CHELONIAN CONSERVATION AND BIOLOGY
International Journal of Turtle and Tortoise Research

Feeding Habits of Amazonian Freshwater Turtles (Podocnemididae and Chelidae) from Peru

BRUNO DE OLIVEIRA FERRONATO[1], CARLOS IGNACIO PIÑA[2], FREDDY COCHACHEZ MOLINA[3],
RENATO A. ESPINOSA[3], AND VÍCTOR R. MORALES[3]

[1]*Institute for Applied Ecology, University of Canberra, ACT 2601, Australia [brunoferronato@hotmail.com];*
[2]*CICyTTP-CONICET. Proyecto Yacaré. UAdER/FCyT. UNER/FCAl. Dr. Materi y España, CP 3105, Diamante, Entre Ríos, Argentina [cidcarlos@infoaire.com.ar];*
[3]*Universidad Ricardo Palma, Facultad de Ciencias Biológicas. Ap. Postal 18-01, Av. Benavides 5440, Las Gardenias, Surco, Lima, Perú [fric_mc@hotmail.com; renatocom86@hotmail.com; victor9901@yahoo.com]*

Chelonian Conservation and Biology, 2013, 12(1): 119–126

Feeding Habits of Amazonian Freshwater Turtles (Podocnemididae and Chelidae) from Peru

BRUNO DE OLIVEIRA FERRONATO[1], CARLOS IGNACIO PIÑA[2], FREDDY COCHACHEZ MOLINA[3],
RENATO A. ESPINOSA[3], AND VÍCTOR R. MORALES[3]

[1]*Institute for Applied Ecology, University of Canberra, ACT 2601, Australia [brunoferronato@hotmail.com];*
[2]*CICyTTP-CONICET. Proyecto Yacaré. UAdER/FCyT. UNER/FCAl. Dr. Materi y España, CP 3105, Diamante, Entre Ríos, Argentina [cidcarlos@infoaire.com.ar];*
[3]*Universidad Ricardo Palma, Facultad de Ciencias Biológicas. Ap. Postal 18-01, Av. Benavides 5440, Las Gardenias, Surco, Lima, Perú [fric_mc@hotmail.com; renatocom86@hotmail.com; victor9901@yahoo.com]*

ABSTRACT. – We describe here the feeding habits of the Yellow-spotted River turtle (*Podocnemis unifilis*) (*n* = 20), Geoffroy's side-necked turtle (*Phrynops geoffroanus*) (*n* = 10), and Gibba turtle (*Mesoclemmys gibba*) (*n* = 4) from central Peru, Pasco Department, and evaluate food overlaps among them. *Podocnemis unifilis* showed a generalist feeding habit, ingesting animal and plant matter, but tending to be herbivorous, because plant matter made up 62.9% of the volume vs. 3.9% for animal material. The most important items in *P. unifilis* diet were seeds from the Fabaceae (Leguminosae) family and bark. *Podocnemis geoffroanus* and *M. gibba* also had generalist feeding habits. The most important items for *P. geoffroanus* were insects, especially Libellulidae larvae, and plant material. *Mesoclemmys gibba* ingested insects, fish, crustaceans, unidentified plant matter, bark, leaves, stem, and algae, with plant matter being more representative by frequency and volume. Low dietary overlap was observed between *P. unifilis* and *P. geoffroanus*, and both species appeared to overlap with *M. gibba*. To our knowledge, this is the first quantitative dietary study of Peruvian freshwater turtles, and the first diet analysis of wild *M. gibba* in the Amazon basin.

KEY WORDS. – Reptilia; Testudines; *Podocnemis unifilis*; *Phrynops geoffroanus*; *Mesoclemmys gibba*; diet; food overlap

Quantitative evaluation of animals' diets is a powerful tool for understanding niche specifications in community dynamics (Krebs 1999). In addition, studying feeding habits of natural populations can serve as a basis for making recommendations for captive husbandry, especially for species with economic importance (Fachin-Teran et al. 1995). The feeding habits of Amazonian freshwater turtle species have been studied since the 1960s but have received more attention the past 2 decades (Medem 1964; Almeida et al. 1986; Fachin-Teran et al. 1995; Balensiefer and Vogt 2006; Caputo and Vogt 2008). However, the diet of some species in the wild, e.g., *Mesoclemmys heliostemma*, *Mesoclemmys gibba*, *Platemys platycephala,* is virtually unknown (Souza 2004).

Turtle assemblages are common in Amazonian habitats (Fachin-Teran et al. 1995) as well as in other tropical and temperate regions (Vogt 1981; Vogt and Guzman 1988; Bjorndal et al. 1997; Alcalde et al. 2010). In living together, species tend to overlap or to partition the food resources. Overlapping usually occurs when resource availability is high (Bjorndal et al. 1997; Godbold et al. 2009; Rocha et al. 2011). Partitioning mechanisms could occur when there are microhabitat segregation of the species, interspecific differences in feeding strategies, and interspecific differences in food organism preference (Vogt 1981; Souza and Abe 1998; Luiselli 2006). Although turtle diversity is high in the Amazon basin (Buhlmann et al. 2009), little is known about resource overlap or mechanisms involved in food partitioning in those species (Fachin-Teran et al. 1995).

