpla.edu.ar; puconpay@yahoo.com.ar; rosset@ilpla.edu.ar];
[2]*Sección Herpetología, Museo de La Plata, Paseo del Bosque s/n, CP 1900, La Plata, Buenos Aires, Argentina;*
[3]*Investigador Asistente, Conicet*

ABSTRACT. – Stomach contents were obtained from 25 Hydromedusa tectifera and 47 Phrynops hilarii that live in syntopy in a pampasic stream in Buenos Aires province, Argentina. Both species are arthropod consumers. Copepods, ostracods, and hemipterans are the preferred items for P. hilarii, and H. tectifera prefers copepods, ostracods, immature dipterans (mainly chironomids), and ephemeropteran larvae. Items that most contribute to the diet of both species are immature chironomids, corixids, and belostomatids. Available food varies little among seasons, being slightly lower in winter months and part of the summer. Diet diversity changes by seasonal variation of prey item abundance in the diet of both species. Diet diversity is higher for P. hilarii (more generalist and broader trophic niche) than in H. tectifera, but there is no niche overlap between them. No significant correlation between the size of turtles and length of prey items was found. There is no evidence that the long neck of H. tectifera relates to piscivorous habits, because fish are a small fraction of its diet and arthropods constitute the bulk of the ingested items.

KEY WORDS. – Reptilia; Testudines; Pleurodira; Chelidae; Hydromedusa tectifera; Phrynops hilarii; diet; feeding; piscivory; Argentina

Most of the present knowledge about diet of freshwater turtles is somewhat unbalanced toward cryptodirans, with emydids and kinosternids the most studied (Raney and Lachner 1942; Lagler 1943, 1966; Knight and Gibbons 1968; Mahmoud 1968; Moll and Legler 1971; Dodd et al. 1988; Chen and Lue 1998; Stuart and Painter 3002; Ottonello et al. 2005; Collins and Lindeman 2006; Lindeman 2006a, b). Dietary aspects of pleurodirans based on large field-collected data sets are known for about the 10% of the species described for the group (Chessman 1986; Lima et al. 1997; Allanson and Georges 1999; Souza 1004; Armstrong and Booth 2005; Caputo and Vogt 2008; Wilson and Lawler 2008, among others). Other works about diet of pleurodirans are documented in captive specimens and miscellaneous field observations (e.g., Luedenvaldt 1926; Gallardo 1987; Malvasio et al. 2003).

There are no detailed long-term studies describing the diet of the most austral species of South American pleurodirans, Hydromedusa *tectifera* and Phrynops *hilarii*. The only published data for the diet of P. hilarii are those of Richard (1999) and Gallardo (1982). The first author considered P. hilarii an unspecific hunter of prey smaller than the turtle head, whereas Gallardo (1982) characterized the species as predominantly a herbivore. Luederwaldt (1926), Gallardo (1956, 1987), and Freiberg 1977) supplied some comments on the diet of H. *tectifera* and noted that the species consumes arthropods, fish, anurans, and gastropods (*Pomacea*).

This study characterizes the trophic niches of the long-necked H. *tectifera* and the short-necked P. hilarii living in syntopy in a polluted stream in Argentina at their austral limits of distribution (Derocco et al. 2005) and

seeks to 1) describe the trophic spectrum of both species and characterize each one as a specialist or generalist, 2) analyze the trophic niche overlap between the species, 3) evaluate the variation of the frequency of each prey item among seasons, and 4) describe the relationship between turtle size and prey item size. Additionally, we discuss the hypothesis of piscivory, as introduced by Pritchard (1984), by comparing the diet of P. hilarii and H. *tectifera* in the context of data for other freshwater turtles.

MATERIALS AND METHODS

The study was conducted at Arroyo Buñirigo (35°01'S; 57°29′W, Buenos Aires Province, Argentina), a stream in the Río de La Plata drainage. Turtles were trapped in 2 sample stations. Sample station 1 was under the influence of the Río de La Plata with daily changes of water depth (0.2–2.5 m) and mostly native vegetation on its margins (e.g., Celtis tala, Erythrina *crista-galli*, *Passiflora* caerulea, Salix *humboldtiana*, Schinus longifolius, Senna corymbosa, *Vigna* luteola) with presence of some introduced shrubs (Lonicera japonica) and trees (*Morus* sp., *Ligustrum* sp., Phoenix sp.). Sample station 2 was more homogeneous in depth (usually 1 m) except during the rainy season. This area had elevational changes at some points, creating small waterfalls (0.5 m height). Cattle ranching in the area impacts the vegetation of the stream banks, leaving some native trees (C. tala, S. longifolius, S. corymbosa) and a few exotic trees (*Morus* sp., Phoenix sp.). Submersed and floating vegetation is scarce (lower than 25%), and the bottom is hard in both areas.

Samples were taken once each month (or bimonthly) from December 2006 to November 2008, a total of 18 sample days. Turtles were trapped using 3 different methods: single-funnel traps, double-funnel traps, and fishing lines without hooks. Characteristics of structure and functioning of the single-funnel traps are specified in Colautti (1998). Double-funnel traps are rectangles that were constructed using a 5-mm net. They are opened at both ends and with ample distance between the external (40×40 cm) and internal (15×15 cm) openings of each funnel. In all cases, we used cow-heart as bait. We put 1 double-funnel trap, 1 single-funnel trap, and 2 fishing lines (20 baits) at each sample station for a period of 24 h and checked the traps and replaced the bait balls at 12-h intervals.

Each turtle was taxonomically identified, sexed, weighed, and measured (straight-line carapace length, maximum carapace width, and maximum head width). Length measurements were obtained using calipers ($\pm$ 0.1 mm) and weights by a digital balance ($\pm$ 1 g). Males of both species were recognized by the presence of a plastral concavity (see Cabrera 1998). Females of both species lack a plastral concavity. Hydromedusa *tectifera* males have a plastral concavity from hatching, and both sexes are identifiable at all sizes. Phrynops hilarii males begin to have a plastral concavity at 180-mm carapace length (L. Alcalde, *pers.* obs.); specimens were considered males (concavity present) or females (concavity absent) when they were longer than 180 mm, whereas smaller individuals were considered juveniles.

Stomach contents were obtained by flushing, following the principles described by Legler (1977) with modifications, and preserved in 70% ethanol. The offer (environmental abundance of aquatic prey items) was estimated passing a hand-net (50-cm diameter, mesh 0.1 mm) 30 times along the vegetated margins and bottoms of each sample station. Fish trapped with the funnel traps were also recorded for prey estimations. Prey items were preserved in 70% ethanol. Water and air temperature ($\pm$ 1°C) were registered.

Stomach contents and prey items were taxonomically classified to order or family level and counted. We measured the maximum length and maximum width of each flushed item using a stereoscopic microscope with measurement accessories ($\pm$ 0.1 mm) to estimate the volume of each item, employing the ellipsoid method (Dunham 1983).

The contribution of each item to the diet was evaluated using the Relative Importance Index (Pinkas et al. 1971) as follows: RII = %OF [%V $+$ %N], where %OF indicates the percent of the stomachs containing a particular prey item, %V is the proportion of the volume of each item in relation to the total volume of all prey items, and %N represents the proportion between the number of individuals of each item and the total of individuals of all prey items. The prey item with the highest value of RII was used to make the percent category of RII values of the remaining ones. The following categories were considered: fundamental (RII values between 50.1 and 75%), secondary (between 75.1 and 100%), accessory (25–50%), and accidental (lower than 25%). The RII was calculated for items grouped at Family level (e.g., Pimelodidae and Loricariidae for siluriform fish or Corixidae, Notonectidae, Ranatridae, and Belostomatidae for hemipteran arthropods) or at high taxonomic levels (e.g., Hyrudinea and other categories that could not be identified with better accuracy). In addition, we calculated this index discriminating prey items as larvae or adults in the case of particular groups (e.g., Coleoptera, Anura, and Diptera).

