Revista mexicana de biodiversidad
ISSN: 1870-3453
ISSN: 2007-8706
Instituto de Biología

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Revista mexicana de biodiversidad, vol. 91, e912852, 2020
Instituto de Biología

DOI: https://doi.org/10.22201/ib.20078706e.2020.91.2852

Available in: https://www.redalyc.org/articulo.oa?id=42571632048

Revista Mexicana de Biodiversidad

Revista Mexicana de Biodiversidad 91 (2020): e912852

Ecology

Variation in diet of hatchlings, juveniles and sub-adults of *Caiman crocodilus chiapasius* in La Encrucijada, Chiapas, Mexico

Variación de la dieta de crías, juveniles y subadultos de Caiman crocodilus chiapasius *en La Encrucijada, Chiapas, México*

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Received: 30 November 2017; accepted: 20 April 2018

Abstract

Little is known about the diet of the Chiapas spectacled caiman, *Caiman crocodilus chiapasius* (Bocourt, 1876), in the southern coast of Mexico. Herein, we analyzed the stomach content of 44 caimans divided into 3 size classes in La Encrucijada, Chiapas, Mexico. Within the contents we identified insects, crustaceans, arachnids, fishes, and birds. Hatchlings fed mainly on insects and arachnids, juveniles on crustaceans and insects and sub-adults on crustaceans and fish. Our data show that while the invertebrate intake decreased along different size classes, vertebrates intake increased, and that diet overlapped greater in adjacent size classes. No differences were found in niche breadth ($p > 0.05$), diet composition ($Q = 2.0$, $p = 0.3678$) and prey abundance ($X^2 = 1.9756$, $p = 0.3759$) among size classes. *Caiman crocodilus chiapasius* is protected by the Mexican law in the category of "special protection".

Keywords: Caiman; Diet; Development; Food niche

Resumen

Para entender la dieta del caimán de anteojos de Chiapas *Caiman crocodilus chiapasius* (Bocourt, 1876) en la costa sur de México, analizamos el contenido estomacal de 44 caimanes de 3 clases de tamaño en La Encrucijada, Chiapas, sur de México. En los contenidos, identificamos insectos, crustáceos, arácnidos, peces y aves. Las crías se alimentaron principalmente de insectos y arácnidos, los juveniles de crustáceos e insectos, y los subadultos de crustáceos y peces. Nuestros resultados muestran que mientras le ingestión de invertebrados disminuye con el aumento del tamaño de los individuos, la ingestión de vertebrados se incrementa y que el solapamiento de dietas es más importante entre clases de tamaño adyacentes. No encontramos diferencias entre clases de tamaño a nivel de ancho de nicho ($p > 0.05$), composición de dieta ($Q = 2.0$, $p = 0.3678$) y abundancia de presa ($X^2 = 1.9756$, $p = 0.3759$). *Caiman crocodilus chiapasius* está catalogado como especie con protección especial por la ley mexicana.

Palabras clave: Caimán; Dieta; Desarrollo; Nicho alimenticio

ISSN versión electrónica: 2007-8706; Universidad Nacional Autónoma de México, Instituto de Biología. https://doi.org/10.22201/ib.20078706e.2020.91.2852

Introduction

The Chiapas spectacled caiman, *Caiman crocodilus chiapasius* (Bocourt, 1876), is distributed along the coasts of the state of Chiapas (Mexico) and of El Salvador (Escobedo-Galván et al., 2011, 2015; Venegas-Anaya et al., 2008). This species inhabits mostly coastal marshes, estuaries and river mouths on the Pacific slope (Álvarez-del Toro, 1974). Although the IUCN considers the species endangered status as "Least Concern", and the Mexican NOM-059 (Semarnat, 2010) classifies it "Under Special Protection", the subspecies status needs further assessment and the implementation of adequate conservation plans. The survival of species depends on their ecosystems status. Through the study of the alimentary habits of an organism we can understand food chains and the impact of populations on the environment (Casas-Andreu & Barrios-Quiroz, 2003). Furthermore, diet analyses allow a better understanding of the ecological role of organism fulfill in the ecosystem (Villegas & Schmitter, 2008). Food affects body condition, growth, behavior and reproduction of crocodiles (Platt, Thorbjarnarson et al., 2013), and analyzing diet from different perspectives, such as its variation throughout development, allows to understand the intraspecific competition through the overlap of food niche between different size classes (Platt et al., 2006; Platt, Thorbjarnarson et al., 2013; Tucker et al., 1996).