Podocnemis unifilis (Podocnemididae) is widespread in the tropical lowlands of northern South America, occurring in Bolivia, Brazil, Colombia, Ecuador, French Guyana, Guyana, Peru, Surinam, and Venezuela (Pritchard and Trebbau 1984). Its feeding habits are known both for wild (Medem 1960; Almeida et al. 1986; Fachin-Teran et al. 1995; Portal et al. 2002; Balensiefer and Vogt 2006) and captive individuals (Malvasio et al. 2003), but no quantitative information is available for this species in Peru (Ferronato and Morales 2012).

Phrynops geoffroanus (Chelidae) is the South American turtle with the widest geographical distribution of all freshwater turtles in the region, ranging from the Colombian Amazon to southern Brazil and northern Argentina (Ernst and Barbour 1989), where they inhabit pristine areas as well-urbanized, often polluted rivers (Souza and Abe 2000; Ferronato et al. 2009; Piña et al. 2009; Martins et al. 2010). *Phrynops geoffroanus* exhibits a carnivorous feeding habit in captivity (Medem 1960; Molina 1990), but, in the wild, its diet varies according to the habitat within which it lives (Medem 1960; Fachin-Teran et al. 1995; Souza and Abe 2000; Dias and Souza 2005; Martins et al. 2010). To date, no diet records of *P. geoffroanus* from Peru have been published (Ferronato and Morales 2012).

Mesoclemmys gibba (Chelidae) is a lowland rainforest species that occurs in Brazil, Colombia, Ecuador, French Guyana, Guyana, Peru, Surinam, Trinidad, and Venezuela (Mittermeier et al. 1978; Pritchard and Trebbau 1984). The species' diet is only known from captive individuals (Fretey 1977; Mittermeier et al. 1978).

The goal of this study was to describe the feeding habits of wild *P. unifilis*, *P. geoffroanus,* and *M. gibba* from the Peruvian Amazon and to verify the degree to which dietary overlap occurs among these species. To our knowledge, this is the first quantitative dietary study of freshwater turtles from Peru and the first quantitative description of wild *M. gibba* diet for the Amazon basin.

METHODS

The study was conducted in the Santa Rosa de Chivis community (260 m above sea level, lat 10°20′13″S, long 74°58′33″W) and surrounding areas. The community is formed by an Asháninka ethnic group and is located in Puerto Bermúdez District, Pasco Department, central Peru. It is located in the buffer zone of the natural protected area ''Bosque de Protección San Matías – San Carlos.'' The average annual temperature is 25.4°C, and average annual rainfall is 3500 mm. The dry season extends from May to September, and the wet season is from October to April. The typical ecological formation in the area is Humid Tropical Forest (Gaviria 1981).

Turtles were captured, twice a month, from July to November 2009. They were collected in 2 oxbow lakes (both approximately 1.7 m deep, 80 m long and 8 m wide) and in a section of the Azupizu River (10-m depth, 25-m width). We used fishing nets (nylon, mesh size 4.5 cm, 2 m deep, 40 m long), a trammel net (mesh size of the inner net was 7 cm between knots and 25 cm for the outer net, 2 m deep, 25 m long), and basking traps (nets under basking logs) to collect turtles in the oxbow lakes, and basking traps for the animals in Azupizu River. We collected the animals during the day, setting the nets and basking traps early in the morning and checking nets every 3 hrs and basking traps every hour. Turtles were identified and sexed based on their morphological characteristics by following Pritchard and Trebbau (1984) and Rueda-Almonacid et al. (2007), marked by shell notching (Cagle 1939), and weighted and measured with calipers (straight-line carapace length [SCL]). We designated all *P. unifilis* less than 13 cm in SCL, *P. geoffroanus* less than 20 cm (Souza and Abe 2000), and *M. gibba* less than 15 cm (Pritchard and Trebbau 1984) as subadults of unknown sex. Turtles were stomach-flushed (Legler 1977), and the items were preserved in 70% ethanol. The turtles were released within 3 hrs of initial capture in the same area where they were trapped.

Stomach contents were examined with a stereoscopic microscope, and the items were identified to the lowest taxonomic level possible. The total volume of each prey item was measured by water displacement by using graduate cylinders to the nearest 0.1 ml (Bjorndal et al. 1997). For each food group, we registered frequency of occurrence (percentage of turtles in which a given food item was found [%F]) and volume percentage (volume percentage of prey category in relation to all food items detected [%V]). The importance of each food item in the diet was quantified in each species by the index of relative importance (IRI) by integrating frequency of occurrence and volume: $\mathrm{IRI} = 100\,(\mathrm{Fo} \times \mathrm{Vi})/\sum (\mathrm{Fo} \times \mathrm{Vi})$, where F is the percentage frequency of occurrence and V is the percentage volume. Values near zero indicate low importance, and values near 100 indicate high importance (Bjorndal et al. 1997). Similarity or niche overlap among the species was measured by the simplified Morisita index (CH): $\mathrm{CH} = 2 \sum (P_{ij} \times P_{ik})/\sum (P^2_{ij}) + \sum (P^2_{ik})$, where j and k are categories to be compared, and P_{ij}, P_{ik} are the proportions represented by item i in such categories; values near zero indicate low similarity and values near 1, high similarity (Krebs 1999). We did not include sediment, a common finding in the stomach contents, in our analysis of IRI and CH because we considered it an incidental ingestion and not a food item; further details are depicted in the Results and Discussion sections.

We performed descriptive statistics for our results. We could not analyze our data into sex or life stage categories due to the small sample size.

