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Feeding habits of *Mesoclemmys vanderhaegei* (Testudines: Chelidae)

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Abstract. We studied the feeding habits of *Mesoclemmys vanderhaegei* in small water bodies in the central region of the Brazilian Cerrado. We captured 80 individuals, 79 of which [41 (52%) females, 27 males (34%), 11 (14%) juveniles] had stomach contents for analysis. We identified 64 food item categories. The turtles were eating more animal than plant material, aquatic invertebrates being the most conspicuous diet item found. Plant material was more abundant in females and rare in the diet of juveniles. *Mesoclemmys vanderhaegei* proved to be an omnivorous and opportunistic chelonian, feeding on a wide range of food items. Although there are differences in the consumption of food items among sexes and age categories, the most consumed food categories were common in all water bodies sampled.

Keywords. Cerrado ecoregion, diet, food habits, foraging ecology, freshwater turtle, prey items, stomach contents, stomach flushing.

INTRODUCTION

Studies of freshwater turtle trophic ecology have shown that feeding habits in populations of the same species vary with the availability of food, life stage, sex, presence of other species of turtles (Moll, 1976; Vogt, 1980; Fachín-Terán et al., 1994; Fachín-Terán et al., 1995), habitat type and seasonality, among other factors (Moll and Moll, 2000).

Diet is one of the most often-discussed aspects of turtle natural history (Souza, 2004). Freshwater turtles in the family Chelidae are generally considered omnivorous (Souza, 2004), and ontogenetic dietary shifts are known in some species (e.g., Bouchard and Bjorndal, 2006). Variations in the diet of turtles in relation to size and sex appear to be important to avoid niche overlap and intraspecific competition (Fachín-Terán et al., 1995; Souza and Abe, 1998).

Although some aquatic turtles possess a general morphology and behavior patterns adapted for carnivory, a variety of plant items are also regularly consumed, including stems, flowers, leaves and fruit (Moll and Moll, 2004). Entirely or primarily carnivorous species can consume items ranging from zooplankton and a large number of aquatic and non-aquatic invertebrates to vertebrates (Moll and Moll, 2004).

Studies on feeding habits of turtles may involve direct observation (focal animal method, see Sabino, 1999), analysis of stomach contents (Legler, 1977) and/or fecal material (Caputo and Vogt, 2008) from live or preserved specimens. Knowledge of the composition and variation in diet and feeding habits across different species can underpin broad ecological and evolutionary studies, as well as aid conservation and management planning (Souza, 2004). Human interference (e.g., trash, offering of arti-

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ficial food, impoundments) may cause important changes in the diet of free-living aquatic organisms, as reported by Sabino et al. (2005), who found "obese" fish populations in areas subjected to intense public visitation in Southwestern Brazil. Changes in the availability of food resources due to water pollution can also reduce the amplitude of the trophic niche and enhance competition amongst sympatric freshwater turtles (Luiselli et al., 2004).

The Vanderhaege's Toad-headed Turtle, *Mesoclemmys vanderhaegei* (Bour, 1973), is a central South American chelid most often recorded in water bodies within ecosystems with naturally open vegetation, such as the Cerrado and Chaco (Brandão et al., 2002; Souza, 2005; Rueda-Almonacid et al., 2007; Vinke et al., 2013; Marques et al., 2014). This species can occur in mountains and on high plateaus, in oligotrophic streams with clear water (Brandão et al., 2002; Brito et al., 2009; Brito et al., 2012). However, individuals have also been found in swampy lowland environments with heavy aquatic vegetation cover, as well as in medium-sized rivers (Vinke et al., 2013), dams and ponds (Marques et al., 2013, 2014). The species also occurs in urban environments, though less frequently (Brito et al., 2012).

Although generally considered carnivorous (Rueda-Almonacid et al., 2007; Vinke et al., 2013; Marques et al., 2014), no detailed studies of the feeding habits of *Mesoclemmys vanderhaegei* have been published. This study aims to identify and quantify the composition of the diet of *M. vanderhaegei* in streams in the Cerrado ecoregion of central Brazil. We investigate the effects of sex, age category, and site on dietary habits of this species and whether individuals are diet specialists or generalists.

MATERIALS AND METHODS

Study site

The study was conducted in the Chapada dos Guimarães National Park (15°25'S; 55°20'W; Datum WGS 84) and its immediate surroundings, in the Chapada dos Guimarães