Among known *Caiman* species, *C. c. chiapasus* has been poorly studied and the information of its basic life history is mostly unknown either in wildlife or captivity (Escobedo-Galván et al., 2004; García-Grajales & López-Luna, 2010; Martínez & Dueñas, 2007). Only González-Desales et al. (2016) describe ecological aspects of nesting of *C.c. chiapasius*, however, there is no information about the diet of the subspecies in Mexico. Studies of diet are fundamental for the understanding of the ecology of an organism (Rosenberg & Cooper, 1990), so given the fact that conservation actions are more effective when based on a thorough understanding of the natural history of individuals (Platt, Thorbjarnarson et al., 2013), diet information is fundamental to create effective protection plans.

Diet of *C. c. crocodilus* and *C. c. fuscus* has been described in Venezuela, Brazil, and Peru (Da Silveira & Magnusson, 1999; Gorzula, 1978; Laverty & Dobson, 2013; Magnusson et al., 1987; Marioni et al., 2008; Seijas & Ramos, 1980; Thorbjarnarson; 1993); and in Costa Rica (Allsteadt & Vaughan 1994), respectively. However, diet of *C. c. chiapasius* in Mexico is known only through natural history notes of Álvarez-del Toro (1974). In general, subspecies of *C. crocodilus* prefer fish, arachnids, insects, mammals, birds, crustaceans, gastropods, amphibians and reptiles, and food composition may vary depending on the season or habitat type. Among other crocodilians (e.g. *C. moreletii*, *C. acutus*, and *C. johnstoni*), food niche shows more overlap in adjacent size classes; consumption of invertebrates decreases with increasing body size while consumption of vertebrates increases. Hatchlings and adults behave more like specialists, while juveniles and sub-adults as generalists (Platt et al., 2006; Platt, Thorbjarnarson et al., 2013; Tucker et al., 1996).

Thus, as little is known on the diet of *C. c. chiapasius*, our study pretends to describe the diet composition of this subspecies in the state of Chiapas, Mexico, and its variation among different size classes following the next questions: *1)* Which prey types (composition) are consumed by *C. c. chiapasius* in the dry season in La Encrucijada, Chiapas? *2)* How much of the diet proportion (prey types) is shared among the size classes? *3)* Is there a variation in the abundance of prey types among size classes? and *4)* Are search for food trends based on the ontogeny of *C. c. chiapasius*?

Materials and methods

The study was done in the Hueyate estuary, within the Nuclear Zone of La Encrucijada Biosphere Reserve, municipality of Acapetahua, Chiapas, Southern México (Fig. 1). The area is covered with tropical dry forest, marshes and mangroves. The area is highly influenced by the rainy season with a precipitation of 1,200 mm to 3,000 mm, and the volume of water bodies change considerably between the dry and the rainy season (Carabias et al., 1999). The Huixtla River supplies fresh water to the Hueyate estuary making it a perennial water body. The water salinity generates a suitable hydrological environment for estuarine organisms. The climate is tropical with monsoon rains in summer, reaching an average annual temperature of 28 °C (Carabias et al., 1999).

Field work was done from March 8 to March 28, 2015 during the dry season. Caimans were captured every night starting at 21:00 hrs., finishing until 05:00 hrs. the next day on board an outboard motor boat (15 HP), paddling when hitting low waters or when we captured the animals. To locate caimans, we used hand lamps (500 lumens) and head lamps (160 lumens) aiming water body edges to detect the light reflection in the *tapetum lucidum* of caimans. We hand captured caimans of less than a meter total length (TL) and for larger ones we used a noose mounted on a steel pole (Borteiro et al., 2009; Platt et al., 2006; Platt, Thorbjarnarson et al., 2013; Wallace & Leslie, 2008).

We measured total length (TL) and snout-vent length (SVL) of all captured caimans to the nearest 0.1 cm using a measuring tape. Since some caimans showed tail maiming, we based size classes on SVL following the classification of Seijas (1983): hatchlings (SVL $\leq$ 19 cm), juveniles (19

< SVL ≤ 59 cm), sub-adults (59 < SVL ≤ 89 cm) and adults (SVL > 89 cm). We marked each individual by cutting caudal scales following a predetermined code, according to the numeration in the same site made by González-Desales et al. (2016).