RESULTS

We captured and stomach-flushed 20 *P. unifilis* (11 males, 4 females, and 5 juveniles), 10 *P. geoffroanus* (all juveniles), and 4 *M. gibba* (1 male and 3 juveniles). The SCL and mass (mean ± SD and range) were 15.9 ± 3.9 cm (8.4–22 cm) and 619.7 ± 382 g (90–1500 g), respectively, for *P. unifilis*; 14 ± 2.8 cm (9.5–18.5 cm) and 298.1 ± 158 g (101–575 g), respectively, for *P. geoffroanus*; and 14 ± 3.1 cm (11.7–18.6 cm) and 302.5 ± 166 g (190–550 g), respectively, for *M. gibba*. Most of the captures occurred during dry season and in one of the oxbow lakes.

Podocnemis unifilis diet was composed of a greater variety of items when compared with the other turtle species (Table 1). *Podocnemis unifilis* consumed 49 food items, including 32 animal and 17 plant items (Table 2). Although animal matter was represented by a greatest number of diet items ($n = 32$ food types) and had a high %F (90%), it comprised a relatively low percentage of the overall food volume (3.9%) in the stomachs that we examined. *Podocnemis unifilis* consumed 16 species of fish (based on scales present in the stomachs contents; one turtle ingested a small and whole fish) and 12 species of insects, with a volume of only 1.6% and 2.3% (Table 1), respectively. In contrast, plant material corresponded to 62.9% of the volume and was found in 95% of the turtles (Table 1). Seeds from the Fabaceae (Leguminosae) family and bark were common items in *P. unifilis* stomachs, which yielded 70% and 85% of frequency, 28.3% and 18.8% of volume, and 42.78 and 34.57 of IRI, respectively (Table 2). Sediment also was commonly

Table 1. Description of groups of food items found in the stomach flushings of *Podocnemis unifilis* (n = 20), *Phrynops geoffroanus* (n = 10), and *Mesoclemmys gibba* (n = 4) in Santa Rosa de Chivis, Pasco Department, Central Peru.[a]

	P. unifilis				*P. geoffroanus*				*M. gibba*			
	Freq.	%F	Vol.	%V	Freq.	%F	Vol.	%V	Freq.	%F	Vol.	%V
U.p.m.	15	75	22.3	4.8	9	90	7.6	29.4	4	100	1.8	28.8
Bark	17	85	86.6	18.8					1	25	0.3	4.9
Flower	7	35	3.7	0.8	1	10	0.1	0.4				
Leaf	18	90	35	7.6	3	30	0.2	0.7	2	50	0.7	11.5
Stem	13	65	5.3	1.1					1	25	0.05	0.8
Seed	17	85	136.1	29.6	1	10	0.01	0.04				
Fruit					1	10	0.5	1.9				
Algae									1	25	0.1	1.6
Fungi	1	5	0.2	0.04								
Plant total	19	95	289.3	62.9	9	90	8.4	32.4	4	100	2.9	47.6
Insect	14	70	10.4	2.3	9	90	14	54.1	4	100	1	17
Crustacean	1	5	0.01	0.002	2	20	0.1	0.4	1	25	0.01	0.2
Fish	16	80	7.6	1.6	1	10	0.1	0.4	1	25	0.4	6,.5
Mollusca	5	25	0.1	0.03	6	60	1.7	6.4				
Arachnida					1	10	0.01	0.04				
Animal total	18	90	18.1	3.9	9	90	15.9	61.4	4	100	1.4	23.7
Sediment	15	75	152.4	33.1	1	10	1.6	6.2	1	25	1.7	28.6
Total	20	100	459.8	100	10	100	25.9	100	4	100	6.1	100

[a] Freq. = frequency, %F = frequency of occurrence, Vol. = volume (ml), %V = volume percentage, U.p.m. = unidentified plant matter.

encountered, because it was present in 75% of the individuals sampled and made up 33.1% of the sample volume (Table 2). Sediment was mainly composed of mud and small rocks. Other frequent items were stem (65%F), unidentified plant matter (75%F), and Fabaceae leafs (80%F). Of the 49 food items consumed by *P. unifilis*, several of them showed a low frequency of occurrence in the stomach samples (Table 2).

Phrynops geoffroanus ingested 23 food items, with 18 of these being animal items and 5 plant items. Sediment was present in one stomach content. Animal matter contributed to 61.4% of the volume and was present in 90% of the *P. geoffroanus* stomachs. Another frequent item was unidentified plant material, which was present in 90% of the animals, contributed to 29.4% of volume (Table 1), and showed an IRI of 39.49 (Table 2). Insects made up the bulk of the *P. geoffroanus* diet, with 13 species ingested from 7 orders (Odonata, Ephemerida, Hemiptera, Neuroptera, Coleoptera, Diptera, and Trichoptera), which contributed 54.1% of the sample volume (Table 1). Insects prey sizes ranged from approximately 10 to 40 mm. Libellulidae larvae was the most frequent item (80% of the stomach contents), which represented 37.5% of the volume, therefore, the most important item in their diet (IRI = 44.78) (Table 2). Other frequent animal dietary constituents in *P. geoffroanus* stomachs included Ephemeridae larvae (50%F) and the gastropod *Biomphalaria anaticus* (60%F) (Table 2).

Mesoclemmys gibba consumed 18 diet constituents, with 12 animal and 6 plant items. Sediment was found in one stomach content. Animal and plant matter were present in the stomachs of the 4 *M. gibba* captured (100% of frequency) and represented 23.7% and 47.6% of the total volume, respectively (Table 1). *Mesoclemmys gibba* ingested 9 species of insects and 2 fishes (only scales were recovered), and the bulk of their diet was represented by unidentified plant material, which represented 28.8% of total sample volume (Table 2).