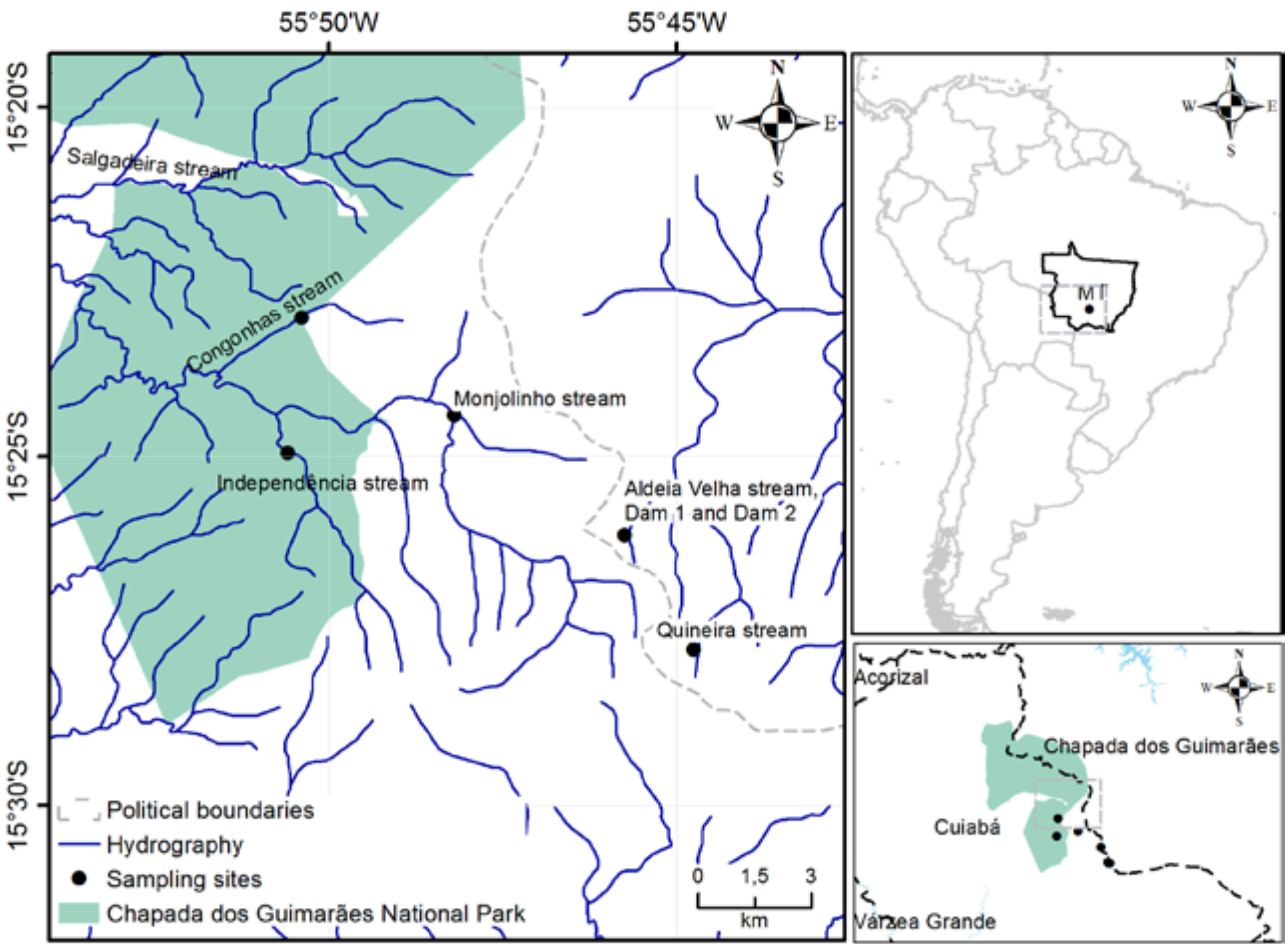

Fig. 1. Map illustrating study site in the Chapada dos Guimarães National Park and surrounding areas, Mato Grosso, Brazil. Black dots represent sampled streams.

municipality, Mato Grosso state, central Brazil (Fig. 1). The area is located in the southwestern portion of the Cerrado ecoregion, a savanna-like vegetation that originally covered nearly two thousand square kilometers, mostly across central Brazil. Seven water bodies were sampled (Table 1), at altitudes between 600 and 800 m a.s.l.

Obtention of specimens and stomach contents

Captures were made between 05 of January and 30 of March 2007. Individuals were hand captured during visual searches or with the aid of baited funnel traps. For details of size, type and arrangement of funnel traps see Brito et al. (2009). At each collecting site, seven traps operated 24 hours a day, for six consecutive days (a total sampling effort of 1008 trap hours per site). Traps were visited three times a day (06:00, 14:00, and 21:00 h). Visual searches by two observers were conducted during trap visits, totaling 36 hours/observer at each collection site.

Individuals were marked following the methods of Cagle (1939), measured (to the nearest 0.05 mm, with a 300 mm Vernier caliper: straight-line carapace length – CL, carapace width – CW; straight-line plastron length – PL; plastron width – PW), weighed (body mass, in g), and sexed, after which they were released at the capture site. Sex was determined by external examination of secondary sexual characteristics: chelid males usually possess a longer and thicker tail than females (Brito et al., 2009). Individuals in which sex could not be determined (n = 11; all with CL < 100 mm) were treated as juveniles and grouped together in this category.

To sample the diet of *M. vanderhaegei* we collected stomach contents using the stomach flushing technique developed by Legler (1977). We considered the stomach empty when, after two consecutive flushing attempts, totaling 60 ml of water, individual turtles regurgitated nothing but water. Samples of stomach contents were stored in containers with 70% alcohol (plant samples and invertebrates) or 10% formalin (vertebrates).

Diet analyses

Stomach contents were examined under a stereo-microscope and the food items were quantified and identified to the lowest possible taxonomic level. Plant fragments that could not be identified because they were in an advanced state of decomposition were categorized as “unidentified plant material”. Parts of exoskeleton, legs, wings and antennae of invertebrates that could not be identified were grouped in the category “unidentified Arthropoda”. Aquatic invertebrates were identified by using dichotomous keys (Pérez, 1988; Costa et al., 2006) and by consulting experts (see acknowledgements). Total length (mm) of entire prey was measured to the nearest 0.01 mm using a digital caliper (BTS®).

Data on stomach contents were analysed by sex (females and males), age categories (adults and juveniles), and water bodies. For each food category we determined the frequency of occurrence, the numerical frequency, and percentage volume (Hyslop, 1980; Marrero, 1994), measured by the displacement of a water column in a 1 ml syringe (graduated to 0.01 ml increments). When food item classes had a volume less than 0.01 ml, we regrouped such items into broader categories for volumetric analysis. The final analytical categories for volume were: aquatic invertebrates, non-aquatic invertebrates, fish, adult amphibians, larval amphibians, vertebrate bones (except fish), mammalian teeth, reptile scales, unidentified animal material, stems, leaves, fruits, seeds, aquatic plants (submerged vegetation), uni-

Table 1. Characteristics of seven capture sites of *Mesoclemmys vanderhaegei* in Chapada dos Guimarães municipality (Mato Grosso, Brazil) and number of turtles captured on each site. Abbreviations: Water body type: Le - lentic; Lo - lotic; Le/Lo - mixed. Natural/Human Impacted: N - natural; HI - human impacted. Presence of aquatic vegetation (submerged and floating): ++ abundant; + present; - absent. Bankside vegetation: Tr - trees; Sr - shrubs; Gr - grasses. Substrate: Mu - mud; Sa - sand; Ro - rock.