To evaluate diet preference, we calculated the Ivlev index (IvI) (Ivlev 1961) as follows: IvI = %n_id – %n_io/ %n_id $+$ %n_io, where %n_id indicates the numerical proportion of each prey item in relation to total items in the diet, and %n_io is the same but for offer items. The IvI index was calculated for aquatic items grouped at Order level (e.g., Siluriform for some fish or Hemiptera for some arthropods). Values of IvI tending to -1 indicate avoidance of the prey, whereas values tending to 1 denote a major prey preference.

Diet diversity of both species and diversity of the prey were calculated using the Shannon diversity index (H') applying natural logarithms (Shannon and Weaver 1949). Comparisons among the 3 H' indices (H' prey, H' Phrynops diet, H' Hydromedusa diet) were made using *t*-tests.

The breadth of the trophic niche was calculated employing the index proposed by Levins (1968) based on Shannon diversity index: H = $-$ $\sigma p_i x \times \log_2 p_i x$, where p_i is the number of each item considering the total of stomachs. Higher values of the index indicate lower diet specialization.

To calculate niche overlap, we used the symmetric index proposed by Pianka (1973, 1974): $O_{jk} = \sigma p_{ij} \times p_{ik}/\sigma p_{ij}^2 \times \sigma p_{ik}^2$, where $p_{ij} \times p_{ik}$ represents the proportion of each item employed for species j and k. This index generates values between 0 (with no overlap of the diet) and 1 (complete overlap).

To test whether prey composition varies between juveniles and adult males and between seasons (autumn–winter vs. spring–summer), we employed Chi-square tests (χ^2) using Yates correction factor. Our null hypothesis (H_0) for these comparisons was that the number of prey items of each category does not vary between pairs of comparisons (autumn–winter vs. spring–summer, males vs. juveniles). Prey items were grouped into inclusive categories to make Chi-square comparisons (e.g., belostomatids, corixids, notonectids, and ranatrids were considered as Hemiptera). In all cases, categories with total values lower than 2 were not compared.

Seasons were grouped by comparing the mean water temperature of the whole year with the mean of each season, yielding 2 groups: autumn–winter (T $<$ 19.8°C) and spring–summer (T $>$ 19.8°C). This pair of seasons was used to evaluate seasonal variation of the diet.

To test whether prey size varies in relation to the size of the turtles, we used Pearson's correlations between carapace length and mean length of the prey ingested by each turtle.

All analyses were made using the software STATISTICA 6.0 (StatSoft 2001) considering only the animal fraction of the diet, excluding plant matter, stones, bait rests, and parasitic nematodes.

RESULTS

Twenty-five H. tectifera (4 females, 21 males) and 64 P. hilarii (16 females, 33 males, 15 juveniles) were caught at Arroyo Buñirigo during this study. Stomach contents were obtained for all H. tectifera and for 47 specimens of P. hilarii (9 females, 27 males, 11 juveniles). Small stones were present in stomachs of 4 H. tectifera (16%; 3 males, 1 female) and 4 P. hilarii (8.5%; 1 male, 1 juvenile, 2 females). Plant material was present in stomachs of 9 males of H. tectifera (36%) and 15 P. hilarii (31.9%; 8 males, 4 juveniles, 3 females). Although plant material had a high frequency of occurrence in both species, the highest volume was verified for P. hilarii (61 fragments, 10.74 ml, 8.2% of the volume of all food items). Plant fragment composition in P. hilarii was 28 flowers, 10 leaves, 6 grasses, 4 fruits (Morus spp.), 4 stems, 4 small floating plants, 3 seeds, and 1 root. In H. tectifera, plant fragment composition was 14 grasses, 11 leaves, 1 root, and 2 entire small floating plants that totalled 1.66 ml (3.2% of the volume of all food items). The frequency of plant material in the stomach contents of both species was moderately high. Considering the composition of plant material (generally incomplete fragments), we discard the hypothesis of herbivory for both species. We believe that vegetal ingestion occurs accidentally when turtles prey upon other items or by confusing plant parts with terrestrial insects that float on the surface of the water.

Twenty nematodes were obtained from the stomachs of 8 individuals of both sexes of H. tectifera. Similarly, we found 24 nematodes in 8 specimens of both sexes of P. hilarii. Nematode sizes ranged 4–35 mm in H. tectifera and 18–35 mm in P. hilarii, and in some cases, they were flushed alive.

The animal items recorded in the diet of both species are in Table 1. This shows the percentage of numeric frequency (%NF), percentage of observed frequency (%OF, percentage of turtles with the food item), and percentage of the total volume of all food items (%TV) for each species. Of the animal items preyed upon by P. hilarii, 99.3% were arthropods, with clear prevalence of microcrustaceans (50.3%) and immature chironomids (30.2%) (Fig. 1A). Similarly, 99.5% of the items ingested by H. tectifera were arthropods, especially immature chironomids (82%), crustaceans (8.8%, mostly microcrustaceans), and adult insects (7.2%) (Fig. 1D). Within the "other items" category described in Figure 1A and D, fish were the most common in H. tectifera (Fig. 1E), with

gastropods the predominant one in P. hilarii (Fig. 1B). In both species, the fraction of terrestrial items was lower than 1%, being slightly higher in P. hilarii than in H. tectifera (Fig. 1C, F).

Ivlev's Index indicates that copepods (IvI: 0.99), ostracods (IvI: 0.93), and hemipterans (IvI: 0.32) are the most preferred aquatic food items in P. hilarii. In H. tectifera, the most preferred aquatic food items are copepods (IvI: 0.99), ostracods (IvI: 0.85), immature chironomids (IvI: 0.8), and ephemeropteran larvae (IvI: 0.51).

The Relative Importance Index indicates that immature chironomids (RII: 100) and hemipterans of the families Corixidae (RII: 50.9) and Belostomatidae (RII: 9.18) are the items that most contribute to H. tectifera diet. Identical results, but with more equal contribution of corixids and belostomatids, was found for P. hilarii: immature chironomids (RII: 100), Corixidae (RII: 26.17), and Belostomatidae (RII: 20.03). Values of RII showing the dietary contribution of all food item categories in both species are in Table 2.

The temporal evolution of the H' indices for the offer and the stomach contents of both species are in Figure 2. This graph shows 2 results: 1) available prey diversity did not vary much during the present study, being lower during winter months and in parts of the summer; and 2) diet diversity of both species varied, resulting in temporal differences of prey being consumed.

The H' index of the prey abundance was higher than the H' values obtained for the diet of both species, with the diet of P. hilarii being more diverse than that of H. tectifera ($H_{prey} = 0.99$; $H_{Phrynops} = 0.68$; $H_{Hydromedusa} = 0.33$). The H values of both species differed ($t = 56.45$, $v = 15,210$, $a = 0.05$) and when each them was compared with prey abundance ($H_{Phrynops}$ vs. H_{prey}: $t = 51.61$, $v = 15,210$, $a = 0.05$; $H_{Hydromedusa}$ vs. H_{prey}: $t = -107.9$, $v = 189,473.6$, $a = 0.05$). In addition, values calculated for the breadth of the trophic niche of P. hilarii ($H = 2.248$) and H. tectifera ($H = 1.06$) indicate that P. hilarii is more generalist than H. tectifera because of the lower value obtained for the latter species. The value of the symmetric index used to calculate trophic niche overlapping was near zero ($O_{jk} = 0.000035$), indicating the almost total absence of niche overlapping between both species.

When the prey item category abundance was compared between both groups of seasons (autumn–winter vs. spring–summer), we observed that particular items showed significant differences in both species (Table 3). In H. tectifera, 6 of 11 categories showed significant variation on prey item abundance between seasons. The species consumes more naiads, larval ephemeropterans, and immature dipterans in the coldest months than in spring–summer. Conversely, higher consumption of hemipterans, crustaceans, and fish characterizes the warmest months.

Table 1. Percentages of numeric frequency (%NF), occurrence frequency (%OF), and total volume (%TV) of each prey item category for both studied species. Spaces without data indicate absence of the item in the diet of the species.