We observed low dietary overlap between *P. unifilis* and *P. geoffroanus* (CH = 0.368), although, when considering the upper limit on tolerable niche overlap (< 0.4) (Bonino et al. 2009), diet compositions of *M. gibba* appeared to overlap with *P. geoffroanus* (CH = 0.521) and *P. unifilis* (CH = 0.456). The foods mutually consumed by *M. gibba* and *P. geoffroanus* included insects (Libellulidae, Tenebrionidae, Culicidae), a crustacean (Ostracoda), and plant material (Fabaceae leaf, unidentified plant material) (Table 2). The diets of *M. gibba* and *P. unifilis* overlapped in the presence of insects (Libellulidae), fishes (*Leporinus* sp., *Hoplias malabaricus*), and plant material (Fabaceae leaf, bark, unidentified plant material) (Table 2).

DISCUSSION

The feeding habits of *P. unifilis* from the Peruvian Amazon are primarily herbivorous, which is similar to the records of the species' diet in other regions of the Amazon basin. We found plant material in 95% of the *P. unifilis* sampled, and it accounted for 62.9% of the sample volume, whereas animal matter represented 3.9% of the sample volume. Fachin-Teran et al. (1995) demonstrated that *P. unifilis* in Guapore River in Brazil ingested 89.5% of the total volume of stomach contents in vegetal items, such as seeds, fruits, leaves, and stems. In addition, *P. unifilis* in Mamirauá Reserve in northern Brazil fed mainly on plant material (79.6% of the volume), with leaves, seeds, and fruits occurring most frequently (Balensiefer and Vogt 2006). Other qualitative records of *P. unifilis* diet (Medem 1964; Almeida et al. 1986;

Table 2. Percentages of frequency of occurrence (F%) and volume (V%), and index of relative importance (IRI) of each prey item ingested by *Podocnemis unifilis* ($n = 20$), *Phrynops geoffroanus* ($n = 10$), and *Mesoclemmys gibba* ($n = 4$), in Santa Rosa de Chivis, Departamento de Pasco, Central Peru.

	P. unifilis			*P. geoffroanus*			*M. gibba*		
Food item[a]	%F	%V	IRI	%F	%V	IRI	%F	%V	IRI
Arthropoda, Insecta	45	0.11	0.1068	40	1.66	0.9899	50	3.27	3.91
Order Odonata	5	0.01	0.0011						
Fam. Libellulidae	25	0.05	0.0269	80	37.55	44.78	25	1.64	0.9784
Fam. Coenagrionidae				40	3.13	1.86			
Order Orthoptera									
Fam. Tettigonidae	5	0.02	0.0021						
Order Ephemerida	35	1.85	1.39	50	6.38	4.75			
Order Hemiptera									
Fam. Naucoridae	10	0.01	0.0021	20	0.46	0.1371			
Fam. Corixidae	20	0.01	0.0043	30	3.32	1.48			
Fam. Pyrrocoridae							25	3.27	1.95
Order Neuroptera									
Fam. Chrysopidae	30	0.12	0.0777	10	0.19	0.0283			
Order Coleoptera	5	0.02	0.0021	10	0.04	0.0059	25	0.16	0.0954
Fam. Curculionidae	5	0.01	0.0011	10	0.08	0.0119			
Fam. Staphylinidae	5	0.01	0.0011						
Fam. Tenebrionidae				20	0.81	0.2415	25	3.27	1.95
Fam. Carabidae				10	0.39	0.0581			
Order Hymenoptera									
Fam. Formicidae	25	0.05	0.0269						
Fam. Pteromalidae							25	0.16	0.0954
Order Lepidoptera									
Fam. Pyralidae							25	0.16	0.0954
Order Diptera							25	4.91	2.92
Fam. Culicidae				10	0.04	0.0059	25	0.16	0.0954
Order Trichoptera									
Fam. Odontoceritidae				10	0.04	0.0059			
Arthropoda, Crustacea	5	0.01	0.0011						
Order Ostracoda				20	0.42	0.1252	25	0.16	0.0954
Arthropoda, Arachnida									
Order Aranae									
Fam. Lycosidae				10	0.04	0.0059			
Vertebrata, Pisces	15	0.92	0.2979	10	0.39	0.0581			
Order Characiformes									
Fam. Anostomidae									
Leporinus sp.	20	0.05	0.0215				25	4.91	2.92
Schizodon sp.	5	0.04	0.0043						
Abramites hypselonotus	5	0.01	0.0011						
Fam. Characidae	5	0.11	0.0118						
Knodus sp.	10	0.02	0.0043						
Astyanax sp.	5	0.01	0.0011						
Subfam. Glandulocaudinae	5	0.04	0.0043						
Fam. Curimatidae									
Steindachnerina sp.	10	0.02	0.0043						
Potamorhina sp.	25	0.06	0.0323						
Fam. Erythryniidae									
Hoplias malabaricus	25	0.09	0.0485				25	1.64	0.9784
Fam. Prochilodontidae									
Prochilodus nigricans	20	0.16	0.0691						
Fam. Gymnotidae									
Gymnotus sp.	5	0.01	0.0011						
Order Perciformes									
Fam. Cichlidae									
Crenicichla sp.	10	0.02	0.0043						

Table 2. Continued.