Water body	Captures	Coordinates	Water body type	Natural/ Human impacted	Submerged vegetation	Floating vegetation	Bankside vegetation	Substrate
Monjolinho	18	15º24’S 55º48’W	Le/Lo	HI	++	++	Tr	Mu/Sa
Dam 1	7	15º26’S 55º45’W	Le	HI	++	+	Gr	Sa
Dam 2	5	15º26’S 55º45’W	Le	HI	+	-	Gr	Sa
Aldeia Velha	5	15º26’S 55º45’W	Lo	N	+	+	Tr/Sr/Gr	Sa/Ro
Quineira	24	15º27’S 55º44’W	Le/Lo	HI	++	+	Tr	Mu/Sa
Independência	8	15º24’S 55º50’W	Lo	N	+	-	Tr/Sr	Sa/Ro
Congonhas	13	15º23’S 55º50’W	Lo	HI	-	-	Tr/Sr/Gr	Sa/Ro

dentified plant material, sediment (sand/stone), material from human activities (food scraps and religious rituals), periphyton, and unidentified material.

Statistical analyses

We used analysis of variance (ANOVA) to test if differences existed in the proportions of animal and plant items consumed by different sexes and ages of *M. vanderhaegei*. For this analysis, food items of animal origin were grouped in four categories: aquatic invertebrates, non-aquatic invertebrates, fish, and amphibians. We excluded the contributions of unidentified invertebrates and small bone fragments, scales and teeth of vertebrates, scarcely represented in our sample. Similarly, plant items were grouped into four categories: aquatic plants, fruits, leaves, and plant material not identified; seeds were excluded due to poor representativity. An ANOVA was also performed to investigate the differences between the consumption of animal and plant items as a whole. For both analyses, data on the proportions of each of the categories considered were transformed into arc sine square root, a transformation recommended when using frequency-based data that is not normally distributed (Zar, 1996). The paired-samples *t* test (Zar, 1996) was used to compare frequency of occurrence of animal and plant material consumed by *Mesoclemmys vanderhaegei* in the seven water bodies sampled.

To test the relationship between the total volume of ingested plant matter and the carapace length (CL) of captured individuals, and between the size of the entire ingested prey and CL, we employed a simple linear regression. For statistical analyses we used the application SYSTAT (Wilkinson, 1990). The level of significance in statistical tests was set at ≤ 0.05.

Based on abundance (quantitative) and presence/absence (qualitative) data for the 12 food categories with higher values of frequency of occurrence, we performed an ordination analysis (non-metric multidimensional scaling – NMDS), using the application PcORD (version 4.0) to reduce the dimensionality of diet composition. We did this for male and female *M. vanderhaegei* (sites combined) and for each studied water body (sexes combined). To give the same weight to each sample (individual), we used the Bray-Curtis index as a measure of dissimilarity between matrices of abundance and presence/absence.

RESULTS

We captured 80 individuals of *Mesoclemmys vanderhaegei* of which 79 had stomach contents. Of these, 41 (52%) were females, 27 were males (34%), and 11 (14%) were juveniles.

We identified 64 food item categories. Items of animal origin were found in 97% (n = 77) of individuals examined, and items of plant origin in 63% (n = 65). Among the animal items, invertebrates of the class Insecta were the most diverse (with material from 25 families in 11 orders; Table 2). Macro-invertebrate species at aquatic larval stage were the most frequently consumed insects, mainly from the orders Odonata, Diptera and Hemiptera. Non-aquatic invertebrates (Hymenoptera, Lepidoptera, Araneae, Diplopoda) were also present, though generally with a frequency of less than 5%.

Among vertebrates, fish of the genus *Astyanax* (Characidae: Characiformes) were most commonly consumed. Amphibians occurred both at low frequency and small numbers when compared to other animal categories, and were mostly tadpoles. For plant material, the most often consumed items were aquatic plants, fruits (mainly from *Ficus* sp., Moraceae, and from *Mauritia flexuosa,* Arecaceae) and leaves, plus periphyton and material from the unidentified category.

Females of *Mesoclemmys vanderhaegei* consumed more plant material than either males or juveniles (Fig. 2), but recorded differences between the three categories were not significant ($F_{3,27} = 0.26$, $P = 0.41$). Juveniles consumed more animal items than adult males and females ($F_{3,106} = 0.26$, $P = 0.02$).

Males consumed significantly more aquatic invertebrates than females ($F_{3,76} = 0.33$, $P < 0.01$). However, individuals in the two sexes did not differ in the consumption of non-aquatic invertebrates ($F_{3,19} = 0.53$, $P = 0.06$), fish ($F_{3,6} = 0.67$, $P = 0.73$) or amphibians ($F_{3,12} = 0.76$, $P = 0.26$). There was no significant relationship between turtle CL (n = 66) and the abundance of aquatic invertebrates consumed ($R^2 = 0.01$, $P = 0.38$).

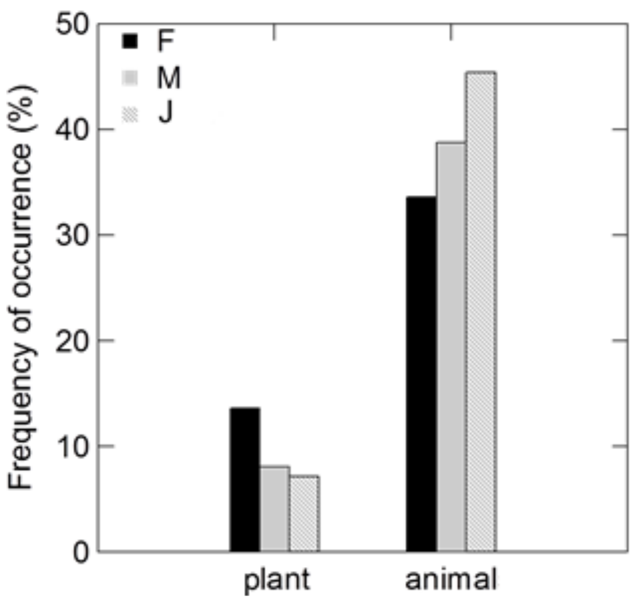

Fig. 2. Frequency of occurrence of animal and plant material consumed by 79 individuals of *Mesoclemmys vanderhaegei* captured in the Chapada dos Guimarães region (Mato Grosso, Brazil) between January and March 2007. Abbreviations: F = females (n = 41), M = males (n = 27) and J = juveniles (individuals ≤ 100 mm; n = 11).