Food item	H. tectifera			P. hilarii		
	%NF	%OF	%TV	%NF	%OF	%TV
Siluriform fish						
Loricaridae				0.02	2.22	0.14
Pimelodidae	0.086	12	10.5			
Characiform fish						
Characidae	0.065	16	3.41	0.07	20	2.98
Cyprinodontiform fish						
Poeciliidae	0.108	8	0.34	0.006	4.44	0.01
Anura						
Hylidae (larvae)				0.06	2.22	0.2
Birds						
Feathers, unidentified family				0.01	4.44	3.51
Mammalia						
Hair and skin rests, unidentified family				0.01	6.66	17.1
Testudines						
Mental barbels, Chelidae (*P. hilarii*)	0.01	4	0.01			
Cnidaria						
Hydrozoa, Hydra spp.				0.06	2.22	0.007
Platyhelminthes						
Turbellarea, unidentified family				0.006	2.22	0.003
Mollusca, Gastropoda						
Ampullaridae				0.006	2.22	0.002
Hydrobiidae	0.054	8	0.21	0.52	8.88	0.62
Planorbidae	0.021	8	0.03			
Annulata						
Hyrudinea, unidentified family				0.06	4.44	2.19
Oligochaeta, unidentified family (aquatic)				0.006	2.22	0.0001
Arthropoda, Chelicerata						
Araneidae, Lycosidae				0.012	4.44	0.008
Acari, Arrenuridae	0.032	8	0.0006	0.006	2.2	0.0002
Arthropoda, Crustacea						
Cladocera, unidentified family				25.47	2.22	0.27
Ostracoda, unidentified family	0.173	20	0.001	0.42	15.55	0.008
Copepoda, unidentified family	5.227	24	0.13	25.47	2.22	0.21
Amphipoda, Hyalellidae	1.76	40	1.58	1.77	11.11	0.83
Decapoda, Brachyura, Trychodactylidae				0.006	2.22	0.002
Decapoda, Sergestidae	0.01	4	0.99			
Isopoda, unidentified family (terrestrial)				0.012	2.22	0.22
Arthropoda, Insecta, Hemiptera						
Heteroptera, Belostomatidae	0.097	24	10.64	0.16	33.33	12.29
Heteroptera, Notonectidae	0.076	16	0.34	0.006	2.2	0.02
Heteroptera, Corixidae	8.47	36	30.49	12.67	20	14.45
Heteroptera, Ranatridae	0.01	4	0.12			
Heteroptera, unidentified family (terrestrial)				0.01	4.44	0.0008
Auchenonyncha, Cercopidea				0.03	6.66	0.01
Arthropoda, Insecta, Lepidoptera						
Larvae, unidentified family				0.01	4.44	0.66
Arthropoda, Insecta, Coleoptera						
Larvae (Dysticidae, Hydrophilidae)	0.021	8	0.02	0.05	6.66	0.03
Adult (Dysticidae, Hydrophilidae)	0.054	16	1.38	0.35	26.66	0.8
Adult (Curculionidae and others) (terrestrial)	0.021	8	0.08	0.15	15.55	2.21
Arthropoda, Insecta, Orthoptera						
Acrididae	0.021	4	0.04	0.01	4.44	0.0008
Arthropoda, Insecta, Hymenoptera						
Formicidae	0.010	4	0.002	0.01	4.44	0.001
Hymenoptera, unidentified family				0.01	4.44	0.001

Table 1. Continued.

Food item	H. tectifera			P. hilarii		
	%NF	%OF	%TV	%NF	%OF	%TV
Arthropoda, Insecta, Diptera						
Chironomidae (larvae)	81.52	24	34.8	31.96	28.88	39.77
Culicidae (larvae)				0.08	8.88	0.009
Culicidae (adult)				0.01	4.44	0.006
Muscidae (larvae)				0.01	2.22	0.15
Muscidae (adult)				0.01	4.44	0.01
Sirphidae (larvae)				0.01	4.44	0.08
Ceratopogonidae (adult)	0.01	4	0.05			
Simulidae (adult)				0.006	2.22	0.0001
Arthropoda, Insecta, Odonata						
Anisoptera larvae, unidentified family				0.006	2.22	0.27
Zigoptera larvae, unidentified family	0.53	24	2.41	0.04	11.11	0.12
Arthropoda, Insecta, Ephemeroptera						
Larvae, unidentified family	0.9	12	2.31	0.36	2.22	0.87
Arthropoda, Insecta, Trichoptera						
Larvae, unidentified family	0.032	4	0.03	0.006	2.2	0.002

Eight of the 11 item categories preyed upon by P. hilarii varied among seasons, with crustaceans, hemipterans, aquatic coleopterans, gastropods, and terrestrial items more abundant in the warmest months. Conversely, the diet of this species shows a higher frequency of ephemeropteran larvae, immature dipterans, and hyrudineans in the coldest months. Immature dipterans, ephemeropteran larvae, and crustaceans correlate with offer variation in the diet of both species. However, both species coincide in a higher consumption of hemipterans in spring–summer than in autumn–winter contrary to the lack of seasonal variation of these insects in the offer.

Seasonal variation of other prey item categories preyed upon by P. hilarii also differed from the seasonal variation of these items in the offer. Aquatic coleopterans, naiads, hyrudineans, gastropods, and fish in the diet did not correlate with seasonal variation of these items. Except for gastropods and hemipterans, the diet of H. tectifera was more correlated to seasonal variations than was the diet of P. hilarii.

Sex variation of the diet could not be made for 2 reasons: 1) the number of females with contents in their stomachs was too small in both species; and 2) the number of items contained in female stomachs was insufficient to perform any statistical analysis. Comparisons between males and juveniles of H. tectifera were not made because this species has secondary sexual dimorphism from hatching. For these reasons, comparisons were made only between adult males and juveniles of P. hilarii (Table 4). This demonstrates that abundance of hemipterans, naiads, crustaceans, hyrudineans, ephemeropterans, immature dipterans, and gastropods was lower in juveniles than in adult males of the species.

Turtles of both species showed no correlation between the mean size of ingested prey and carapace length of the turtles (Fig. 3A, B). Although there was no significant correlation in either species (Pearson's r $_{Phrynops}$ = 0.0294, $P > 0.5$; Pearson's r $_{Hydromedusa}$ = 0.002, $P > 0.5$), graphs show that larger individuals of H. tectifera tend to eat larger preys. The largest prey fed upon by P. hilarii was the characiform fish, *Pseudocorynopoma doriai* (total length: 46 mm), whereas the smallest prey was a cladoceran (0.7 mm). The smallest prey ingested by H. tectifera was a small copepod (0.5 mm) and the largest was the silunform fish, *Pimelodella laticeps* (total length: 40 mm).

DISCUSSION

Hydromedusa tectifera and P. hilarii are generalist carnivorous species. Both prey upon aquatic and terrestrial arthropods, and their diets have a low contribution of items such as fish, tetrapods (as carrion), larval anurans, and other invertebrates. Plant matter occurs by involuntary ingestion in both species.

Diet Preferences. — Item preference indices have been studied for few species of freshwater turtles because such indices require knowledge of both the diet of the species and the environmental abundance (offer) of prey items. Only Parmenter (1980) for *Trachemys scripta* and Spencer et al. (1998) for *Emydura macquarii* have used these indices. Spencer et al. found that only 1 of the 4 most preferred items of E. macquarii also had a high diet contribution. Similarly, Parmenter did not find more than one coincidence between the most preferred and the most important dietary items in the 3 populations of T. scriptu he studied.

