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Diet of *Podocnemis unifilis* (Testudines, Podocnemididae) During the Dry Season in the Mamirauá Sustainable Development Reserve, Amazonas, Brazil

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ABSTRACT. – **Stomach contents of *Podocnemis unifilis* sampled in white water *varzéa* forest during the dry season in the Mamirauá Sustainable Development Reserve (Middle-Solimões River) had plant material in 100% of cases, with Poaceae and Bombacaceae the most frequently recorded. Poaceae leaves (67.7% frequency) and seeds (21.5% frequency) were common, as were fibers of the fruit *Pseudobombax munguba* (Bombacaceae; 38.5% frequency), with fruits in general contributing 45.9% of volume. Animal material was consumed in much lesser quantities—only 0.8% of total volume—but had a 37% frequency.**

Ontogenetic changes and sexual differences in the composition of the turtle diet have been noted for some species of turtles (Graham 1971; Plummer and Farrar 1981; Hart 1983; Bury 1986; Moll 1990). The influence of age is perhaps due to changes in the physiological needs of the turtles, with an ontogenetic change from animal to plant matter. Smaller turtles often need to assimilate animal protein rich in calcium and proteins to allow them to grow rapidly (Hart 1983). As the turtle grows, energy restrictions may partially explain why they reduce the intake of animal prey. Small turtles, having less mass, spend less energy searching for prey compared to larger individuals (Parmenter and Avery 1990), and the return obtained from small prey does not make up for the energetic cost for obtaining them (Georges 1982).

The influence of sex on variation in diet might be related to distinct physiological needs between males and females. Ramo (1982), studying *Podocnemis vogli* in Venezuela, found that males fed mainly on plant matter, while females fed more on mollusks and fish, and that this difference may have been due to calcium requirements for the formation of eggs. However, this remains hypothetical for turtles.

Podocnemis unifilis is widely distributed throughout the Amazon Basin in rivers and lakes, making it an important protein source for local inhabitants. There is marked sexual dimorphism, with females reaching 46.5 cm in carapace length and males 33.5 cm (Pritchard and Trebbau 1984). Previous studies on the diet of *P. unifilis* have been conducted in the wild (Medem 1964; Smith 1979; Almeida et al. 1986; Portal et al. 2002), in captivity (Acosta et al. 1995; Malvasio et al. 2003), and in black water habitat (Fachín et al. 1995). However, no study has focused on possible ontogenetic and sexual shifts in the diet of this species in *várzea* habitat (white water flooded forest). This was the aim of our study.

Methods. — We studied *P. unifilis* in the dry season in the Mamirauá Sustainable Development Reserve (MSDR). The MSDR is located on the floodplain between the Middle-Solimões and Japurá rivers, near Tefé, Amazonas, Brazil, covering an area of 1,124,000 ha. Being inundated by white water rivers, the forest in the MSDR is classified as *várzea*. The main characteristic of this environment is seasonal variation in water levels (Junk et al. 1989), associated with high loads of suspended and dissolved fertile matter (Junk 2000), allowing the production of large amounts of macrophytes, with the predominant species in the MSDR being *Paspalum repens*, *Echinochloa polystachya*, *Eichhornia crassipes*, *Pistia stratiotes*, and *Salvinia* spp. (Cramptom 1999).

The wet season in the region extends from December to March, with the mean annual rainfall more than 2500 mm for Tefé. Temperature is practically constant year round; the daily average in 1984 was 29.5°C (Sociedad Civil Mamirauá 1996). Our study was undertaken in the Jarauá sector of the MSDR, located at 2°51′S, 64°55′W. Sampling included 15 lakes and 5 *ressacas* (portions of river channels that dry up or have their surfaces totally covered by macrophytes during the dry season).