Table 2. Composition of stomach contents of 79 individuals of *Mesoclemmys vanderhaegei* from Chapada dos Guimarães, Mato Grosso, Brazil, sampled between January and March 2007. Frequency of occurrence and numerical frequency of each prey type by sex and age category: M - adult males (n = 27); F - adult females (n = 41); J - juveniles (individuals ≤ 100 mm; n = 11). Abbreviations: n.i. - not identified due to digestion state. Food items' life stage: A - adult (invertebrates and vertebrates; I - imago (invertebrates only*)*; L - larva (vertebrates only); P - pupa.

FOOD ITEMS	Frequency of occurrence			Numerical frequency		
	M	F	J	M	F	J
INVERTEBRATES	322.09	268.05	418.14	74.47	57.71	75.16
Odonata - Anisoptera (I)	14.81 (4)	9.75 (4)	9.09 (1)	1.11 (4)	1.31 (5)	1.07 (1)
Libellulidae (I)	25.92 (7)	19.51 (8)	9.09 (1)	15.59 (56)	12.36 (47)	3.22 (3)
Gomphidae (I)	11.11 (3)	4.87 (2)		2.50 (9)	1.31 (5)	
Aeshnidae (I)	14.81 (4)	17.07 (7)		2.78 (10)	2.89 (11)	
Odonata - Zygoptera (I)		2.43 (1)			0.26 (1)	
Coenagrionidae (I)		2.43 (1)			0.26 (1)	
Lestidae (I)	14.81 (4)	9.75 (4)		20.89 (75)	7.63 (29)	
Blattaria (A)		2.43 (1)			0.26 (1)	
Orthoptera (A)	14.81 (4)	12.19 (5)	18.18 (2)	1.11 (4)	1.31 (5)	2.14 (2)
Neuroptera (I)		4.87 (2)	9.09 (1)		0.52 (2)	1.07 (1)
Corydalidae (I)	3.70 (1)			0.27 (1)		
Diptera (I)	3.70 (1)	4.87 (2)	9.09 (1)	0.27 (1)	0.78 (3)	4.30 (4)
Diptera - Culicomorpha (A)	3.70 (1)	14.63 (6)	9.09 (1)	0.27 (1)	1.57 (6)	1.07 (1)
Chironomidae (P)	29.62 (8)	17.07 (7)	18.18 (2)	3.34 (12)	2.89 (11)	2.15 (2)
Culicidae (P)	3.70 (1)	4.87 (2)		3.34 (12)	1.31 (5)	
Simuliidae (P)	3.70 (1)		9.09 (1)	1.11 (4)		2.15 (2)
Diptera - Brachycera (A)						
Sarcophagidae (A)		2.43 (1)			0.26 (1)	
Hemiptera (A)	14.81 (4)	12.19 (5)		1.11 (4)	1.31 (5)	
Hemiptera - Auchenorrhyncha (A)	14.81 (4)	2.43 (1)	27.27 (3)	1.39 (5)	0.26 (1)	8.60 (8)
Hemiptera - Heteroptera						
Belostomatidae (A)	3.70 (1)		9.09 (1)	0.27 (1)		1.07 (1)
Corixidae (A)		2.43 (1)	9.09 (1)		0.26 (1)	1.07 (1)
Naucoridae (A)			9.09 (1)		0.26 (1)	1.07 (1)
Pleidae (A)	3.70 (1)		18.18 (2)	0.27 (1)		3.22 (3)
Trichoptera - Annulipalpia (I)	11.11 (3)	7.31 (3)	9.09 (1)	1.11 (4)	1.05 (4)	1.07 (1)
Hydropsychidae (I)		7.31 (3)	18.18 (2)		1.31 (5)	2.15 (2)
Macronema sp. (I*)*	7.40 (2)	2.43 (1)	18.18 (2)	1.11 (4)	0.52 (2)	5.37 (5)
Polycentropodidae (I)		2.43 (1)	9.09 (1)		0.52 (2)	4.30 (4)
Trichoptera - Integripalpia						
Leptoceridae (I)	3.70 (1)		9.09 (1)	0.27 (1)		1.07 (1)
Coleoptera (A)	3.70 (1)	12.19 (5)	18.18 (2)		1.31 (5)	2.15 (2)
Coleoptera (I)		2.43 (1)	9.09 (1)		0.26 (1)	1.07 (1)
Coleoptera - Adephaga (A)						
Dytiscidae (A)	3.70 (1)	7.31 (3)	9.09 (1)	1.11 (4)	1.05 (4)	1.07 (1)
Coleoptera - Elateroidea (A)						
Elateridae (A)	3.70 (1)			0.27 (1)		
Ephemeroptera (I)	14.81 (4)	2.43 (1)	9.09 (1)	1.94 (7)	0.52 (2)	1.07 (1)
Ephemeroptera - Pisciforma (I)						
Baetidae (I)	14.81 (4)	4.87 (2)	9.09 (1)	5.57 (20)	0.78 (3)	5.37 (5)
Hymenoptera (A)		9.75 (4)	18.18 (2)		1.31 (5)	2.15 (2)
Formicidae (A)	3.70 (1)	9.75 (4)	18.18 (2)	0.27 (1)	1.57 (6)	2.15 (2)

(continued)

Table 2. (continued).