In order to know food habits of caimans, we washed their stomachs to obtain food remains using a modified method of Taylor et al. (1978) here described. After placing the PVC tube that keeps open the snout of the caiman, we introduced one end of a flexible plastic hose, previously lubricated, into the stomach. The other end of the hose was attached to a four-liter Flow Master® water sprinkler. Hoses were set according to the size of each caiman, and were previously marked to indicate the distance from the tip of the snout to the stomach. Once the hose was in the stomach of the caiman, the sprinkler water was allowed to flow filling the stomach, monitoring the distension of it. Then, the body of the caiman was tilted 90°, facing the snout downwards. Using our hands, we pressed the stomach to provoke regurgitation. The same procedure was repeated until the stomach was completely empty. The stomach content was recovered in a bucket and filtered using a 20 cm diameter strainer with a 0.5 mm screen. Stomach content remains were fixed with 10% formaldehyde (Borterio et al., 2009) and has been kept in 50 to 250 ml containers to be analyzed in the Colección Nacional de Anfibios y Reptiles (CNAR) of the Instituto de Biología, Universidad Nacional Autónoma de México.

The remains were identified to the lowest possible taxonomic level and were assigned to major prey categories: insects, arachnids, crustaceans, fish and birds. Seeds, vegetation, algae, parasites, and solid waste was not classified as food.

We calculated the percent occurrence for each prey category by size class. The percentage of occurrence is defined as the number of samples in which a particular prey item occurs divided by the sample size per size class of crocodile, multiplied by 100. It is appropriate to use the percentage of occurrence instead of the total occurrence when preys cannot be quantified since individual preys are dissociated within the stomach (Platt et al., 2006; Platt, Thorbjarnarson et al., 2013). Subsequently, percentage of occurrence was transformed using the arcsine of the square root for linearization (Zar, 1984) to evaluate the simple lineal regression between size classes and occurrence of prey type at major taxonomic ranks.

We estimated order 1 true diversity index (1D), which considers all species weighted by their abundance and they are also weighted by their abundance (Jost, 2006, 2007). This was calculated using the Shannon entropy exponential 1D = exp (H') (Jost, 2006) to know the number of dominant prey types per size class. The analysis was done using SpadeR software (Chao & Shen, 2003). The values of true diversity were plotted in a box and mustache diagram to see if there are differences between the 3 diversity indices.

The niche overlap between size classes was calculated using the percentage of prey type overlap (P) per size classes (Krebs, 1989; Platt et al. 2006, Platt, Thorbjarnarson et al., 2013; Tucker et al. 1996). Dietary niche overlap among size classes was determined using percent of prey type overlap (P). P is estimated

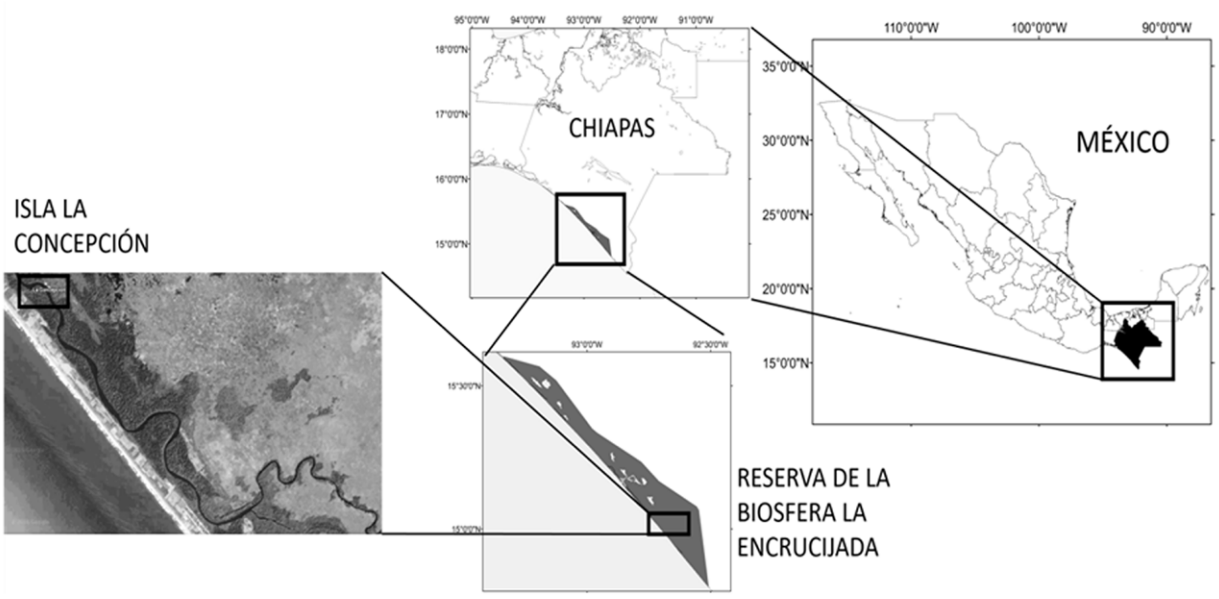

Figure 1. Location map of the study area.