We captured turtles in the dry season from September to December 2001. Turtle populations are more concentrated during the dry season than wet season, when animals are dispersed in the high waters of the flooded forest. We captured turtles using trammel nets; in each site, we used 430 m^2 of netting, corresponding to 2 trammel nets 82-m long and 2.65-m high each. The mesh size of the inner net was either 10 or 20 cm between knots, which allowed the capture of mid-size and large turtles. We

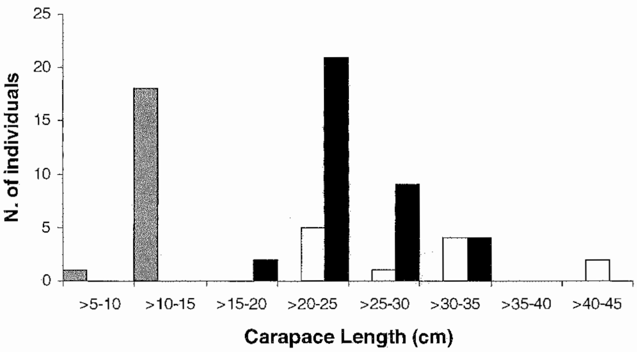

Figure 1. Number of individuals of *P. unifilis* sampled per size class (SLC). Gray = subadults, black = males, white = females.

Table 1. Description of groups of food items found in the stomach contents of *Podocnemis unifilis* ($n = 65$) during the dry season in the Jarauá sector of Mamirauá Sustainable Development Reserve in 2001.

Groups	Frequency	F (%)	Volume (ml)	V (%)
Unidentified plant matter	65	100	57.73	15.15
Leaf	53	81.5	50.99	13.38
Flower	16	24.6	1.98	0.52
Fruit	33	50.8	174.92	45.91
Seed	40	61.5	13.64	3.58
Stem	12	18.5	0.96	0.25
Root	10	15.4	0.05	0.01
Algae	4	6.1	3.21	0.84
Bryophythe	1	1.5	0.02	0.01
Plant total	65	100	303.5	79.65
Unidentified animal matter	2	3.1	1.01	0.27
Anthropod	22	33.8	0.69	0.18
Fish	3	4.6	1.15	0.3
Sponge	2	3.1	0.05	0.01
Animal total	24	37	2.9	0.76
Sediment	11	17	57.33	15.05
Not identified matter	64	98.5	17.3	4.54
Total	65	100	381.03	100

deployed nets for 30 hours for the first 12 sites and 9 daylight hours for the remaining sites, checking nets every 3 hours; we modified our methodology due to insignificant captures after sunset. For each individual captured, we recorded straight-line carapace length (SCL) and mass. We marked the turtles utilizing a marginal notching system adapted from Cagle (1939). We designated all turtles less than 15 cm in SCL as indeterminate sex subadults; turtles larger than 15 cm SCL were sexed based on external characteristics.

We flushed stomach contents of the turtles using the methodology of Legler (1977). Pérez-Eman and Paolillo (1997) demonstrated the efficiency of this method while working with *Peltocephalus dumerilianus*. We used plastic tubing of 3- and 5-mm diameter, and syringes of 5 and 35 ml for subadults and larger turtles, respectively, sampled stomach contents usually within 2 hours after capture of the turtles, and stored the contents in 40% alcohol. We released the turtles at the site of capture after stomach flushing.

We sorted and classified food items to the lowest possible taxon with the aid of a stereo microscope. Plant groups were sorted into leaves, flowers, fruits, seeds, stems, roots, algae, bryophytes, and unidentified; animal groups into arthropods, fish, sponges, and unidentified. Rocks and earth were grouped as sediments. For each turtle captured, we measured the volume of food items with graduated syringes precise to the nearest 0.01 ml. For each food group, we registered frequency of occurrence and volume of these categories in all individuals.

We analyzed the relationship between the volume of plant and animal matter and SCL of the captured individuals to determine whether ontogenetic shifts occurred in the diet. We used linear regression to analyze whether the animal and plant matter volumes were related, because if there is an ontogenetic effect on the diet of *P. unifilis*, there would be a negative correlation between these 2 categories. Items not identified as plant, animal, or sediment represented less than 5% of the total (see results), and were not included in the analysis.