	P. unifilis			*P. geoffroanus*			*M. gibba*		
Food item[a]	%F	%V	IRI	%F	%V	IRI	%F	%V	IRI
Bujurquina sp.	10	0.02	0.0043						
Mesonauta sp.	5	0.02	0.0021						
Order Siluriformes									
Fam. Locaridae	10	0.02	0.0043						
Mollusca, Gastropoda	5	0.01	0.0011						
Order Basommatophora									
Fam. Planorbidae									
Biomphalaria anatinus	20	0.03	0.0129	60	4.91	4.39			
Mollusca, Bivalvia									
Order Veneroida									
Fam. Pisidiidae									
Sphaerium sp.				40	1.51	0.9005			
Plant, Unindentified plant matter	75	4.86	7.86	90	29.43	39.49	100	28.81	68.75
Plant, Stem	65	1.15	1.61				25	0.82	0.4892
Plant, Fruit				10	1.93	0.2877			
Plant, Bark	85	18.84	34.57				25	4.91	2.92
Plant, Leaf	60	3.03	3.92				25	4.91	2.92
Order Fabales									
Fam. Fabaceae	80	3.32	5.73	30	0.66	0.2952	50	6.56	7.82
Order Urticales									
Fam. Cecropiaceae	5	0.3	0.0323						
Fam. Urticaceae	5	0.74	0.0798						
Order Myrtales									
Fam. Melastomataceae	5	0.17	0.0183						
Order Poales									
Fam. Poaceae	5	0.04	0.0043						
Plant, Flower	5	0.29	0.0313						
Order Poales									
Fam. Juncaceae	20	0.48	0.2072						
Fam. Poaceae	10	0.04	0.0086	10	0.39	0.0581			
Plant, Seed	35	1.05	0.7933						
Order Rosales									
Fam. Moraceae	5	0.11	0.0118						
Order Fabales									
Fam. Fabaceae	70	28.31	42.78						
Order Poales									
Fam. Poaceae	40	0.15	0.1295	10	0.04	0.0059			
Fungi, Basidiomycetis									
Order Agaricales	5	0.04	0.0043						
Algae, Chlorophycea							25	1.64	0.9784
Sediment	75	33.14		10	6.19		25	28.64	

[a] Fam. = family.

Portal et al. 2002; Malvasio et al. 2003) also underscore the importance of plant material in its diet (Balensiefer and Vogt 2006).

In this study, the plant item most important for *P. unifilis* diet was Fabaceae (Leguminosae) seeds (IRI = 42.78). Fabaceae seeds are known for their high nutritional values, including elevated protein and fat content (Sotelo et al. 1995; Duranti and Gius 1997; Portal et al. 2002). It is possible that *P. unifilis* ingested these seeds due to their nutritional value and high caloric content to more efficiently reach their energetic and physiological requirements. There is evidence that marine turtles (e.g., *Chelonia mydas*) select food items with higher protein and nutrients levels in their diet (Godley et al. 1998; Brand-Gardner et al. 1999; Nagaoka et al. 2012).

Fachin-Teran et al. (1995) and Balensiefer and Vogt (2006) identified 30 and 15 species of plants, respectively, in *P. unifilis* stomach contents, whereas we found only 7 species. Perhaps the lower variety of plant species found in Peruvian turtles is due to the lesser number of sample sites, lesser types of habitat, or smaller sample size when compared with these previous dietary studies of Amazonian turtles (Fachin-Teran et al. 1995; Balensiefer and Vogt 2006). Nonetheless, our results still demonstrate that *P. unifilis* diet consists mostly in vegetal materials.

Sediment, represented mainly by mud, was a common component of *P. unifilis* diet in Peru, which accounted for 75% of frequency and 33.4% of sample volume. This likely is evidence that, at our study site, *P. unifilis* consumes foods that are closely associated with the riverbed and perhaps in the process, sediment is incidentally consumed. Balensiefer and Vogt (2006) also reported the presence of sediment in *P. unifilis* stomach contents (15% sample volume) and suggested that this may be due to incidental ingestions associated with bottom feeding or that turtles could be purposefully consuming substrate to obtain trace minerals not available in plants (Moll and Legler 1971; Beyer et al. 1994). Due to the elevated frequency and volume found in this investigation, we suggest further studies on the role that sediments play in freshwater turtle digestive processes.

The presence of a small whole fish and several large scales in the stomach contents indicates that *P. unifilis* can take live fish as well eat them as carrion, which also was observed by Fachin-Teran et al. (1995). Aquatic insect larvae also were part of the diet in many of the turtles in this study, which could have been eaten by active predation or neustophagia or been consumed incidentally along with plant matter (Belkin and Gans 1968; Balensiefer and Vogt 2006; Alcalde et al. 2010).

Although *P. unifilis* is considered primarily an herbivorous species due to the high amounts of plant matter it ingests (Belkin and Gans 1968; Malvasio et al. 2003; Balensiefer and Vogt 2006), analysis of our results suggests that it is a generalist species because we found animal items to be a common component of its diet. The consumption of animal matter by *P. unifilis* occurred with a large number of individuals (90%F), but in substantially lower volume (3.9%V). Similar results were obtained across the range of *P. unifilis* (Fachin-Teran et al. 1995; Balensiefer and Vogt 2006), which suggests additional evidence of diet mixing and possible benefits in digestive additive effects in freshwater turtles (Bjorndal 1991).