by P = ∑ (mínimo pij, pik) * 100, where pij and pik are the proportion of prey item (i) used by size class j and k, respectively, and ranges from 0 (no overlap) to 1 (complete overlap) (Krebs, 1989).

We used the non-parametric Cochran Q test to determine if the composition of the diet between size classes was similar. Cochran Q test is calculated as:

$$Q = ((k - 1)\ (k\ \Sigma^{k}_{j} = 1\ x_j^2 - N^2)) / (kN - \Sigma^{n}_{i} = 1\ x_i^2)$$

where *k* is the number of class sizes, *xj* is the summation of presence or absence of all types of prey in a size class, *xi* is the summation of presence or absence of a prey in all size classes and *N* is the summation of the summation of presence or absence of a prey in all size classes. Finally, a non-parametric analysis Friedman test was performed to know if the quantity of food consumed per size classes was similar (Zar, 1984). Friedman test is calculated as:

$$Xr^2 = (12 / nJ\ (J+1))* \Sigma i\ Ri^2 - 3n\ (J+1))$$

where *n* is the number of size classes and *J* is the number of types of prey, while the value of Ri^2 is given by the sum of squares of the sum of the ranges given to each type of prey in each size classes. These analyzes were conducted using Rstudio 3.3.3 software with the RVAideMemoire package ver. 0.9-69-3 and stats, respectively (Harvé, 2018).

Results

We captured 50 individuals of *C. c. chiapasius* with SVL between 159 and 960 mm, and TL from 325 to 1,540 mm. Of all captures, 16 individuals were hatchlings, 30 juveniles, 3 sub-adults and 1 adult. We washed the stomach of all captured caimans. Six caimans were excluded from analyzes because food remains were either highly digested making contents impossible to identify, or stomachs were

Table 1.

Number and percentage (in parentheses) of recovered remains (RR) and occurrence number and percentage (in parentheses) of each type of prey (OC) in the stomach contents of 44 spectacled caimans of La Encrucijada, Chiapas.