Individuals of P. hilarii studied herein preferred copepods, ostracods, and aquatic hemipterans, whereas H. tectifera preferred copepods, ostracods, immature chironomids, and ephemeropteran larvae. Among these last items, only immature chironomids coincided in having a high IRI and Ivlev values in H. tectifera, with the same
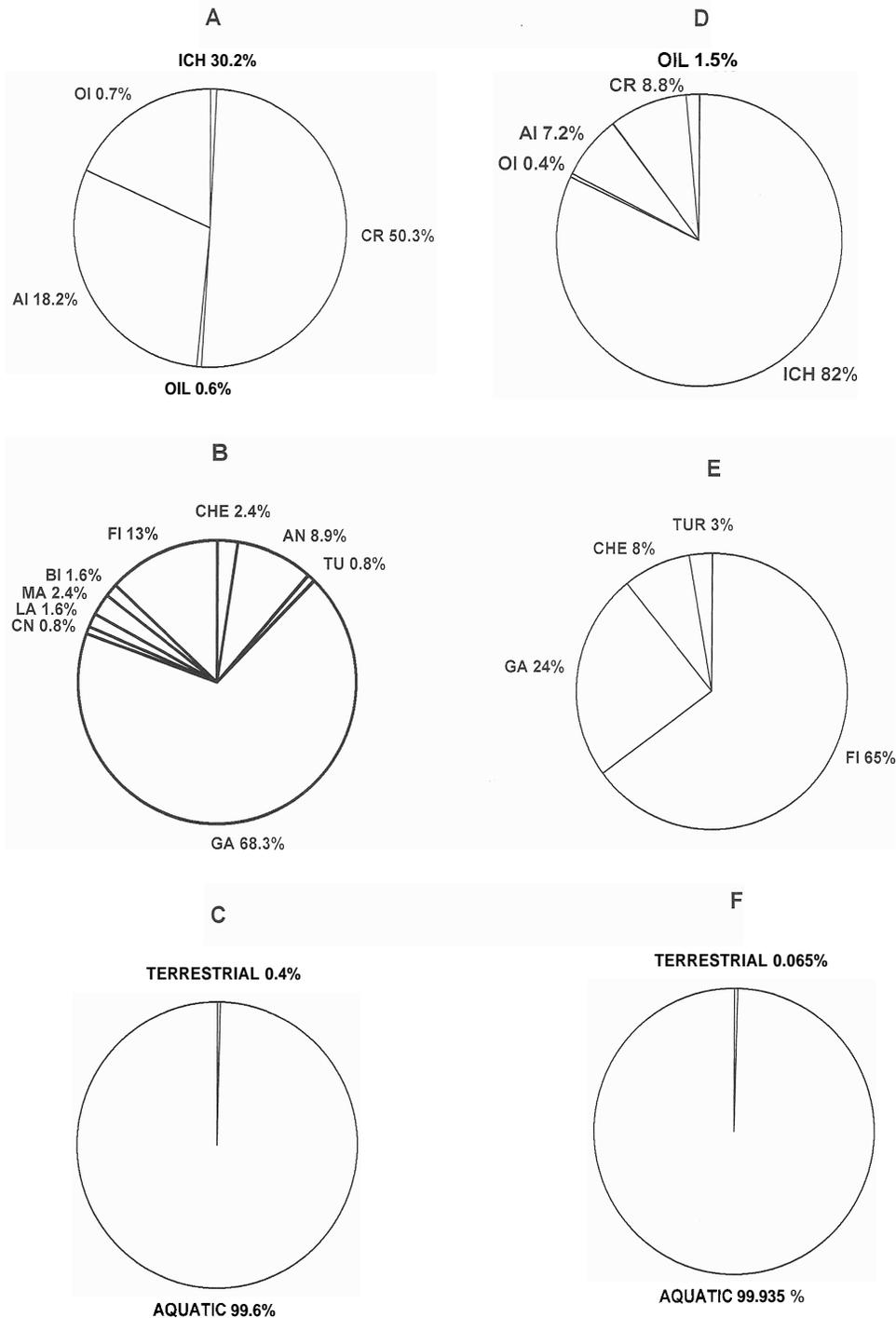
Figure 1. Pie charts showing prey category percentages for *Phrynops hilarii* (A–C) and *Hydromedusa tectifera* (D–F). *A* and D show the percentages of the most inclusive prey categories. B and E represent percentages of categories included within the "other" fraction shown in A and D. C and F are the percentages of terrestrial and aquatic prey items, respectively. Abbreviations: AI, adult insects; AN, annulata; BI, bird rests; CHE, chelicerata; CN, cnidaria; CR, crustacea; FI, fish; GA, gastropoda; ICH, immature chironomids; LA, larval anurans; MA, mammal rests; OI, other items; OIL, other insecta larvae; TU, turbellarea; TUR, turtle rests.

occurring for corixids in P. *hilarii*. Reasons for some prey preferences are difficult to determine, but we recommend that future studies should focus more attention on the preferred items that also have high diet contribution. Microcrustaceans are one of the most abundant items in the diet of the characiform fish ingested by the turtles studied by us (Escalante 1982, 1983). This would indicate

that microcrustaceans might have been ingested as "trojan" items. However, we prefer to reject this mechanism, at least for P. *hilarii,* because the 7 individuals that contained microcrustaceans had no trace of fish. As an alternative explanation, we believe that microcrustacean ingestion in *P. hilarii* occurred by neustophagia (see Belkin and Gans 1967). However, the

Table 2. Relative importance index values of each prey category for both studied species.

H. *tectifera*	P. *hilarii*
Fundamental	Fundamental
Immature Chironomidae (100)	Immature Chironomidae (100)
Secondary	Accesory
Corixidae (50.09)	Corixidae (26.17)
Accidental	Accidental
Belostomatidae (9.18)	Belostomatidae (20.03)
Amphipoda (4.78)	Mammal rests (5.5)
Copepoda (4.61)	Characidae (2.95)
Pimelodidae (4.52)	Copepoda (2.75)
Zigoptera larvae (2.52)	Cladocera (2.7)
Characidae (1.98)	Terrestnal Coleoptera (1.78)
Ephemeroptera larvae (1.37)	Adult aquatic Coleoptera (1.49)
Adult aquatic Coleoptera (0.81)	Amphipoda (1.39)
Notonectidae (0.24)	Bird rests (0.75)
Sergestidae (0.14)	Hydrobiidae (0.49)
Ostracoda (0.12)	Hyrudinea (0.48)
Poecilidae (0.12)	Ostracoda (0.32)
Adult Ceratopogonidae; Planorbiidae; Ranatridae; Turtle rests; Hydrobiidae; Formicidae; Acrididae; Arrenuridae; Trichoptera larvae; Terrestrial Coleoptera; larval aquatic Coleoptera (each them lower than 0.1)	Lepidoptera larvae (0.14)
	Ephemeroptera larvae (0.13)
	Notonectidae; Zigoptera larvae; Formicidae; Acrididae; Arrenuridae; Trichoptera larvae; Hydrozoa; Trychodactylidae; Turbellarea; Muscidae larvae; Culicidae larvae; adult Culicidae; unidentified adult Diptera; Isopoda; Sirphidae larvae; larval aquatic Coleoptera; Hymenoptera unidentified; unidentified terrestrial Heteroptera; Loricariidae; Auchenorrincha; Ampullaridae; Lycosidae; Anuran larvae; adult Simulidae; adult Muscidae; Anisoptera larvae; Aquatic Oligochaeta; Poecilidae (each them lower than 0.1)

situation is different in H. *tectifera,* with microcrustaceans present in 6 individuals and 4 of these also containing fish remains, suggesting that the species ingested microcrustaceans as trojan items.

Turtles of both studied species ingested large amounts of immature chironomids of the genus *Chironomus*. The fact that there are very few areas of the sampled sections of Arroyo Buñirigo that have soft bottoms with interstitial spaces indicates that chironomids are easy prey for turtles. In fact, these chironomids usually live over the hard stream bottom and are frequently found over algae, trunks, and other submersed substrates. Similar situations of diets based on large quantities of immature chironomids have been reported for turtle populations that survive in polluted habitats, as occurs in *Chrysemys picta, Graptemys pseudogeographica,* and *Phrynops geoffroanus* (Knight and Gibbons 1968; Moll 1976; Souza and Abe 2000). Curiously, these species have a non-chironomid diet in populations from unpolluted waters. Cooley et al. (2003) described the diet of 2 populations of *C. picta* and found that the most ingested items were gastropods, naiads, trichopteran larvae, terrestrial isopods, and aquatic vegetation but not immature chironomids. Similarly, Dias and Souza (2005) and Fachin-Terán et al. (1995) reported that individuals of P. *geoffroanus* from unpolluted habitats ate fish, macrocrustaceans, mollusks, insects, and fruits of river-margin trees.