In this investigation, *P. geoffroanus* had a more onmivorous diet than that of *P. unifilis*, with animal matter and plant materials constituting 61.4%V and 32.4%V, respectively. Our results show some similarity with the diet of *P. geoffroanus* in another locality within the Amazon basin, where plant items and animal matter also were consumed (Fachin-Teran et al. 1995), but some of the animal groups consumed were different between our study site (arachnida, gastropods, bivalvia, and ostracoda) and that in the Guapore River (anurans, shrimp, crabs) (Fachin-Teran et al. 1995). Likewise, we found the proportion of animal:plant matter to be 2:1 vs. 1:1 (48% of volume each) found by Fachin-Teran et al. (1995). Contrasting with our results of animal and plant matter consumption, free-living *P. geoffroanus* were primarily carnivorous in Colombia (Medem 1960) and in Parana River in Brazil (Dias and Souza 2005), and the species fed mainly on Chironomidae larvae and pupa in Brazilian urban rivers (Souza and Abe 2000; Martins et al. 2010).

Although results of some studies suggest that plant material is incidentally ingested by *P. geoffroanus* (Souza and Abe 2000; Dias and Souza 2005; Martins et al. 2010), this was not the case at our study site because plant matter was found in 90% of the turtles and contributed to more than 32% of the sample volume. Souza and Abe (2000), Dias and Souza (2005), and Martins et al. (2010) showed that plant material was substantially less frequent (28.1%, 10.7%, and 2.6%, respectively) and occurred in much lower volumes (1.7% in Souza and Abe [2000], 1.2% in Martins et al. [2010]). We instead observed a high frequency of occurrence and high portion of the volume represented by plant material. Fachin-Teran et al. (1995) also found that plant matter, represented by seeds and fruits of legumes (35.6%V), was one of the principal dietary groups consumed by *P. geoffroanus* in the Guapore River in Rondonia State in Brazil.

The most important item in *P. geoffroanus* diet in Peru was Libellulidae larvae (IRI = 44.78) with the presence in most of the stomach contents of the turtles (80%) and represented the majority portion of the sample volume (37.5%). Fachin-Teran et al. (1995) also found Libellulidae larvae to be a very frequent item in *P. geoffroanus* stomach contents in a similar Amazonian habitat. We are not sure at this time if Libellulidae larva is a preferred item or its elevated consumption is a reflection of high availability of this resource in our study area. Future studies should focus on evaluating resource availability and diet preferences in Amazonian freshwater turtles.

Fishes were commonly consumed by *P. geoffroanus* in Colombia (Medem 1960) and in northern Brazil (Fachin-Teran et al. 1995). In the present study, we recorded scales of fish in only one turtle, and it was probably eaten as carrion. The gastropod *Biomphalaria anatinus* has been found in 60% of the stomachs in our study site. Gastropods were also recorded but to a lesser extent in the diet of *P. geoffroanus* in polluted urban rivers (1.8%F and 2.6%F) (Souza and Abe 2000; Martins et al. 2010) and in Parana River (17.9%F) (Dias and Souza 2005). Our results are additional evidence of the opportunistic and omnivorous feeding habits of *P. geoffroanus* because the species diet drastically shifts according to the habitat within which it lives (Medem 1960; Fachin-Teran et al. 1995; Souza and Abe 2000; Dias and Souza 2005; Martins et al. 2010).

Captive *M. gibba* are known to feed almost exclusively on animal prey (Pritchard and Trebbau 1984). Fretey (1977) reported that captive individuals fed on live frogs, worms, and pieces of red meat, and Mittermeier et al. (1978) also observed that captive *M. gibba* consumed fish, meat, insects, dog food, and newborn mice, but sometimes would ingest plant matter (leaves of *Colocacia* sp). Our investigation shows that wild *M. gibba* is an omnivorous species, because animal and plant matter were ingested by all individuals captured (23.7%V and 47.6%V, respectively). *Mesoclemmys gibba* has eaten insects, fish, and crustaceans, in addition to unidentified plant matter, bark, leaves, stems, and algae, plant matter was more representative by frequency and sample volume. The presence of sediment in one stomach, which represented 28.6% of the volume, shows that the species can feed in the bottom of the oxbow lakes. In Rio Negro Basin, in northern Brazil, *M. gibba* has been found to feed almost exclusively on palm fruits during part of the year, which could be due to a more scattered distribution of aquatic animal prey when the forest was flooded (R.C. Vogt, *pers. obs.* in Caputo and Vogt 2008). We suggest future investigation on ontogenetic and seasonal variation in *M. gibba* diet to better understand its feeding habits.

Food partitioning has been observed in Neotropical turtle communities, in different systems, and with various species (Vogt and Guzman 1988; Fachin-Teran et al. 1995; Alcalde et al. 2010). Some reasons for partitioning could be due to specialized feeding habits of some species (e.g., *Mesoclemmys raniceps* is a mollusk specialist and *Chelus fimbriatus* is a fish specialist [Fachin-Teran et al. 1995]) in addition to differences in foraging strategies and microhabitat use (Vogt and Guzman 1988). In the present study, we observed low dietary overlap between *P. unifilis* and *P. geoffroanus* (CH = 0.368). Although both species tend to have a generalist diet, *P. unifilis* fed on a large variety of items compared with *P. geoffroanus*, and the former preferred seeds and bark, contrary to *P. geoffroanus*, which fed largely on Libellulidae larvae and unidentified plant material.