	Hatchlings (n = 16)		Juveniles (n = 25)		Sub-adults (n = 3)		Total	
	RR	OC	RR	OC	RR	OC	RR	OC
Invertebrates	432 (100)	16 (100)	697 (100)	25 (100)	50 (100)	3 (100)	1,179 (100)	44 (100)
Insecta	256 (59.2)	13 (81.3)	462 (66.2)	18 (72.0)	2 (4.0)	2 (66.7)	720 (61.06)	33 (75)
Coleoptera	94 (21.7)	6 (37.5)	146 (21.0)	8 (32.0)	0 (0)	0 (0.0)	240 (20.3)	14 (31.8)
Hemiptera	106 (24.5)	6 (37.5)	130 (18.6)	5 (20.0)	0 (0)	0 (0.0)	236 (20.0)	11 (25.0)
Orthoptera	0 (0.0)	0 (0.0)	24 (3.4)	4 (16.0)	0 (0)	0 (0.0)	24 (2.0)	4 (9.1)
Diptera	7 (1.6)	2 (12.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	7 (0.5)	2 (4.5)
Hymenoptera	0 (0.0)	0 (0.0)	3 (0.5)	1 (4.0)	0 (0.0)	0 (0.0)	3 (0.2)	1 (2.3)
Unidentified insects	49 (11.3)	9 (56.3)	158 (22.6)	13 (52.0)	2 (4.0)	2 (66.7)	209 (17.7)	24 (54.6)
Aracnidae	117 (27.0)	9 (56.3)	21 (3.0)	4 (16.0)	1 (2.0)	1 (33.3)	139 (11.7)	14 (31.8)
Araneae	113 (26.1)	8 (50.0)	17 (2.4)	3 (12.0)	0 (0.0)	0 (0.0)	130 (11.0)	11 (25.0)
Acaria	0 (0.0)	0 (0.0)	2 (0.2)	2 (8.0)	0 (0.0)	0 (0.0)	2 (0.2)	2 (4.5)
Unidentified arachnids	4 (0.9)	1 (6.3)	2 (0.2)	1 (4.0)	1 (2.0)	1 (33.3)	7 (0.5)	3 (6.8)
Crustaceae	59 (13.6)	7 (43.8)	214 (30.7)	15 (60.0)	47 (94.0)	3 (100)	320 (27.1)	25 (56.8)
Decapoda	41 (9.4)	4 (25.0)	153 (22.0)	9 (36.0)	38 (76.0)	2 (66.7)	232 (19.8)	15 (34.1)
Unidentified crustaceae	18 (4.2)	3 (18.8)	61 (6.5)	6 (24.0)	9 (18.0)	1 (33.3)	78 (6.6)	10 (22.7)
Vertebrates	6 (100)	3 (18.8)	6 (100)	3 (12.0)	138 (100)	2 (66.7)	150 (100)	8 (18.2)
Osteichthyes	6 (100)	3 (18.8)	6 (100)	3 (12.0)	78 (56.5)	2 (66.7)	90 (60)	8 (18.2)
Aves	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	60 (43.4)	1 (33.3)	60 (40)	1 (2.3)
Jacanidae	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	60 (43.4)	1 (33.3)	60 (40)	1 (2.3)
Other	20 (100)	7 (43.8)	108 (100)	21 (84.0)	32 (100)	3 (100)	160 (100)	31 (70.5)
Solid waste	0 (0.0)	0 (0.0)	1 (1.0)	1 (4.0)	1 (3.1)	1 (33.3)	2 (1.2)	2 (4.5)
Parasites	0 (0.0)	0 (0.0)	6 (5.5)	8 (32.0)	0 (0.0)	0 (0.0)	6 (3.7)	8 (18.2)
Vegetation (leafs and wood pieces)	20 (100)	7 (46.0)	67 (62.0)	18 (72.0)	31 (96.8)	3 (100)	118 (73.7)	28 (63.6)
Seeds of Poaceae	0 (0.0)	0 (0.0)	30 (27.7)	2 (8.0)	0 (0)	0 (0.0)	30 (18.75)	2 (4.5)
Algae	0 (0.0)	0 (0.0)	4 (3.7)	3 (12.0)	0 (0)	0 (0.0)	4 (2.5)	3 (6.8)

empty. We worked with a total sample of 44 caimans (16 hatchlings, 25 juveniles and 3 sub-adults).

We recognized 1,329 body parts considered as food (Table 1). Insects were the most abundant, being present in 75.0% of the caimans, followed by crustaceans (56.8%), arachnids (31.8%), fish (18.2%), and birds (2.3%). We were able to identify aquatic coleopterans of the families Hydropilineae (*Hydrophilus* sp.), Dysticidae (*Megadytes* sp.), Noteridae and Cuculionidae; arachnids of the family Lycosidae; crustaceans of the family Grapsidae, unidentified fishes (Osteichthyes) and a bird of the family Jacanidae (*Jacana* sp.); we were unable to identify fishes to a lower taxonomic level (Table 2). Juveniles presented more invertebrates remains (n = 697) than the other size classes, followed by hatchlings (n = 432) and sub-adults (n = 50); but more vertebrate remains were found in sub-adult stomach contents (n = 138), compared to hatchlings (n = 6) and juveniles (n = 6) (Table 1). In hatchlings, most remains were insects (n = 256) followed by arachnids (n = 117), crustaceans (n = 59), fishes (n = 6), and also some vegetation remains (pieces of leaves and wood, n = 20). In juveniles, insect remains were the most important (n = 462), followed by crustaceans (n = 214), arachnids (n = 21) and fishes (n = 6) remains (Table 1). In juveniles, we also found a solid waste residue (plastic piece, n = 1), vegetation (n = 67), seeds (n = 30) and algae (n = 4) (Table 1). In addition, juvenile was the only size class that presented gastrointestinal parasites (n = 6). In sub-adults, vertebrate remains were the most important (n = 138), corresponding to fishes (n = 78) and birds (n = 60), followed by crustaceans (n = 47), insects (n = 2) and arachnids (n = 1). In this size class we also found solid waste remains (a piece of fishing net, n = 1) and vegetation (n = 31) (Table 1).