FOOD ITEMS	Frequency of occurrence			Numerical frequency		
	M	F	J	M	F	J
Lepidoptera (I)		2.43 (1)			0.26 (1)	
Cossidae (I)	3.70 (1)			0.27 (1)		
Notodontidae (I)	3.70 (1)		9.09 (1)	0.27 (1)		1.07 (1)
Araneae	3.70 (1)	2.43 (1)		0.27 (1)	0.26 (1)	
Diplopoda (A)		2.43 (1)			0.26 (1)	
Oligochaeta	3.70 (1)			0.55 (2)		
Unidentified Arthropoda (I)	3.70 (1)	4.87 (2)	18.18 (2)	0.27 (1)	0.78 (3)	2.15 (2)
Unidentified Arthropoda (A)	55.55 (15)	41.46 (17)	72.72 (8)	5.57 (20)	8.94 (34)	10.75 (10)
AMPHIBIANS	18.05	7.30	9.09	2.49	1.04	1.07
Leptodactylidae (L)	3.70 (1)			0.27 (1)		
Hylidae - *Dendropsophus minutus* (A+L)		4.87 (2)			0.78 (3)	
AMPHIBIANS (n.i.) (A)	7.40 (2)			0.55 (2)		
AMPHIBIANS (n.i.) (L)	7.40 (2)	2.43 (1)	9.09 (1)	1.67 (6)	0.26 (1)	1.07 (1)
FISH	48.13	58.51	27.27	5.54	12.09	3.22
Astyanax sp.	37.03 (10)	53.65 (22)	27.27 (3)	4.45 (16)	11.57 (44)	3.22 (3)
Rivulus sp.	3.70 (1)			0.27 (1)		
Vertebrate bones (n.i.)	3.70 (1)			0.55 (2)		
Reptile scales	3.70 (1)	2.43 (1)		0.27 (1)	0.26 (1)	
Mammalian teeth (n.i)		2.43 (1)			0.26 (1)	
PLANT MATERIAL	96.26	136.55	72.72	7.75	22.06	8.59
Aquatic plants (submerged vegetation)	22.22 (6)	34.14 (14)	18.18 (2)	2.22 (8)	4.73 (18)	2.15 (2)
Stems	7.40 (2)	14.63 (6)	9.09 (1)	0.55 (2)	1.57 (6)	1.07 (1)
Leaves	18.51 (5)	21.95 (9)	18.18 (2)	1.11 (4)	2.36 (9)	2.15 (2)
Seeds	3.70 (1)	2.43 (1)		0.27 (1)	0.26 (1)	
Fruit of *Ficus* sp. (fig)	11.11 (3)	17.07 (7)		0.83 (3)	8.15 (31)	
Fruit of *Mauritia flexuosa* (buriti)	7.40 (2)	17.07 (7)	18.18 (2)	0.55 (2)	1.84 (7)	2.15 (2)
Unidentified plant material	25.92 (7)	29.26 (12)	9.09 (1)	2.22 (8)	3.15 (12)	1.07 (1)
ALGAE						
Periphyton	7.40 (2)	3.70 (1)	3.70 (1)	0.27 (1)	0.27 (1)	0.27 (1)
MATERIAL FROM HUMAN ACTIVITIES (religious food-offerings)	29.62 (8)	7.30 (3)	9.09 (1)	6.12 (22)	4.99 (19)	5.37 (5)
SEDIMENT (sand/gravel)	29.62 (8)	14.62 (6)	54.54 (6)	3.06 (11)	1.57 (6)	6.44 (6)

Among the four categories of commonly eaten plant material, there was a significant difference between sexes and age categories for the consumption of leaves ($F_{3,11} = 1.00$, $P < 0.01$), aquatic plants ($F_{3,21} = 0.96$, $P < 0.01$), and plant material not identified ($F_{3,19} = 0.86$, $P < 0.01$), but not for fruit ($F_{3,14} = 0.17$, $P = 0.35$). Females were the largest consumers of plants. The two axes of the NMDS captured much of the variation of *M. vanderhaegei* diet (62% for qualitative data – presence/absence, and 59% for quantitative data – abundance), but it was not possible to separate the diets of males and females (Fig. 3).

Items of animal origin represented the largest proportion of stomach contents volume for females (46%), males (53%), and juveniles (75%; Table 3). For all these three categories, sediment constituted less than 1% of total stomach contents volume. For animal prey the commonest food items by volume were fish and aquatic invertebrates, for plants it was fruits. Periphyton also occupied large volumes. Although periphyton was the bulkiest item, only four individuals (one juvenile, one female and two males, 5% of stomachs analyzed) contained this type of food item. In 4% of females and juveniles and 7% of males, the stomachs contained material from human activities: e.g. beans, eggshell and popcorn. This type of material represented 15% of the volume of the diet of individuals caught in Congonhas stream, the