We used Hybrid Multidimensional Scaling (HMDS) to determine whether differences existed among subadults, males, and females regarding volume and variety of items consumed. The HMDS was carried out using the PATN software (Belbin 1992). We used the ratio between the volume of each group item and SCL for each individual as the variable for volume to eliminate the influence of turtle size in the analysis among sexes. We used transformed standardized values for each food group through division by the sum (per column) to avoid the problem of categories with more volume having more influence in the results than those with less. We used Euclidean distance to build a dissimilarity matrix among the individuals according to the volumes of the different food categories and then a HMDS was undertaken, reducing the matrix to 2 dimensions. We used HMDS with information about the presence or absence of the different food categories for each turtle to test the differences in the variety of items consumed. The axes created for the HMDS were utilized as dependent variables when testing for effect of sex on the diet in a MANOVA.

The differences between the sexes (excluding subadults) for a particular food category were analyzed by ANOVA, utilizing the ratio between the volume of each food category and the SCL to eliminate the effect of size differences between individuals.

Results. — We captured 67 *P. unifilis*: 19 (28.4%) were subadults, 36 (53.7%) were males, and 12 (17.9%) were females. The SCL and mass were 12.6 ± 1.2 cm (9.8–14.8) and 310 ± 78 g (160–465) for subadults, 24.9 ± 3.3 cm (15.5–31.0) and 1809 ± 720 g (500-3175) for males, and 30.3 ± 7.8 cm (22.5–44.4) and 4160 ± 3515 g (1370–12,000) for females (Fig. 1).

The total volume of stomach flushings of 65 individuals (2 turtles had empty stomachs) yielded 79.6% plant material, 0.8% animal material, 15.1% sediment (pebbles and clay soil), and 4.5% unidentifiable

Table 2. Animals recorded in the diet of *P. unifilis* (from Table 1).

Animal category	Order	Family	F (%)
Sponges	—	—	2 (3.1)
Insects	—	—	6 (9.2)
	Coleoptera	—	2 (3.1)
	Coleoptera	Curculionidae	2 (3.1)
	Coleoptera	Hydrophilidae	2 (3.1)
	Coleoptera	Scolytidae	1 (1.5)
	Diptera	—	2 (3.1)
	Diptera	Brachycerae	1 (1.5)
	Diptera	Ceratopogonidae	1 (1.5)
	Diptera	Chironomidae	2 (3.1)
	Diptera	Culicidae	1 (1.5)
	Diptera	Sciaridae	2 (3.1)
	Diptera	Psychodidae	2 (3.1)
	Diptera	Tabanidae	2 (3.1)
	Ephemeroptera	—	1 (1.5)
	Ephemeroptera	Polymitarcidae	1 (1.5)
	Hemiptera	—	2 (3.1)
	Hemiptera	Corixidae	1 (1.5)
	Hymenoptera	—	2 (3.1)
	Hymenoptera	Formicidae	4 (6.1)
	Hymenoptera	Vespidae	1 (1.5)
	Lepidoptera	—	1 (1.5)
	Orthoptera	—	2 (3.1)
	Plecoptera	Perlidae	2 (3.1)
Spider mites	—	—	3 (4.6)
Spiders	—	—	1 (1.5)
Crustaceans	Conchostraca	—	1 (1.5)
Fish	Characiformes	—	1 (1.5)
	Perciformes	Cichlidae	2 (3.1)
	Siluriformes	—	1 (1.5)
	Siluriformes	Loricariidae	1 (1.5)

Table 3. Plants recorded in the diet of *P. unifilis* (from Table 1).