True diversity index (1D) indicated very similar effective prey diversity for all 3 size classes (Fig. 2). Sub-adults had the highest value with 4.5 types of effective prey followed by hatchlings (3.5) and juveniles (3.1). The percentage of niche overlap obtained between the 3 size classes was high (> 75.0%). This value was more important among adjacent size classes (i.e., among juveniles and sub-adults = 81.68%, or among hatchlings and juveniles = 79.99%), and lower among remote classes (i.e., among hatchlings and sub-adults = 75.68%). In addition, no difference was found in the composition of the diet among hatchlings, juveniles and sub-adults ($Q_{[Cochran]} = 2.0$, 2 g.l., $p = 0.3678$). Ontogenic tendencies may show that the consumption of insects and arachnids decreases with size, while the consumption of crustaceans and fish increases (Fig. 3). However, no significant differences were found in the abundance of the diet among the 3 size classes ($X^2_{[Friedman]} = 1.9756$, 2 g.l., $p = 0.3759$).

Table 2

Taxonomy of identified remains of 44 spectacled caimans of La Encrucijada, Chiapas.

Identified remains	
Invertebrates	Unidentified insects
Insecta	Arachnidae
Coleoptera	Araneae
Hydropilineae	Lycosidae
Hydrophilus sp.	Acaria
Dysticidae	Unidentified arachnids
Megadytes sp.	Crustaceae
Noteridae	Decapoda
Curculionidae	Brachyura
Hemiptera	Grapsidae
Belostomatidea	Unidentified crustaceae
Lethocerus sp.	Vertebrates
Gerridae	Osteichthyes
Orthoptera	Aves
Acrididea	Charadriiformes
Diptera	Jacanidae
Hymenoptera	*Jacana* sp.
Formicidae	

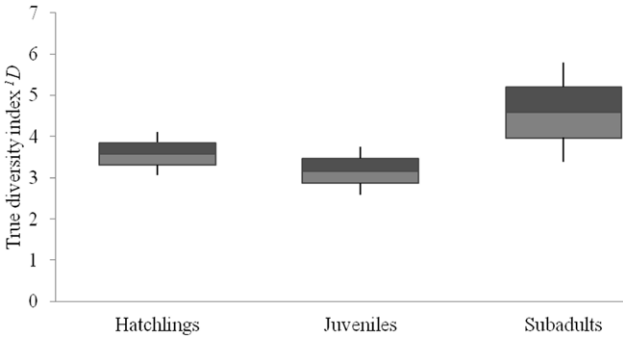

Figure 2. True diversity index of prey of 3 size classes of spectacled caiman at La Encrucijada, Chiapas, with first quartile (dark grey), third quartile (light grey), minimum and maximum (dark lines).

Discussion

The Chiapas spectacled caiman (*C. c. chiapasius*) eats 5 major preys: insects, arachnids, crustaceans, fish and birds. It has been described that *C. c. crocodilus* in Venezuela, Brazil and Peru eats from 4 type of preys:

insects, mollusks, fish and crustaceans (Magnusson et al., 1987; Seijas & Ramos, 1980) to 9 different preys: insects, arachnids, crustaceans, fish, birds, gastropods, amphibians, reptiles and mammals (Da Silveira & Magnusson, 1999; Laverty & Dobson, 2013; Thorbjarnarson, 1993).

The preys number also differs from those found in other crocodilians such as *Crocodylus acutus* and *Crocodylus moreletii* in Belize (Platt et al., 2006; Platt, Thorbjarnarson et al., 2013), *Crocodylus niloticus* in Botswana (Wallace & Leslie, 2008) and *Crocodylus johnstoni* in Australia (Tucker et al., 1996) where amphibians, reptiles, mammals and gastropods were found in high frequencies. The lack of these preys in the diet of *C. c. chiapasus*, points at diet differences with respect to its sister subspecies *C. c. crocodilus* (Da Silveira & Magnusson, 1999; Laverty & Dobson, 2013) or other crocodilians (Platt et al., 2006; Platt, Thorbjarnarson et al., 2013; Tucker et al., 1996; Wallace & Leslie, 2008). It is possible that preys of *C. c. chiapasus* in La Encrucijada tend to be smaller because the caimans are small, and may prevent the intake of larger preys such as terrestrial vertebrates (amphibians, reptiles and mammals). However, it is impossible to be sure due to the lack of sample of sub-adults and adults. In Brazil and Venezuela, it has been reported that the intake of terrestrial vertebrates in *C. c. crocodilus* increases in larger size classes (sub-adults and adults; Magnusson et al., 1987; Thorbjarnarson, 1993). Our sample size of sub-adults and adults was reduced to only 4 caimans, and only sub-adults were used in the study, likely biasing our results.