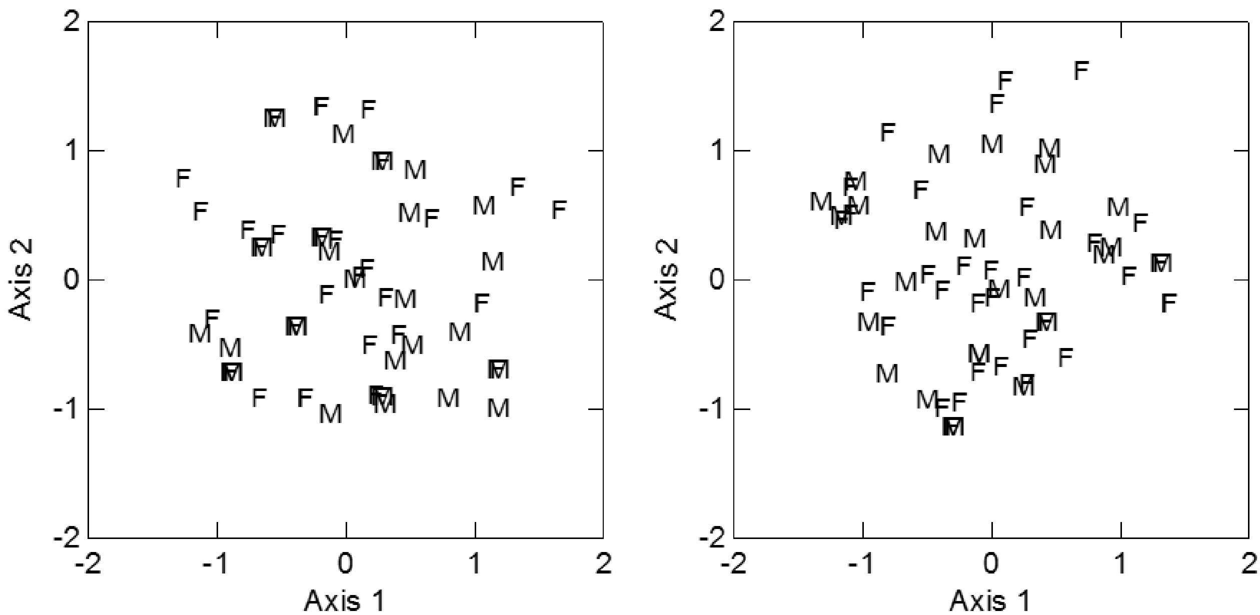

Fig. 3. Non-metric multidimensional scaling (NMDS) plots of food items consumed by *Mesoclemmys vanderhaegei* from Chapada dos Guimarães, Mato Grosso, Brazil, according to (A) presence/absence and (B) abundance. Only turtles that were sexed were considered (n = 69; F - females; M - males).

only locality in which such items were recorded from *M. vanderhaegei* stomachs.

In all water bodies sampled, diet items of animal origin were more commonly consumed than those of plant origin (t = 2.77; df = 6; P = 0.03; Fig. 4). Water bodies where there was greatest consumption of plant items were mostly dammed streams (Monjolinho, Quineira, Dam 1, and Dam 2), all anthropogenic environments. Fruit consumption was recorded only in Monjolinho and Quineira dammed streams.

The volume of plant ($R^2 < 0.03$, P = 0.13) and animal material ($R^2 < 0.01$, P = 0.72) in the stomachs was not significantly related to the CL of individuals caught. Similarly, there was no significant relationship between prey size and the CL of captured individuals ($R^2 = 0.01$, P = 0.13, n = 45 entire prey).

Qualitative data on sampling sites captured much of the variation in the diet between water bodies (63%), but the resulting ordination did not allow us to group water bodies according to the consumed food items (Fig. 5).

DISCUSSION

In the area, and during the period of study, *Mesoclemmys vanderhaegei* was found to be omnivorous with a general tendency to carnivory, as briefly pointed in a recent species's account by Marques et al. (2014). In many communities of vertebrates, omnivorous species represent the greater part of the consumers (Polis, 1991; Polis and Strong, 1996), and species identified as primarily carnivorous may include plant material in their diet (McTigue and Zimmerman, 1991). Omnivory has been reported frequently among members of the family Chelidae (e.g., Medem, 1960; Mittermeier et al., 1978; Souza, 2004; Caputo and Vogt, 2008; Martins et al., 2010). However, some species of this family, such as *Chelus fimbriatus*, *Hydromedusa tectifera*, *Phrynops hilarii*, and *Platemys platycephala* are exclusively carnivorous (Vogt and Villarreal, 1993; Alcalde et al., 2010).

Mesoclemmys vanderhaegei is one of the largest aquatic vertebrates in the water bodies studied, along with the Cuvier's Dwarf Caiman (*Paleosuchus palpebrosus*) and the Green Anaconda (*Eunectes murinus*), and like these two, appears to occupy the higher levels of the local trophic chain (E. Brito, pers. comm. 2007). Items of animal origin were those most frequently used by all age and sex categories of *M. vanderhaegei,* with aquatic invertebrates being the most important, both in terms of proportional contribution to the diet and as number of individuals. High consumption of aquatic invertebrates (larvae and pupae) is frequently recorded for freshwater turtles (e.g., Lagler, 1943; Moll, 1990; Souza and Abe, 1998, 2000; Moll and Moll, 2004; Caputo and Vogt, 2008; Bonino et al., 2009; Alcalde et al., 2010; Martins et al., 2010; Brasil et al., 2011). However, consumed non-aquatic invertebrates

Table 3. Composition of stomach contents of 79 individuals of *Mesoclemmys vanderhaegei* from Chapada dos Guimarães, Mato Grosso, Brazil, sampled between January and March 2007. Volume (V) - in ml and in percentual - of each food item category, by sex and age category: M - adult males (n = 27); F - adult females (n = 41); J - juveniles (individuals ≤ 100 mm; n = 11). Food items' life stage: A - adult; L - larva.

Food item category	Age category					
	M		F		J	
	V (ml)	V (%)	V (ml)	V (%)	V (ml)	V (%)
INVERTEBRATES	10.98	16.96	15.91	17.11	2.27	17.53
Aquatic invertebrates	8.41	12.99	13.39	14.40	1.06	8.19
Non-aquatic invertebrates	2.57	3.97	2.52	2.71	1.21	9.34
VERTEBRATES	10.58	16.32	26.05	28.01	7.46	57.55
Amphibians (A)	0.12	0.19	0.00	0.00	0.00	0.00
Amphibians (L)	1.92	2.96	0.06	0.06	0.02	0.15
Fish	7.86	12.13	23.24	24.99	7.44	57.40
Vertebrate bones (except fish)	0.10	0.15	0.00	0.00	0.00	0.00
Mammalian teeth	0.00	0.00	0.05	0.05	0.00	0.00
Reptilian scales	0.08	0.12	0.60	0.65	0.00	0.00
Unidentified vertebrates	0.50	0.77	2.10	2.26	0.00	0.00
PLANT MATERIAL	1.76	3.64	15.05	16.16	0.77	5.94
Stems	0.19	0.29	1.18	1.27	0.02	0.15
Leaves	0.13	0.20	0.05	0.05	0.04	0.31
Fruits	1.34	2.07	12.04	12.95	0.50	3.86
Seeds	0.10	0.15	0.02	0.02	0.00	0.00
Aquatic plant (submerged vegetation)	0.16	0.25	0.87	0.94	0.11	0.85
Unidentified plant material	0.44	0.68	0.89	0.96	0.10	0.77
SEDIMENT (sand/gravel)	0.07	0.11	0.06	0.06	0.04	0.31
MATERIAL FROM HUMAN ACTIVITIES (religious food-offerings)	2.61	4.03	7.05	7.58	0.50	3.86
ALGAE - Periphyton	26.60	41.26	20.89	27.17	1.30	9.87
UNIDENTIFIED MATERIAL	11.30	17.67	8.00	3.88	0.62	4.93

include adults of Orthoptera, Coleoptera and Formicidae, indicating that *M. vanderhaegei* is an opportunistic predator, a feature common among aquatic turtles (Moll, 1976; Chessman, 1984; Souza and Abe, 1998, 2000; Luiselli et al., 2004; Alcalde et al., 2010; Brasil et al. 2011).