There are no published data on the diet of H. *tectifera,* and the only data for P. *hilarii* are those of Richard (1999) describing the diet of 2 feral populations

from artificial unpolluted lakes. He reported a diet based on small fish, shrimps, naiads, aquatic coleopterans, larval culicids, aquatic hemipterans (belostomatids and corixids), tadpoles, and some terrestrial insects (lepidopterans, orthopterans) but not chironomids. We hypothesize a pattern in which a generalist species experiences radical changes in diet composition in accord with environmental variations affecting prey abundance. Diet displacement from a non-chironomid to a chironomid-based diet fits this pattern. Similar displacements in trophic ecology
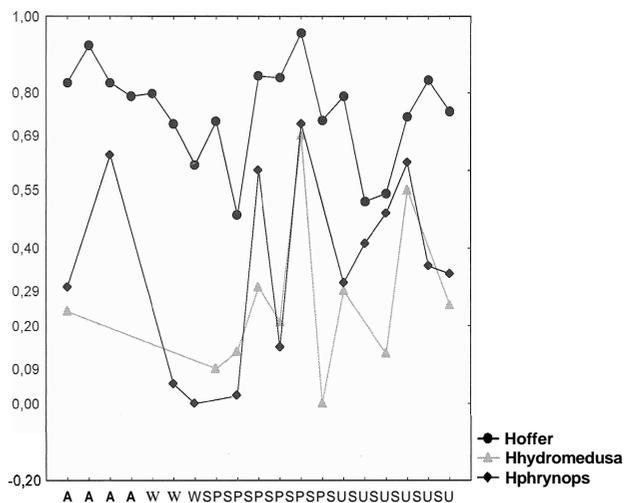

Figure 2. Seasonal variation of the H′ indices for prey abundance and diet of both species studied. Abbreviations: A. autumn; SP, spring; SU, summer; W, winter.

Table 3. Seasonal variation in prey items among seasons and species and prey abundance, compared using Chi-square tests. Spaces without data indicate absence of the item. Boldface values represent significant differences between seasons (calculated $\chi^2 >$ table χ^2 at $\alpha = 0.05$) and in such cases, the null hypothesis was rejected (see data analysis).

Item	Prey [A–W vs. S–S (χ^2)]	*H. tectifera* [A–W vs. S–S (χ^2)]	*P. hilarii* [A–W vs. S–S (χ^2)]
Fish	1253 **vs.** 1812 (101.94 $>$ 3.8)	6 **vs.** 19 (6.8 $>$ 3.8)	5 vs. 12 (2.93 $<$ 3.8)
Odonata larvae	758 **vs.** 363 (138.61 $>$ 3.8)	38 vs. **11** (14.89 $>$ 3.8)	4 vs. 4 (0.125 $<$ 3.8)
Crustacea	437 **vs.** 1248 (393.34 $>$ 3.8)	24 **vs.** 201 (139.23 $>$ 3.8)	5 **vs.** 8292 (8277 $>$ 3.8)
Hyrudinea	2 vs. 3 (0.4 $<$ 3.8)		9 **vs.** 1 (6.5 $>$ 3.8)
Acari	3 vs. 7 (1.7 $<$ 3.8)	3 vs. 0 (3.26 $<$ 3.8)	
Aquatic Coleoptera	55 vs. 53 (0.045 $<$ 3.8)	4 vs. 5 (0.2 $<$ 3.8)	8 **vs.** 63 (44.61 $>$ 3.8)
Hemiptera	230 vs. 269 (2.04 $<$ 3.8)	6 **vs.** 800 (782.17 $>$ 3.8)	60 **vs.** 1957 (1784.1 $>$ 3.8)
Ephemeroptera	24 **vs.** 4 (22.51 $>$ 3.8)	83 vs. 0 (83 $>$ 3.8)	57 **vs.** 0 (57.008 $>$ 3.8)
Diptera larvae	733 **vs.** 7 (713.26 $>$ 3.8)	3590 **vs.** 3 (3581 $>$ 3.8)	4925 **vs.** 108 (2305 $>$ 3.8)
Gastropoda	88 **vs.** 320 (131.92 $>$ 3.8)	2 vs. 5 (1.42 $<$ 3.8)	0 **vs.** 44 (44.02 $>$ 3.8)
Trichoptera		3 vs. 0 (3.26 $<$ 3.8)	
Tetrapods			1 vs. 5 (2.83 $<$ 3.8)
Terrestrial items		3 vs. 3 (0.166 $<$ 3.8)	4 **vs.** 50 (39.2 $>$ 3.8)

appear well supported in published data about fish diets (Tobler 2008). However, specialized turtles, such the strictly piscivorous *Chelus fimbriata* (Fachin-Terán 1995) or the molluscivorous females of *Graptemys* spp. (Lindeman and Sharkey 2001), seem to change diet composition across different environments less radically than in generalized species.

Diet Diversity. — There are few studies comparing the diet of freshwater turtles living in syntopy. It has been studied for the following syntopic pairs and assemblages: *Sternotherus minor–Sternotherus odoratus* (Berry 1975), *Graptemys geographica–Graptemys ouachitensis–G. pseudogeographica* (Vogt 1981), *Kinosternon flavescens–Emydoidea blandingii* (Kofron and Schreiber 1985), *Kinostemon leucostomum–Staurotypus triporcatus–T. scripta*

Table 4. Prey abundance variation between males and juveniles of *Phrynops hilarii* tested using Chi-square tests. Boldface values represent significant differences between males and juveniles (calculated $\chi^2 >$ table χ^2 at a = 0.05), and in such cases, the null hypothesis was rejected (see data analysis).

Item	Sex	N	M VS. J (χ^2)
Fish	M	11	2.31 $<$ 3.8
	J	5	
Odonata larvae	M	7	**5.5 $>$ 3.8**
	J	2	
Crustacea	M	8288	**8312 $>$ 3.8**
	J	3	
Hyrudinea	M	10	**10.1 $>$ 3.8**
	J	0	
Aquatic Coleoptera	M	30	3 $<$ 3.8
	J	45	
Hemiptera	M	1892	**1555.55 $>$ 3.8**
	J	122	
Ephemeroptera	M	57	**57.1 $>$ 3.8**
	J	0	
Diptera larvae	M	4989	**4942.8 $>$ 3.8**
	J	48	
Gastropoda	M	83	**83.1 $>$ 3.8**
	J	0	
Tetrapods	M	5	0.68 $<$ 3.8
	J	2	
Terrestrial items	M	26	0.019 $<$ 3.8
	J	26	

(Vogt and Guzman Guzman 1988), and *Podocnemis unifilis–Podocnemis expansa–Phrynops geoffvoanus–Mesoclemmys raniceps–C. fimbriata* (Fachin-Terán et al. 1995). Most of these cases show absence of competition for food resources except by *S. minov* and *S. odoratus.* Although there is no niche overlap between P. *hilarii* and *H. tectifera,* both them show a tendency toward consumption of large quantities of immature chironomids as adaptation to habitat disturbance.

Seasonal Variation. — Seasonal variation of diet composition occurs in many species, but most studies do not correlate diet variations with the seasonal abundance of prey items. In fact, very few studies have included estimations of environmental abundance of prey items (e.g., Parmenter 1980; Spencer et al. 1998), and none of them has studied prey abundance during more than one season. Diet abundance vaned seasonally for 6 prey items consumed by H. *tectifera* and for 8 ingested by P. *hilarii.* Both species varied the consumption of 3 item categories in relation to seasonal variation of prey abundance. This was the case for dipteran larvae, ephemeropteran larvae, and crustaceans. Of the items consumed by H. *tectifera,* 33% varied in relation with prey abundance, whereas of those consumed by P. *hilarii,* 66% correlated with seasonal variations. These differences indicate more dependence of H. *tectifera* on seasonal variation of particular prey items.