In *C. c. chiapasius*, aquatic insects appear to be the prey with greater occurrence in the diet of hatchlings and juveniles. About 33.0 to 87.7% of evaluated stomach of *C. c. crocodilus* in Venezuela, Brazil, and Peru (Laverty & Dobson, 2013; Seijas & Ramos, 1980; Thorbjarnarson, 1993) and other crocodilians (Borteiro et al., 2009; Platt et al., 2006; Platt, Thorbjarnarson et al., 2013; Saalfeld et al., 2011; Walace & Leslie, 2008) smaller than 60 cm of SLV, presented insect remains. In contrast, other studies in Brazil and Venezuela (Gorzula, 1978, Magnusson et al., 1987), found that insects are not even part of the normal diet of *C. c. crocodilus*. They suggest that food type intake depends on the habitat where the studies were conducted; e.g., lagoons and rivers (Gorzula, 1978; Magnusson et al., 1987). In contrast to most of the studies published before, our sampling was done in an estuary, probably affecting caiman food type selection.

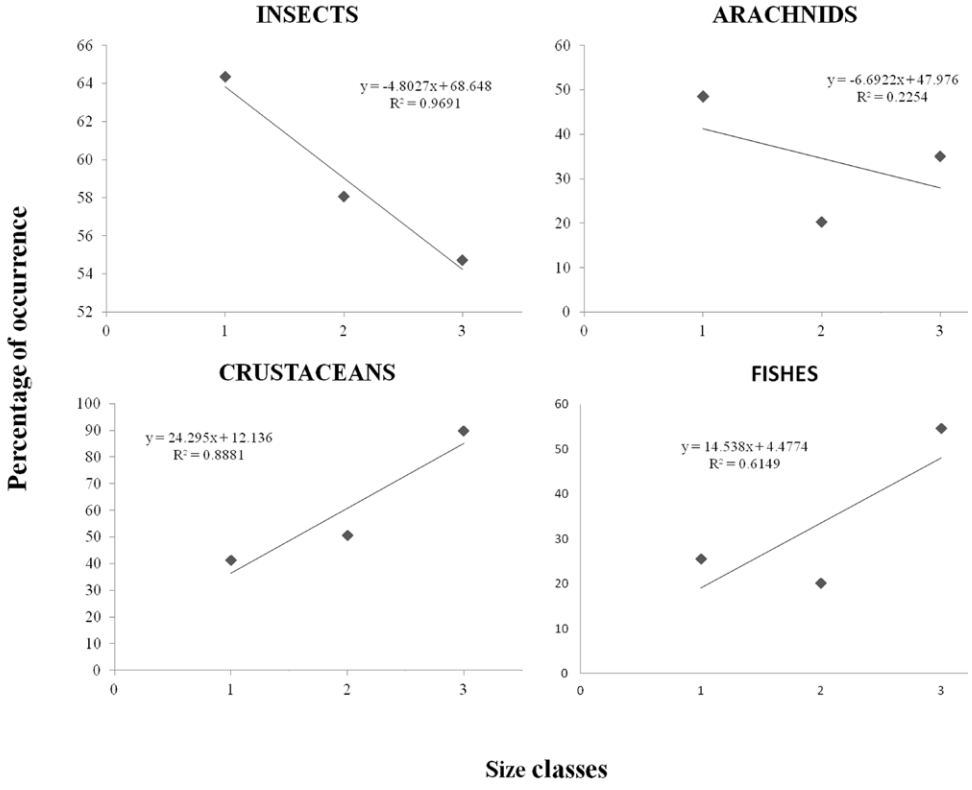

Figure 3. Relationship between size classes and the percentage of occurrence of insects, crustaceans, fish and arachnids. 1: Hatchlings, 2: juveniles, and 3: sub-adults.

The occurrence of crustaceans was significant, being present in all size classes (57.0% total). Former reports in Brazil, Peru and Venezuela indicate that *C. c. crocodilus* also have a high abundance of crustaceans in stomach contents (Da Silveira & Magnusson, 1999; Magnusson et al., 1987; Thorbjarnarson, 1993), or a very low or no consumption of this prey type (Gorzula, 1978; Laverty & Dobson, 2013; Seijas & Ramos, 1980). Since Hueyate estuary is a perennial water body (Carabias et al., 1999), the availability of crustaceans should not be affected throughout the year, becoming the second most important food resource.