Plant category	Family	Species	F (%)
Leaves	Araceae	*Pistia* sp.	1 (1.5)
	Azzolaceae	*Azzola* sp.	3 (4.6)
	Melastomataceae	—	1 (1.5)
	Poaceae	—	44 (67.7)
	Pontederiaceae	*Eichhornia* sp.	1 (1.5)
	Salviniaceae	*Salvinia* sp.	2 (3.1)
Flowers	Araceae	*Pistia* sp.	1 (1.5)
	Leguminosae	—	1 (1.5)
	Myrtaceae	—	1 (1.5)
	Sapindaceae	*Toulisia* sp.	1 (1.5)
Seeds	Asteraceae	—	5 (7.7)
	Euphorbiaceae	*Phyllanthus* sp.	4 (6.1)
	Mimosaceae	—	3 (4.6)
	Moraceae	—	1 (1.5)
	Poaceae	—	14 (21.5)
	Polygonaceae	—	1 (1.5)
Algae	Desmidiaceae	—	4 (6.1)
Bryophythe	—	—	1 (1.5)

(Table 1). Animal material (fish, arthropods, sponges, unidentifiable) occurred in 37% of the individuals. The fish parts identified were Siluriformes, Characiformes, and Perciformes (Table 2). Parts of the arthropods were identified as insects, spider mites, spiders, and crustaceans. Sponges were found in 3.1% of individuals sampled. Plant material was found in all stomach contents sampled (Table 1). Only 15.2% of the plant material was unidentifiable. Leaves, seeds, and fruits occurred most frequently; in 81.5, 61.5, and 50.8% of the samples, respectively. Fruits from 4 families of plants (Bombacaceae, Leguminosae, Myrtaceae, Sapindaceae) made up the largest volume of plant material consumed (45.9%). Fibers from the fruit of *Pseudobombax munguba* (Bombacaceae) were found in 38.5% of turtles sampled.

A large portion of plant material was macerated and partially digested, with only 15.4% of the leaves identified to family (Table 3). Poaceae occurred in 67.7% of the turtles, with other plant families apparently contributing less than 5% per family. We found 50 different seed varieties, but only 12% were identified to family, of which the most frequent was Poaceae (21.5%), followed by Asteraceae (7.7%), and Euphorbiaceae (6.1%). Flowers represented 0.52% of the total volume with a 24.6% frequency of occurrence.

Nematodes were found in 90.8% of individuals sampled, with the most frequent being *Goezia* sp. (Heterocheilidae). We also found different stages of *Atractis* spp. (Atractidae) (Thatcher 1991; Vicente et al. 1993).

The volume of plant material was significantly related to the SCL ($r^2 = 0.09$; $F_{1.63} = 6.223$; $p = 0.015$). Because this value was low (the size of the individual turtles explained less than 10% of the variance in the volume of plants consumed), we ran a simple linear regression (excluding subadults) to test this relationship. Results showed that the size of the turtles did not affect the amount of plant material consumed ($r^2 = 0.027$; $F_{1.45} = 1.25$; $p = 0.27$), and the former result could have occurred because larger individuals—with proportionately larger stomachs—have a larger volume of stomach contents compared to smaller individuals. Size of the turtles did not affect the volume of animal material consumed ($r^2 = 0.001$; $F_{1.63} = 0.087$; $p = 0.769$). There was no significant relationship between the volumes of plant and animal materials consumed by these turtles ($r^2 = 0.054$; $F_{1.63} = 3.628$; $p = 0.061$).

The HMDS for the volumes consumed demonstrated no apparent differences in the volume of each category consumed by subadults, males, and females. There were no sexual differences in volume of diet (MANOVA; $F_{4.122} = 0.11$; $p = 0.979$) (ANOVA; $p > 0.05$; $n = 47$). However, when the HMDS was tested for the variety of items consumed, we found a significant difference among the diets of subadults, males, and females (MANOVA; $F_{4.122} = 6.73$; $p = 0.000$).