Fish, particularly those of the genus *Astyanax* (Characiformes), are among the three most common animal items consumed by *M. vanderhaegei*. They are also the commonest prey item by volume recorded during the study. Although they are known to be important in the diet of carnivorous and omnivorous freshwater turtles belonging to suborder Cryptodira, fish are generally considered to be more easily captured by individuals belonging to those turtle species with longer necks (Moll and Moll, 2004) – the Pleurodira – for which *Hydromedusa tectifera* is a good example (Alcalde et al., 2010). On several occasions during the field study, individuals of *M. vanderhaegei* were observed to chase fish of the genus *Astyanax*. However, none of these attempts resulted in a successful capture. It appeared that individuals of *M. vanderhaegei* soon gave up chasing individuals when they were not caught immediately and would go in pursuit of other fish when there were schools on site (E. Brito, pers. comm. 2005). At least five species of *Astyanax* occur in the Chapada dos Guimarães National Park, all of them considered regular and abundant members of the local fish community (ICMBio, 2009). Additionally, species in the genus *Astyanax* can form large schools (e.g., Suzuki and Orsi, 2008). Some of the individuals from these schools occasionally enter in the funnel traps (E. Brito, pers. comm. 2007), where they could be more easily captured by imprisoned turtles and result in an overestimation of fish as a prey for *M. vanderhaegei*.

Although both sexes have higher consumption of animal items than of plants, the consumption is proportionately greater in females than in males. Similar studies in other species of Chelidae give conflicting results for this aspect: for the Neotropical species *Phrynops*

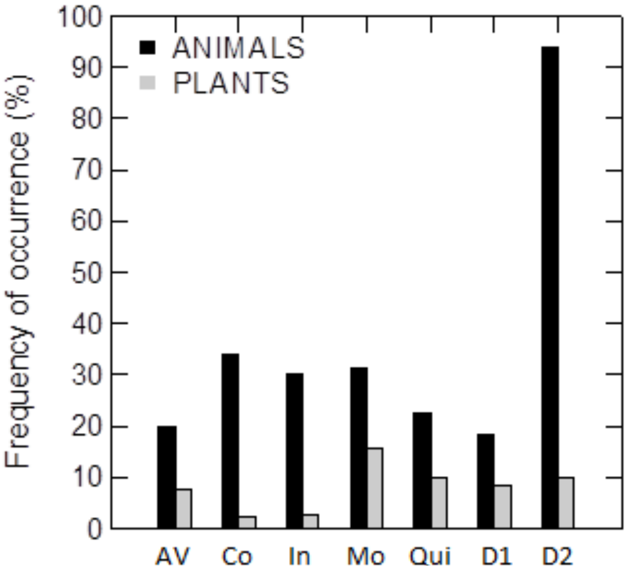

Fig. 4. Frequency of occurrence of animal and plant material consumed by *Mesoclemmys vanderhaegei* in the seven water bodies sampled in the Chapada dos Guimarães region, Mato Grosso, Brazil. Subtitle: AV - Aldeia Velha stream; Co - Congonhas stream; In - Independência stream; Mo - Monjolinho stream; Qui - Quineira stream; D1 - Dam 1; D2 - Dam 2.

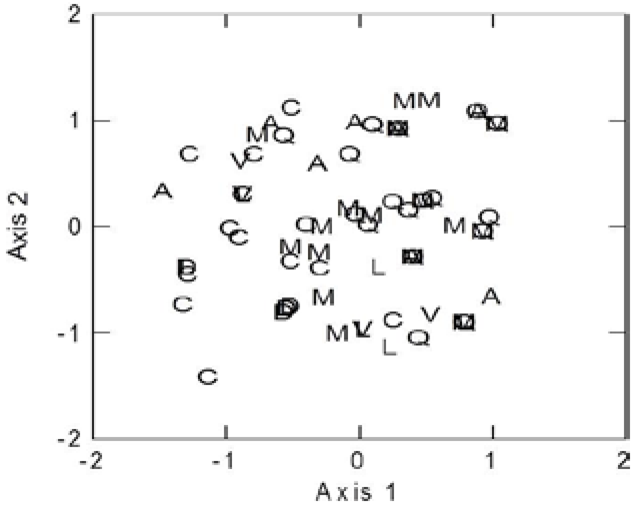

Fig. 5. Non-metric multidimensional scaling (NMDS) plots of food items consumed by *Mesoclemmys vanderhaegei* in the seven sites sampled in Chapada dos Guimarães municipality, Mato Grosso, Brazil. A = Independência stream; C = Congonhas stream; V = Aldeia Velha stream; L = Dam 1; D = Dam 2; M = Monjolinho stream; Q = Quineira stream.

geoffroanus, no significant differences were found in diet composition of males and females (Fachín-Terán et al., 1994), while in *Emydura krefftii* from Australia (Georges, 1982), and *Acanthochelys spixii*, in the Brazilian Cerrado (Brasil et al., 2011), females consumed more plant material, while males ate more animal items.

Considering the different reproductive strategies of the sexes, with females having to increase their weight and maintain nutritional reserves during egg development and laying (Schoener, 1971), such differences in the diets of males and females are not unexpected. The fact that our study found no differences in the composition and abundance of food items consumed by male and female *M. vanderhaegei* suggests a possible food niche overlap between the two sexes. This could be related to the opportunistic consumption of the most abundant items in the environment by both sexes. Although another chelid – *Phrynops geoffroanus* – is frequently recorded in lower sections of the streams studied, no other freshwater turtle but *M. vanderhaegei* occurs at the study site. Therefore, it is also possible that in the absence of competition, individuals in this species have such a broad niche that there is no need for between-sex partitioning. The occurrence of dietary changes in the presence of potential competitors is an interesting hypothesis that could be tested for *M. vanderhaegei*, in the drainages mentioned here.