Prey and Turtle Sizes. — Both species studied herein consumed prey items within a similar range of total length (0.5–0.7 mm to 4 0 4 6 mm), and there was no significant correlation between turtle size and prey size. However, several studies show that correlations between prey item size and turtle size are usually positive, with the largest turtles being those that eat the largest items. Bury (1986) reported that differences in prey size between juveniles, males, and females of *Actinemys marmorata* diminished intraspecific competition for resources. Prévot-Julliard et al. (2007) studied the diet of feral populations of *Trachemys scripta elegans* from France and found that juveniles consumed more invertebrates than adults in

A

X   = 10,848 ,0132 * CL
Correlation r = -,1716

B

X   = 7.9404 + ,00698 * cl
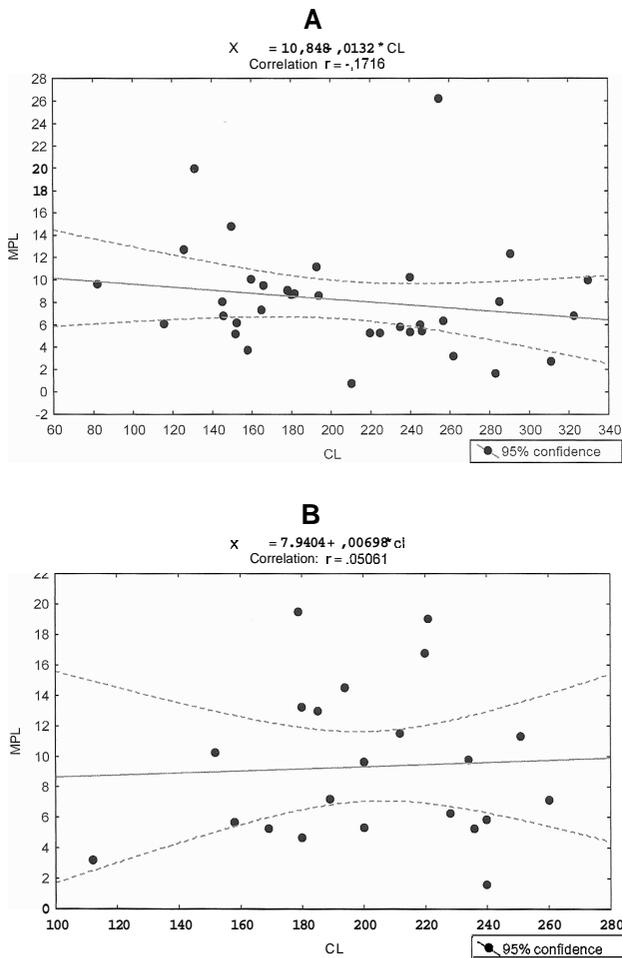Correlation: r = .05061

Figure 3. Pearson correlation between size of turtles (x-axis; straight-line carapace length in mm) and mean size of prey items (y-axis; mean prey length in mm) for *Phrynops hilarii* (A) and *Hydromedusa tectifera* (B).

relation to turtle size. Lahanas (1982) descnbed a positive correlation between the size of the snails preyed upon by *Graptemys nigrinoda,* with the largest turtles eating the largest snails. Georges (1982) for *Emydura macquarii krefftii* and Tucker et al. (1995) for *Malaclemys terrapin* also described positive correlations between turtle size and prey size. Wilson and Lawner (2008) reported that large specimens of E. *m. krefftii* consumed lesser amounts of *Cabomba* and fruits of *Ficus* than did smaller turtles, without commenting on the size of such items. Souza and Abe (2000) did not find any correlation between turtle size and prey item size for *Phrynops geoffroanus.*

Long-Necked Chelids and Piscivory. — Particular and divergent morphological patterns within some groups are usually related to ecological adaptation. A clear example is the hypothesis that proposes piscivory for crocodilíans with slender snouts relative to cranial length (Iordansky 1973). But this hypothesis is not always based on evidence, because these crocodilians reflect a more diverse diet than expected for piscivorous forms (Tucker et al. 1996). An alternative hypothesis proposes that slender snouts represent adaptation to living in riverine

habitats (Magnusson et al. 1987). Similarly, Pritchard (1984) proposed that the long neck of some chelid turtles would increase their capability of feeding on agile prey, particularly fish, but studies on the diet of long-necked chelids have not always supported the relationship between piscivorous habits and long necks. Fish consumption as carrion was reported for E. *m. krefftii* (Wilson and Lawner 2008); E. *macquarii* (Spencer et al. 1998); *G. pseudogeographica,* G. *geographica,* and *G. ouachitensis* (Vogt 1981); *Kinosternon sonoriense* (Hulse 1974); and some populations of T. *s. elegans* (Parmenter 1980; Prévot-Julliard et al. 2007). However, other aquatic turtles are capable of active predation upon small fish. Table 5 shows the published percentages of occurrence frequency, numeric frequency, and relative total volume for fish consumption of many species of freshwater turtles. This table makes 3 interesting points: 1) the only long-necked pleurodiran that completely occupies the piscivorous feeding niche is *C. fimbriata;* 2) contrary to the expected, some long-necked pleurodirans that live in environments in which fish are common do not fed upon them, as in *Hydromedusa maximiliani* and *Chelodina longicollis*; 3) the amount of fish fed upon by some long-necked pleurodirans (such as H. *tectifera)* do not differ from the amount ingested by short-necked turtles, and in some extreme cases, fish consumption is lower in long-necked pleurodirans than in short-necked species. The finding that *Chelus* is the species that best correlates with piscivorous habits is in agreement with the better capabilities of the species for suction feeding in comparison with other aquatic turtles, as has been demonstrated in works on turtle feeding kinematics (Lauder and Prendergast 1992; Van Damme and Aerts 1997; Summers et al. 1998; Aerts et al. 2001; Lemell et al. 2002). Differences in neck length between H. *tectifera* and *P. hilarii* are not expressed in dietary composition differences, because immature chironomids are the bulk of the diet in both species. Finally, the extant data and the evidence presented herein do not support the hypothesis that longer necks have a better capability of preying upon fish. Although some prey are capable of rapid movements (e.g., aquatic hemipterans, decapods), we do not consider them as agile, because they spend most of the time either quiet or making slow movements. We consider that nonagile prey represent 80% of the items ingested by the long-necked H. *tectifera,* with fish and other agile prey representing only a small fraction of the trophic spectrum of the species.

Table 5. Literature-based list of turtle species that feed actively upon fish. The table includes the following percentages: occurrence frequency (%OF), numenc frequency (%NF) and percentage of total volume (%TV). The symbol (?) indicates no available data.

Species	Source	Fish		
		%FN	%OF	%TV
Short-Necked Cryptodirans				
Actinemys marmorata	Bury 1986	0.17	6.89	21.92
Emydoidea blandingii	Kofron and Schreiber 1985	15.21	46.6	?
Kinosternon flavescens	Kofron and Schreiber 1985	6.79	44	?
K. leucostomum	Vogt and Guzman Guzman 1988	?	10	9.1
Staurotypus triporcatus	Vogt and Guzman Guzman 1988	?	33.3–38.4	4.9–17.3
Trachemys scripta elegans	Parmenter and Avery 1990; Outerbridge 2008	?	16.92	?
Short-Necked Pleurodirans				
Acanthochelys spixii	Richard 1999	9	?	
A. pallidipectoris	Richard 1999	7	?	
Phrynops geoffroanus	Fachin-Teran et al. 1995	?	?	
	Dias and Souza 2005			29.8
P. hilarii	Present paper	0.096	36.17	3.13
Podocnemis unifilis	Fachin-Teran et al. 1995	?	?	1.027
Rhinemys rufipes	Caputo and Vogt 2008	3.8	19.4	23.5
Long-Necked Pleurodirans				
Chelodina longicollis	Georges et al. 1986	0	0	0
Chelus fimbriata	Fachin-Teran et al. 1995	100	100	100
Hydromedusa tectifera	Present paper	0.259	36	14.25
H. maximiliani	Souza and Abe 1995	0	0	0
Macrochelodina expansa	Legler 1978	?	7–25	
	Chessman 1983			1.4–7.6
M. rugosa	Kennett and Tory 1996	2.7–30.1	31.3–79.3	18.3–58.2 (g)

tion of some arthropods, L. Protogino who shared her expertise for fish identification, and L. Protogino and B. Semeniuk who helped us during many of the sample days. This paper is contribution 773 of the Instituto de Limnología Dr R.A. Ringuelet.