Dietary overlap was observed in our investigation between *P. geoffroanus* and *M. gibba* (CH = 0.512) and *P. unifilis* and *M. gibba* (CH = 0.456). The 3 turtle species shared some food items in our study site (insects: Libellulidae; plant material: Fabaceae leaf, unidentified plant material), but only crustaceans (Ostracoda) and some insects (Tenebrionidae and Culicidae) were found in diets of both *P. geoffroanus* and *M. gibba*. Fish (*Leporinus* sp. and *Hoplias malabaricus*) and bark were overlapped by *P. unifilis* and *M. gibba*. However, the food overlap results could be partially inflated because we captured few *M. gibba* ($n = 4$), and a food item eaten by one individual represents 25% of frequency of occurrence. We suggest future investigation, with a larger sample size to verify the degree of niche overlap between these species in Amazonian habitats.

Our results demonstrate that the 3 freshwater turtles have generalist feeding habits in consuming both plant and animal matter, although they differ in some of the items consumed. This pattern fits with other descriptions of turtle diets, where, although there is a tendency of these species to consume specific items, they also are opportunists by taking advantage of local availability of food items (Souza 2004). To our knowledge, this is the first quantitative diet study of Peruvian freshwater turtles, in addition is the first quantitative description of *M. gibba* diet for the Amazon basin.

Acknowledgments

We would like to thank F. L. Souza for suggestions on the structure of this manuscript; S. Rosse, T. S. Marques, and R. Benrhard for helping with literature; and the editor J. Seminoff for his comments and contributions of this article. We are in debt to the people who helped in food items identification: P. Huamán Maita (mollusks and crustaceans), R. Zuñiga Acosta (fungus), M. Gonzales de la Cruz and A. Daza (plant material), R. Quispe Chuquihuamaní (fish), D. Lopez and I. Samanes (algae), and D.C. Sanchez (insects). Special thanks to native people from Santa Rosa de Chivis. The ''Amazon Turtles Ecology Project'' was supported by Rufford Small Grant Foundation (ref.03.01.09), and Cleveland Metroparks Zoo and Cleveland Zoological Society Foundation grants. Turtles were captured under Ministerio de Agricultura scientist collect permit (no. 0057-2009-AG-DGFFS-DGEFFS).

LITERATURE CITED

Alcalde, L., Derocco, N.N., and Rosset, S.D. 2010. Feeding in syntopy: diet of *Hydromedusa tectifera* and *Phrynops hilarii* (Chelidae). Chelonian Conservation and Biology 9:33–44.

Almeida, S.S., Sa, P.G.S., and Garcia A. 1986. Vegetais consumidos como alimento por *Podocnemis* (Chelonia) na região de Baixo Rio Xingu (PA). Bulletin Museum Paraense Emilio Goeldi 2:199–211.

Balensiefer, D.C. and Vogt, R.C. 2006. Diet of *Podocnemis unifilis* (Testudines, Podocnemididae) during the dry season in the Mamiraua Sustainable Development Reserve, Amazonas, Brazil. Chelonian Conservation and Biology 5:312–317.

Belkin, D.A. and Gans, C. 1968. An unusual chelonian feeding niche. Ecology 49:768–769.

Beyer, W.N., Connor, E.E., and Gerould, S. 1994. Estimates of soil ingestion by wildlife. The Journal of Wildlife Management 58:375–382.

Bjorndal, K. 1991. Diet mixing: nonadditive interactions of diet items in an omnivorous freshwater turtle. Ecology 72:1234–1241.

Bjorndal, K., Bolten, A.B., Lagueux, C.J., and Jackson, D.R. 1997. Dietary overlap in three sympatric congeneric freshwater turtles (*Pseudemys*) in Florida. Chelonian Conservation and Biology 2:430–433.

Bonino, M.F., Lescano, J.N., Haro, J.G., and Leynaud, G.C. 2009. Diet of *Hydromedusa tectifera* (Testudines-Chelidae) in a mountain stream of Corboda province, Argentina. Amphibia-Reptilia 30:545–554.

Brand-Gardner, S.J., lanyon, J.M., and Limpus, C.J. 1999. Diet selection by immature green-turtles, *Chelonia mydas*, in subtropical Moreton Bay, south-east Queensland. Australian Journal of Zoology 47:181–191.

Buhlmann, K.A., Akre, T.S.B., Iverson, J. B., Karapatakis, D., Mittermeier, R.A., Georges, A., Rhodin, A.G.J., van Dijk, P.P., and Gibbons, J.W. 2009. A global analysis of tortoise and freshwater turtle distributions with identification of priority conservation areas. Chelonian Conservation and Biology 8:116–149.

CAGLE, F.R. 1939. A system of marking turtles for future identification. Copeia 1939:170–173.

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

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

DURANTI, M. AND GIUS, C. 1997. Legume seeds: protein content and nutritional value. Field Crops Research 53:31–45.

ERNST, C.H. AND BARBOUR, R.W. 1989. Turtles of the World. Washington, DC: Smithsonian Institution Press, 313 pp.

FACHIN-TERAN, 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.

FERRONATO, B.O. AND MORALES, V.M. 2012. Biology and conservation of the freshwater turtles and tortoises of Peru. IRCF Reptiles & Amphibians: Conservation and Natural History 19:103–116.

FERRONATO, B.O., MARQUES, T.S., SOUZA, F.L., VERDADE, L.M., AND MATUSHIMA, E.R. 2009. Oral bacterial microbiota and traumatic injuries of free-ranging *Phrynops geoffroanus* (Testudines, Chelidae) in southeastern Brazil. Phyllomedusa 8:19–25.

FRETEY, J. 1977. Les cheloniens de Guyane francaise. I. Etude preliminaire. Thesis, University of Paris, Paris, France, 201 pp.