On the contrary, the greater frequency of occurrence of plant materials in the stomachs of individuals of *Mesoclemmys vanderhaegei* may be simply the result of accidental ingestion during predation of animal items. In fact, when analyzing the diet of omnivorous turtles, it is often not possible to determine whether the plant material was ingested intentionally or accidentally (Parmenter and Avery, 1990; Lindeman, 1996; Rowe and Parsons, 2000). Another aspect potentially indicating accidental ingestion of plant items was the fact that only small fragments of such material were found in the stomach contents. On the other hand, the large volume of periphyton found in four stomachs of *M. vanderhaegei* during our study is suggestive of deliberate intake (Tables 2 and 3). The same can be inferred for bulkier plant items – fruits of *Ficus* sp. and exocarp and mesocarp of *Mauritia flexuosa* were found almost whole in the stomachs, suggesting that they had been purposely ingested. In general, chelid turtles appear to supplement their diets with fruits or seeds, particularly when these items are readily available or when aquatic prey becomes more dispersed, as in the rainy season (Fachín-Terán et al., 1995; Lima et al., 1997; Caputo and Vogt, 2008). Our results reinforce the suggestion by Caputo and Vogt (2008) that turtle diets ideally should be investigated by using both stomach flushing and fecal analyses. In a study of the diet of *Rhinemys rufipes* in Brazilian Amazonia, those authors found that bulky stomach contents (e.g., large fruit seeds), generally not regurgitated by turtles by using the stomach flushing technique, do however appear in analyses of fecal contents (Caputo and Vogt, 2008).

The consumption of animal items in greater numerical frequency and percentage volume by juveniles than by adult males and females corroborates what is reported elsewhere. The record of ontogenetic diet changes in chelonian species is common and usually juvenile freshwater turtles are more carnivorous, while adult freshwater turtles are more herbivorous (Clark and Gibbons, 1969; Moll, 1976; Parmenter and Avery, 1990; Kennett and Tory, 1996; Spencer et al., 1998) or omnivorous (Bouchard and Bjorndal, 2006). This change may be related to protein requirements for growth (Schoener, 1971), considering that the juvenile turtles are more susceptible to predation and need to grow fast. Change in diet upon reaching reproductive maturity has also been reported in *Emydura krefftii* (Chelidae), a species where juveniles are carnivorous and adults omnivorous (Georges, 1982), and in *Hydromedusa maximiliani* (Chelidae) (Souza and Abe, 1998), where small crabs accounted for 75% of all food items consumed by juveniles but only 5% of the food items consumed by adults.

A curious result of this study is the similarity of *M. vanderhaegei* diet in water bodies with apparently very different environmental characteristics. In Congonhas Stream, for example, there are no fish (J. Penha, pers. comm. 2007) but a sporadic supply of biological material from human activities does occur (picnics and religious food-offerings). This material comprised a large variety of fruits (e.g., kiwi, grapevines, pear, peach, apple, banana, watermelon), vegetables (okra), cooked grains (rice, popcorn), beans, and eggs, arranged in plastic or wood trays, at the margins of the stream. The broad trophic plasticity recorded for *M. vanderhaegei* indicates that individuals of this species have very generalist diets. The identification of unusual food items, for example, scales of reptiles (snakes and lizards) and mammalian teeth, as well as material from human activities (see Table 2), may also reflect a common tendency for freshwater turtles to be scavengers (Souza, 2004).

The categories of food eaten by individuals of *M. vanderhaegei* indicate that they may forage in several different strata of the water column. Benthic foraging was indicated by the consumption of such aquatic invertebrates as Trichoptera (which live mostly under rocks, logs and plant materials, in running water; Pérez, 1988) and Odonata (whose larvae have strong associations with lentic and aquatic vegetation, but may also occur in lotic environments, where they live buried in the sand; Pérez, 1988). Meanwhile, the consumption of large amounts of fish (*Astyanax* sp.), of fruits (e.g., *Ficus* sp.), and of non-aquatic invertebrates active on understory vegetation (e.g. various ant species) indicate that individuals of *M. vanderhaegei* also forage both nektonically and directly from the surface.

As with most omnivorous vertebrates, in which feeding is related to a variety of foraging opportunities in their habitat, female, male and juvenile *M. vanderhaegei* all showed a mixed diet of plants and animals items. While a mixed diet implies less efficient digestion, since it requires a diverse gut microflora, it also involves less loss of time and energy in the search for more nutritious foods (Bjorndal, 1991). In addition, a mixed plant-animal diet provides a broader spectrum of nutrients than does an item-restricted diet, which may explain why most organisms are to some extent omnivorous and hence have an enhanced ability to optimize their nutritional balance (Bjorndal, 1991).

The present study provides detailed information on the diet of *Mesoclemmys vanderhaegei* in natural and anthropogenic disturbed environments in headwater streams in Cerrado. Much of the original area occupied by this ecoregion is presently modified by anthropogenic changes derived from agriculture. Such modifications have strongly impacted aquatic ecosystems, severely altering species composition, functioning and structure of freshwater habitats throughout Cerrado (Agostinho et al., 2005), in such an extent that this ecoregion is considered a global biodiversity hotspot (Klink and Machado, 2005). A close relative of *M. vanderhaegei* – *Mesoclemmys hogei*, native to another Brazilian hotspot, the Atlantic Forest – was recently recognized by the governmental environmental agency as Critically Endangered, being the first and the only continental Brazilian chelonian to be considered as a threatened species (ICMbio, 2015). Additional studies on actual and potential effects of anthropogenic and natural disturbances on the feeding habits of *M. vanderhaegei*, among other biological aspects, might help to prevent extinction risks to this species.

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