LITERATURE CITED

AERTS, P., VAN DAMME, J., AND HERREL, A. 2001. Intrinsic mechanics and control of fast cranio-cervical movements in aquatic feeding turtles. American Zoologist 41:1299–1310.

ALLANSON, M. AND GEORGES, A. 1999. Diet of *Elseya puwisi* and *Elseya georgesi* (Testudines: Chelidae), a sibling species pair of freshwater turtles from eastem Australia. Chelonian Conservation and Biology 3:473–477.

ARMSTRONG, G. AND BOOTH, D.T. 2005. Dietary ecology of the Australian freshwater turtle (*Elseya* sp.: Chelonia: Chelidae) in the Bumett River, Queensland. Wildlife Research 32:349–353.

BELKIN, A.D. AND GANS, C. 1967. An unusual chelonian feeding niche. Ecology 49:768–769.

BERRY, J.F. 1975. The population effects of ecological sympatry on musk turtles in Northern Florida. Copeia 1975:692–701.

BURY, R.B. 1986. Feeding ecology of the turtle, *Clemmys marmorata*. Joumal of Herpetology 20:515–521.

CABRERA, M.C. 1998. Las tortugas continentales de Sudamérica austral. Córdoba, Argentina: ed. del autor, 108 pp.

CAPUTO, F.P. AND VOGT, R.C. 2008. Stomach flushing vs. fecal analysis: the example of *Phrynops rufipes* (Testudines: Chelidae). Copeia 2008:301–305.

CHEN, T.H. AND LUE, K.Y. 1998. Ecological notes on feral populations of *Trachemys scripta elegans* in northern Taiwan. Chelonian Conservation and Biology 3:87–90.

CHESSMAN, B.C. 1983. Observations on the diet of the broad-shelled turtle *Chelodina expansa* Gray (Testudines: Chelidae). Australian Wildlife Research 10:169–172.

CHESSMAN, B.C. 1986. Diet of the Murray turtle, *Emydura macquarii* (Gray) (Testudines: Chelidae). Australian Wildlife Research 13:65–69.

COLAUTTI, D.C. 1998. Sobre la utilización de trampas para peces en las lagunas pampásicas. Revista de Ictiología 6:17–23.

COLLINS, D. AND LINDEMAN, P.V. 2006. The influence of body size and trophic morphology on the size of molluscan prey of female Texas map turtles (*Graptemys versa*). Herpetological Review 37:416–418.

COOLEY, C.R., FLOYD, A.O., DOLINGER, A., AND TUCKER, P.B. 2003. Demography and diet of the painted turtle (*Chuysemys picta*) at high-elevation sites in southwestem Colorado. Southwestern Naturalist 48:47–53.

DEROCCO, N.N., ALCALDE, L., AND ROSSET, S.D. 2005. Ampliación de la distribución geográfica de *Phrynops hilarii* (Pleurodira: Chelidae) en Argentina. Cuadernos de Herpetología 19:63.

DIAS, L.C., AND SOUZA, F.L. 2005. *Phuynops geoffroanus* (Geoffroy's side-necked turtle). Diet. Herpetological Review 36:56–57.

DODD, C.K., JR., ENGE, K.M., AND STUART, J.N. 1988. Aspects of the biology of the flattened musk turtle, *Sternotherus depressus* in Northern Alabama. Bulletin of the Florida State Museum, Biological Sciences 34:1–64.

DUNHAM, A.E. 1983. Realized niche overlap, resource abundance and intensity of interspecific competition. In: Huey, R.H., Pianka E.R., and Schoener, T.W. (Eds.). Lizard Ecology. Cambridge, MA: Harvard Univ. Press, pp. 261–280.

ESCALANTE, A.H. 1982. Contribution to the knowledge of the trophic relationships of freshwater fishes in the platense area. I. Astyanax eigenmanniorum (Osteichthyes Tetragonopteridae). Limnobios 2:311–322.

ESCALANTE, A.H. 1983. Contribution to the knowledge of the trophic relationships of freshwater fishes in the platense area. II. Other Tetragonopteridae. Limnobios 2:379–402.

FACHIN-TERÁN, A., VOGT, R.C., AND GOMEZ, M.F.S. 1995. Food habits of an assemblage of five species of turtles in the Rio Guapore, Rondonia, Brazil. Journal of Herpetology 29:536–547.

FREIBERG, M.A. 1977. Reptilia. Testudines o Chelonia. Fauna de agua dulce de la Republica Argentina (FECIC, Bs. As.) 42:1–55.

GALLARDO, J.M. 1956. Tortuga acuática Hydromedusa *tectifera* Cope en cautividad. Ichtys 1:183–188.

GALLARDO, J.M. 1982. Anfibios y reptiles del Parque Nacional El Palmar de Colón, Prov. de Entre Ríos. Anales de Parques Nacionales 15:65–75.

GALLARDO, J.M. 1987. Anfibios y reptiles del Partido de Magdalena (provincia de Buenos Aires). Buenos Aires, Argentina: Fundación Elsa Shaw de Pearson, 46 pp.

GEORGES, A. 1982. Diet of the Australian freshwater turtle Emydura *krefftii* (Chelonia: Chelidae), in an unproductive lentic environment. Copeia 1982:331–336.

GEORGES, A., NORRIS, R., AND WENSING, L. 1986. Diet of the freshwater turtle *Chelodina longicollis* (Testudines: Chelidae) from the coastal dune lakes of the Jervis Bay territory. Australian Wildlife Research 13:301–308.

HULSE, A.C. 1974. Food habits and feeding behavior in Kinosternon sonoriense (Chelonia: Kinosternidae). Journal of Herpetology 8:195–199.

IORDANSKY, N.N. 1973. The skull of the crocodilia. In: Gans, S., and Parsons, T.S. (Eds.). Biology of the Reptilia. IV. Morphology. London: Academic Press, pp. 201–262.

IVLEV, V.S. 1961. Experimental ecology of the feeding of fishes. New Haven, CT: Yale Univ. Press, 302 pp.

KENNETT, R. AND TORY, 0 . 1996. Diet of two freshwater turtles, *Chelodina* rugosa and *Elseya dentata* (Testudines: Chelidae) from the wet–dry tropics of northem Australia. Copeia 1996:409–419.

KNIGHT, A.W. AND GIBBONS, J.W. 1968. Food of the painted turtle, *Chrysemys* picta, in a polluted river. American Midland Naturalist 80:558–562.

KOFRON, Ch.P. AND SCHREIBER, A.A. 1985. Ecology of two endangered aquatic turtles in Missouri: Kinosternon *flavescens* and Emydoidea blandingii. Journal of Herpetology 19:27–40.

LAGLER, K.F. 1943. Food habits and economic relations of the turtles of Michigan with special reference to fish management. American Midland Naturalist 29:257–312.

LAHANAS, P.N. 1982. Aspects of the life history of the southem black-knobbed sawback (Graptemys nigrinoda delticola). Unpublished M.S. thesis, Aubum University, Auburn, Alabama.

LAUDER, G.V. AND PRENDERGAST, T. 1992. Kinematics of aquatic prey capture in the snapping turtle Chelydra serpentina. Joumal of Experimental Biology 164:55–78.

LEGLER, J.M. 1966. Notes on the natural history of a rare Central American turtle Kinosternon *angustipons* Legler. Herpetologica 22:118–122.

LEGLER, J.M. 1977. Stomach flushing: a technique for chelonian dietary studies. Herpetologica 33:281–284.

LEGLER, J.M. 1978. Observations on behavior and ecology in an Australian turtle, *Chelodina* expansa (Testudines: Chelidae). Canadian Journal of Zoology 56:2449–2453.