Discussion. — Plant material was found in all *P. unifilis* stomachs that had some food, and comprised 79.6% of the total volume. This is similar to the results of Fachín et al. (1995) in the Guaporé River, a black water river in Rondônia, Brazil, where plant material represented 89.5% of the volume consumed by *P. unifilis*. Other qualitative studies in different parts of the range of *P. unifilis* (Medem 1964; Smith 1979; Almeida et al. 1986; Malvasio et al. 2003) have also noted the importance of plants in its diet. The food categories most frequently eaten were leaves and seeds of the family Poaceae, indicating that *P. unifilis* in this study were utilizing the banks of macrophytes (that border the lakes and *ressacas* during the dry season) as a food source. This is corroborated by the presence of leaves of *Azzola* sp., *Eichhornia* sp., *Salvinia* sp., and *Pistia* sp. in the stomach contents of some individuals; these plants are floating macrophytes that make up part of the banks of floating meadows. Fruit production is low during the dry season in the *várzea*, with most trees fruiting during high water season as an adaptation for aquatic seed dispersal and also dispersal by migrating fish (Gottsberger 1978; Kubitzki and Ziburski 1994), and possibly turtles. The low availability of fruit during the dry season in the *várzea* probably influenced the low frequency of fruit we observed in relation to that of leaves and seeds, which contrasted with Fachin et al. (1995), who found that fruits and seeds were items most frequently found in the diet of *P. unifilis* in both the dry and wet seasons in the Guaporé River.

Although fruit did not have a high frequency, it had the highest volume of all food consumed by *P. unifilis*. Fiber from the fruit of *Pseudobombax munguba* was found in 38.5% of the turtles and accounted for much of the volume. This fiber is used in the wind dispersal of the seeds, and floats on the surface of the water for several days (Worbes 1997). During our sampling period, the water surface in some lakes was covered with a blanket of these fibers. The seed of *P. munguba* is small, but rich in protein and fats (Waldhoff and Maia 2000).

Food of animal origin had a low volume (0.8%), but the frequency occurrence of these items (37%) and the difference found among the variety of food items consumed by subadults, males, and females indicate that *P. unifilis* is a dietary generalist, consuming a wide diversity of food items—many of which are eaten in low quantities. Malvasio et al. (2003) studied the behavior and food preferences of *P. unifilis* in captivity, noting that this species will eat both plant and animal material throughout its life stages.

Many species of insects identified were Hymenoptera and terrestrial Diptera (Borror et al. 1989; Merrit and Cummins 1996). When these insects fall into the water, they probably remain on the surface and are ingested by the turtles using neustophagia (Belkin and Gans 1968; Rhodin et al. 1981), which is also probably the method of consumption of the floating fibers of *Pseudobombax*. In some lakes, we observed turtles floating on the surface with only the point of their nostrils above the water surface, suggesting that they may be feeding in this manner as reported in captivity (Legler 1976). The sieves used to collect and filter the stomach contents of the turtles had holes too large to retain most of these small insects. Future studies should concentrate on collecting these small particles. The aquatic arthropods found in the stomach contents could have been eaten along with leaves and roots when the turtles were foraging in the floating meadows. These floating mats of plants offer protection and food for both larvae and adult insects, making these mats the most species-rich biotope in the margins of the *várzea* forest (Junk 1976).

Consumption of small, live, moving prey by large turtles does not have a positive cost–benefit relationship (Parmenter and Avery 1990). The energy expended on capturing the small prey found in these *P. unifilis* could not be compensated by the few calories obtained. However, Bjorndal (1991) demonstrated that a mixed diet of animal and plant protein had higher usable nutritional value, greater than that of a diet composed of purely plants or animals. It could be that *P. unifilis* is obtaining this nutritional benefit without expending any extra energy by ingesting these small arthropods along with the plant material.

The parts of fish we found (scales and vertebrae) were from large fish, suggesting that the turtles were feeding on carrion. The turtles may have consumed these fragments when foraging along the bottom. There was no evidence that they were feeding on fresh-caught fish in the trammel nets.

A factor that aids turtles in the efficiency of digesting and assimilating plant material is the presence of nematodes in the digestive tracts (Bjorndal and Bolten 1990). The presence of nematodes in 90.8% of the turtles indicated the possibility that these are commensals important in digestion.