GAVIRIA, A. 1981. La fauna silvestre y su aprovechamiento por las comunidades campa del río Pichis. Revista Forestal del Perú 10:192–201.

GODBOLD, J.A., ROSENBERG, R., AND SOLAN, M. 2009. Species-specific traits rather than resource partitioning mediate diversity effects on resource use. PLoS ONE 4:e7423.

GODLEY, B.J., THOMPSON, D.R., WALDRON, S., AND FURNESS, R.W. 1998. The trophic status of marine turtles as determined by stable isotope analysis. Marine Ecology Progress Series 166: 277–284.

KREBS, C.J. 1999. Ecological Methodology. Second edition. Menlo Park, CA: Addison-Welsey Eucational Publishers, 620 pp.

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

LUISELLI, L. 2006. Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. Oikos 114:193–211.

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

MARTINS, F.I., SOUZA, F.L., AND COSTA, H.T.M. 2010. Feeding habits of *Phrynops geoffroanus* (Chelidae) in an urban river in Central Brazil. Chelonian Conservation and Biology 9:294–297.

MEDEM, M.F. 1960. Observaciones sobre la distribución geográfica y ecología de la tortuga *Phrynops geoffroanus* spp. en Colombia. Informe sobre reptiles Colombianos (V). Novedades Colombianas 1:291–300.

MEDEM, M.F. 1964. Morphologie, okologie und verbreitung der schildkrote *Podocnemis unifilis* in Kolumbien. In: Pritchard, P.C.H. and Trebbau, P. (Eds.). The Turtles of Venezuela. Contributions to Herpetology 2. Athens, OH: Society for the Study of Amphibians and Reptiles, 403 pp.

MITTERMEIER, R.A., RHODIN, A.G.J., MEDEM, F., SOINI, P., HOOGMOED, M.S., AND CARRILLO, N.E. 1978. Distribution of the South American Chelidae turtle *Phrynops gibbus*, with observation on habitat and reproduction. Herpetologica 34:94–100.

MOLINA, F.B. 1990. Observações sobre os hábitos e o comportamento alimentar de *Phrynops geoffroanus* (Schweigger, 1812) em cativeiro (Reptilia, Testudines, Chelidae). Revista Brasileira de Zoologia 7:319–326.

MOLL, E.O. AND LEGLER, J.M. 1971. The life story of a neotropical slider turtle, *Pseudemys scripta* (Schoepff) in Panama. Bulletin of the Los Angeles County Museum of Natural History Science 11:1–102.

NAGAOKA, S.M., MARTINS, A.G., SANTOS, R.S., TOGNELLA, M.M.P., FILHO, E.C.O., AND SEMINOFF, J.A. 2012. Diet of juvenile green turtles (*Chelonia mydas*) associating with artisanal fishing traps in a subtropical estuary in Brazil. Marine Biology 159:573–581.

PIÑA, C.I., LANCE, V.A., FERRONATO, B.F., GUARDIA, I., MARQUES, T.S., AND VERDADE, L.M. 2009. Heavy metal contamination in *Phrynops geoffroanus* (Schweigger, 1812) (Testudines: Chelidae) in a River Basin, São Paulo, Brazil. Bulletin of Environmental Contamination and Toxicology 83:771–775.

PORTAL, R.R., LIMA, M.A.S., LUZ, V.L.F., BATAUS, Y.S.L., AND REIS, I.J. 2002. Espécies utilizadas na alimentação de *Podocnemis unifilis*, Troschel 1948 (Reptilia, Testudinidae, Pelomedusidae) na região do Pracuuba – Amapá-Brasil. Ciência Animal Brasileira 3:11–19.

PRITCHARD, P.C.H. AND TREBBAU, P. 1984. The Turtles of Venezuela. New York: Society for the Study of Amphibians and Reptiles, 403 pp.

ROCHA, A.A.F., SANTOS, N.C.L., PINTO, G.A., MEDEIROS, T.N., AND SEVERI, W. 2011. Diet composition and food overlap of *Acestrorhynchus britskii* and *A. lacustris* (Characiformes: Acestrorhynchidae) from Sobradinho reservoir, Sao Francisco river, Bahia State. Acta Scientarum. Biological Sciences 33: 407–415.

RUEDA-ALMONACID, J.V., CARR, J.L., MITTERMEIER, R.A., RODRÍGUEZ-MAHECHA, J.V., MAST, R.B., VOGT, R.C., RHODIN, A.G.J., DE LA OSSA-VELÁSQUEZ, J., RUEDA, J.N., AND MITTERMEIER, C.G. 2007. Las tortugas y los cocodrilianos de los países andinos del trópico. Serie de guías tropicales de campo N°6. Conservación Internacional. Colombia: Editora Panamericana, Formas e Impresos, 538 pp.

SOTELO, A., CONTRERAS, E., AND FLORES, S. 1995. Nutritional value and content of antinutritional compounds and toxics in ten wild legumes of Yucatan Peninsula. Plant Foods for Human Nutrition 47:115–123.

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

SOUZA, F.L. AND ABE, A.S. 1998. Resource partitioning by the Neotropical freshwater turtle, *Hydromedusa maximiliani*. Journal of Herpetology 32:106–112.

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

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, S.G. 1988. Food partitioning in a Neotropical freshwater turtle community. Copeia 1988: 37–47.

Received: 3 June 2011

Revised and Accepted: 21 September 2012

Handling Editors: Anders G.J. Rhodin and Jeffrey A. Seminoff