LEMELL, P., LEMELL, Ch., SNELDERWAAR, P., GUMPENBERGER, M., WOCHESLANDER, R., AND WEISGRAM, J. 2002. Feeding pattems of *Chelus fimbriatus* (Pleurodira: Chelidae). Joumal of Experimental Biology 205:1495–1506.

LEVINS, R. 1968. Evolution in changing environments – some theoretical exploration. Princeton, New Jersey: Princeton University Press, 132 pp.

LIMA, A.C., MAGNUSSON, W.E., AND DA COSTA, V.L. 1997. Diet of the turtle Phrynops *rufipes* in central Amazonia. Copeia 1997:216–219.

LINDEMAN, P.V. 2006a. Zebra and quagga mussels (Dreissena sp.) and other prey of a Lake Erie population of common map turtles (Emydidae: Graptemys geographica). Copeia 2006:268–273.

LINDEMAN, P.V. 2006b. Diet of the Texas map turtle (Graptemys versa): relationship to sexually dimorphic trophic morphology and changes over five decades as influenced by an invasive mollusk. Chelonian Conservation and Biology 5:25–31.

LINDEMAN, P.V. AND SHARKEY, M.J. 2001. Comparative analyses of functional relationships in the evolution of trophic morphology in the map turtles (Emydidae: Graptemys). Herpetologica 57:313–318.

LUEDERWALDT, H. 1926. Os chelonios brasileiros, com a lista das especies do Museu Paulista. Revista do Museo Paulista 14:405–470.

MAGNUSSON, W.E., VIEIRA DA SILVA, E., AND LIMA, A.P. 1987. Diets of Amazonian crocodilians. Joumal of Herpetology 21:85–95.

MAHMOUD, I.Y. 1968. Feeciing behavior in kinosternid turtles. Herpetologica 24:300–305.

MALVASIO, A., DE SOUZA, A.M., DE BARROS MOLINA, F., AND DE ARRUDA SAMPAIO, F. 2003. Comportamento e preferencia alimentar em Podocnemis expansa (Schweigger), P. *unifilis* (Troschel) e P. *sextuberculata* (Comalia) em cativerio (Testudines, Pelomedusidae). Revista Brasileira de Zoologia 20:161–168.

MOLL, D. 1976. Food and feeding strategies of the Ouachita rnap turtle (Graptemys pseudogeographica ouachitensis). American Midland Naturalist 96:478–482.

MOLL, E.O. AND LEGLER, J.M. 1971. The life history of a Neotropical slider turtle, Pseudernys scripta (Schoepff), in Panama. Bulletin of Los Angeles County Museum of Natural History (Sci.) 11:1–102.

OTTONELLO, D., SALVIDIO, S., AND ROSECCHI, E. 2005. Feeding habits of the European pond terrapin *Emys* orbicularis in Camargue (Rhône delta, Southern France). Amphibia-Reptilia 26:562–565.

OUTERBRIDGE, M.E. 2008. Ecological notes on feral populations of Trachemys scripta *elegans* in Bermuda. Chelonian Conservation and Biology 7:265–269.

PARMENTER, R.R. 1980. Effects of food availability and water temperature on the feeding ecology of pond sliders (*Chrysemys* s. scripta) Copeia 1980:503–514.

PARMENTER, R.R. AND AVERY, H.W. 1990. The feeding ecology of the slider turtle. In: Gibbons, J.W. (Ed.). Life History of the Slider Turtle. Washington, DC: Smithsonian Institution Press, pp. 257–265.

PIANKA, E.R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4:53–74.

PIANKA, E.R. 1974. Niche overlap and diffuse competition. Procedures of the National Academy of Sciences 71:2141–2145.

PINKAS, L., OLIPHANT, M.S., AND IVERSON Z.L. 1971. Food habits of albacore bluefins, tuna and bonito in California waters. California Department of Fish Game, Fish Bulletin 152:1–350.

PREVOT-JULLIARD, A.C., GOUSSET, E., ARCHINARD, C., CADI, A., AND GIDONDORT, M. 2007. Pets and invasion risks: is the

slider turtle strictly carnivorous? Amphibia-Reptilia 28:139–143.

PRITCHARD, P.C.H. 1984. Piscivory in turtles, and evolution of long-necked Chelidae. Symposia Zoological Society of London 1984:87–110.

RANEY, E.C. AND LACHNER, E.A. 1942. Summer food of Chysemys picta marginata in Chautauqua Lake, New York. Copeia 1942:83–85.

RICHARD, E. 1999. Tortugas de las regiones áridas de Argentina: Contribución al conocimiento de las tortugas de las regiones áridas de Argentina (Chelidae y Testudinidae) con especial referencia a los aspectos eto-ecológicos, comerciales y antropológicos de las especies del complejo chilensis (Chelonoidis chilensis y Ch. donosobarrosi) en la provincia de Mendoza. Buenos Aires, Argentina: Monografía especial L.O.L.A. N° 10, 24 pp.

SHANNON, C.E. AND WEAVER, W. 1949. The mathematical theory of communication. Urbana: Univ. of Illinois Press, 144 pp.

SOUZA, F.L. 2004. Uma revisão sobre padrões de atividade, reprodução e alimentação de cágados brasileiros (Testudines, Chelidae). Phyllomedusa 3:15–27.

SOUZA, F.L. AND ABE, A.S. 1995. Observations on feeding habits of Hydromedusa *maximiliani* (Testudines: Chelidae) in southeastern Brazil. Chelonian Conservation and Biology 1:320–322.

SOUZA, F.L. AND ABE, A.S. 2000. Feeding ecology, density and biomass of the freshwater turtle, Phynops geoffroanus, inhabiting a polluted urban river in southeastern Brazil. Journal of Zoology 252:437–446.

SPENCER, R.J., THOMPSON, M.B., AND HUME, I.D. 1998. The diet and digestive energetics of an Australian short-necked turtle, Emydura macquarii. Comparative Biochemistry and Physiology Part A 121:341–349.

STATSOFT INC. 2001. Statistica (data analysis software system). Version 6.0. StatSoft Inc.

STUART, J.N. AND PAINTER, Ch.W. 2002. Observations on the diet of Trachemys gaigeae (Testudines: Emydidae). Bulletin of the Maryland Herpetological Society 38:15–22.

SUMMERS, A.P., KAYVAN, F.D., RICHMOND, A.M., AND BRAINERD, E.L. 1998. Kinematics of aquatic and terrestrial prey capture in Terrapene carolina, with implications for the evolution of feeding in cryptodire turtles. Journal of Experimental Zoology 281:280–287.

TOBLER, M. 2008 Divergence in trophic ecology characterizes colonization of extreme habitats. Zoological Journal of the Linnean Society 95:517–528.

TUCKER, A.D., FRITZSIMMONS, N.N., AND GIBBONS, I.W. 1995. Resource partitioning by the estuarine turtle Malaclemys terrapin: thropic, spatial, and temporal foraging constraints. Herpetologica 51:167–181.

TUCKER, A.D., LIMPUS, C.J., MCCALLUM, H.I., AND MCDONALD, K.R. 1996. Ontogenetic dietary partitioning by Crocodilus johnstoni during the dry season. Copeia 1996:978–988.

VAN DAMME, J. AND AERTS, P. 1997. Kinematics and functional morphology of aquatic feeding in Australian snake-necked turtles (Pleurodira; Chelodina). Journal of Morphology 233:113–125.

VOGT, R.C. 1981. Food partitioning in three sympatric species of map turtle, genus Graptemys (Testudinata, Emydidae). American Midland Naturalist 105:102–111.

VOGT, R.C. AND GUZMAN GUZMAN, S. 1988. Food partitioning in a Neotropical freshwater turtle comrnunity. Copeia 1988:37–47.

WILSON, M. AND LAWLER, I.R. 2008. Diet and digestive performance of an urban population of the omnivorous freshwater turtle (Emydura *krefftii*) from Ross River, Queensland. Australian Journal of Zoology 56:151–157.