We did not find any ontogenetic differences in the diet of *P. unifilis* during the dry season in MSDR. Clark and Gibbons (1969) found that *Trachemys scripta* changed from a diet of animals to a plant diet in the second year of growth. The smallest subadults we captured were probably in their third or fourth growing season, therefore, if ontogenetic changes occur during the first years of life of *P. unifilis*, they could not be demonstrated in our study. However, Fachín et al. (1995) found a significant negative relationship between the consumption of animals and the carapace length of *P. unifilis* in the Rio Guaporé, despite the smallest animals in their study having a carapace length greater than 10 cm.

We did not find a difference between males and females in the volume of different food items consumed. Fachín et al. (1995) found that females of *P. unifilis*, in a black water river, consumed more fruits and seeds than males. The differences between these populations could be the result of the availability of resources at the 2 localities or the effect of different collecting seasons. *Peltocephalus dumerilianus* was not found to have any sexual dietary differences (Pérez-Eman and Paolillo 1997). The presence of pebbles and soil (15% by volume) might suggest that the turtles are obtaining trace minerals not available in plants (Moll and Legler 1971), or the material could be ballast or just incidental take associated with bottom feeding.

We conclude that *P. unifilis* is a dietary generalist, consuming resources abundantly available locally, suggesting that food is not a limiting factor in this population. This characteristic allows a species to recuperate more rapidly if human-threat factors that affect populations—

such as consumption of adults and eggs—can be curtailed, and the turtles allowed to feed, grow, and reproduce.

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Claw Function of Hatchling and Adult Red-Eared Slider Turtles (*Trachemys scripta elegans*)

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ABSTRACT. – **We examined variation in claw length of hatchling and adult red-eared slider turtles (*Trachemys scripta elegans*). Hind claw length of adult females was greater than that of adult males, and we suggest that increased hind claw length in females (a previously unrecognized sexually dimorphic trait) may serve as an adaptation for nest construction. In addition, front and hind claws of hatchlings newly emerged from their eggs were longer than the front and hind claws of hatchlings that were captured during their migration toward aquatic habitats; relatively long claws could aid hatchlings in their escape from nests and migration to aquatic habitats.**

The function of claws can vary dramatically among and within turtle species. For example, the strong claws and forearms of several tortoise species (e.g., *Gopherus polyphemus*) are uniquely adapted for burrowing (Auffenberg 1966). Claws are often used to tear apart food when feeding and are sometimes used in courtship behaviors of many freshwater turtles (i.e., *Graptemys* species; Cagle 1948; Gibbons and Lovich 1990; Legler 1990). The number of claws can also vary geographically within a species (e.g., *Terrepene carolina*; Milstead 1969; Minx 1992).

Claws may also perform functions unique to each life history stage of the animal. For instance, hatchlings of the red-eared slider use their front claws to open the egg at hatching (Ewert 1979; Tucker 1995) and to dig out of nest cavities in the spring after overwintering (Tucker 1997, 1999a; Tucker and Packard 1998). As adults, female sliders use their hind feet and claws to dig nests, sometimes in extraordinarily hard-packed substrates such as gravel road shoulders (Tucker 1999b). Adult males often use their elongated front claws during courtship behaviors (Thomas 2002), and foreclaws are sometimes used by females during courtship as well (Lovich et al. 1990).

This variation in the function of claws prompted us to investigate several questions relating to adult sex differences and ontogenetic changes in claw morphology of the red-eared slider turtle. First, we asked whether the claws of newly hatched turtles in autumn differed from hatchlings caught in the spring after their migration from nests toward aquatic habitats. We expected that the front claws of newly hatched turtles would be longer than those of turtles whose claws had been worn during hatching and digging out of their nests. Secondly, we asked if the rear claws of adult females differed from those of adult males, considering that males do not construct nest cavities, and thus do not use their hind claws in this manner. We expected that hind claws of females would be longer than those of males, reflecting an adaptation for efficient nest construction by