Arachnids are the third most important prey for the Chiapas caiman (27.0% total). The occurrence is similar to that reported for *C. c. crocodilus* in Brazil (46% including insects and arachnids; Da Silveira & Magnusson, 1999) and for *C. latirostris* in Uruguay (27.9%; Borteiro et al., 2009). The intake of arachnids in the diet of *C. c. crocodilus* seems to be very low, varying from 0.0% to 3.0% in reports from Brazil, Venezuela and Peru (Gorzula, 1978; Laverty & Dobson, 2013; Magnusson et al., 1987; Seijas & Ramos, 1980; Thorbjarnarson, 1993). In contrast to our results, arachnids appear to have little relevance in caiman's diet.

Fish was consumed in low frequencies (18.0% total) in all size classes of *C. c. chiapasus* in the Hueyate estuary. Our result differed with those reported by Seijas and Ramos (1980), and Da Silveira and Magnusson (1999) who did not found fish traces in smallest size classes of *C. c. crocodilus* in Venezuela and Brazil. In general, crocodilians are piscivorous, principally the adults (Borteiro et al., 2009; Da Silveira & Magnusson, 1999; Laverty & Dobson, 2013; Magnusson et al., 1987; Platt et al., 2006, Platt, Thorbjarnarson et al., 2013; Seijas & Ramos, 1980, Thorbjarnarson, 1993; Tucker et al., 1996; Villegas & Schmitter-Soto, 2008). Within our sample, the consumption of fish in sub-adults increased considerably to 66.6%; however, it must be considered that the number of sub-adults captured was very small and adults are absent in this work. The report of low fish consumption by *C. c. chiapasus* can also be related to the sampling season. In this work we only have data from the dry season and the intake of prey can vary according to water levels (Da Silveira & Magnusson, 1999; Gorzula, 1978; Thorbjarnarson, 1993). Da Silveira and Magnusson (1999) reported that the amount of fish ingested by *C. crocodilus* increases when there is more water in rivers. Thus, information from rainy season is necessary to have a complete image of the diet of *C.c. chiapasius* along the year. Another explanation for the low consumption of fish could be intra-specific and/or inter-specific competition with larger caimans and the larger sympatric American crocodile (*Crocodylus acutus*), respectively. Some captured caimans showed attack marks on their bodies (e.g., broken tail, scars on the back, recent bites on the skull and belly), probably caused by these large crocodilians. There is a possible influence of *C. acutus* on fish availability for caimans; further studies are needed to confirm this.

Terrestrial vertebrates (amphibians, reptiles and mammals) did not appear to be important for the diet of *C. c. chiapasius*, and only 1 bird was found in a single sub-adult specimen. The low consumption of terrestrial vertebrates differs from values of 1.6% and 23% reported for *C. c. crocodilus* in Brazil and Venezuela, respectively (Magnusson et al., 1987; Thorbjarnarson, 1993). Other crocodilians fed on terrestrial vertebrates in higher percentages (3.5 to 51.7%; Borteiro et al., 2009; Casas-Andreu & Barrios-Quiroz, 2003; Horna et al., 2003; Platt et al., 2006; Saalfeld et al., 2011; Villegas & Schmitter-Soto, 2008). The absence of amphibians may be an effect of the salinity of the estuary (10 to 25 ppm; Ocampo & Flores, 1995), which is not suitable for their survival. The absence of mammals and reptiles in stomach contents is surprising as expected in other caimans and crocodiles where these vertebrates are normally present in larger size classes (Magnusson et al., 1987; Thorbjarnarson, 1993). Mammals and reptiles have slow digestion parts, such as scales, or hair, that cannot be digested (Casas-Andreu & Barrios-Quiroz, 2003). If mammals or reptiles would have been eaten by caimans, remains would have been found in the stomach contents.

Shannon entropy index has been used to estimate food intake diversity in crocodilian diet analysis. It has been shown that this index does not represent the real diversity of a community, but it rather throws an uncertainty value of the identity of the species in a sample (Jost, 2006, 2007). To correct this fault, we decided to use the true diversity value (1D), which represents the effective number of species in the sample, in this case, the number of effective preys in the diet of the Chiapas caiman. In juveniles, the effective number of prey types is 1D = 3.1 (= 3 items), which means that 1 of the 4 prey types sampled in this age class (insects, crustaceans, arachnids and fish), is likely to be hunted casually and probably represents an item of low importance for this class. This prey is probably fish, the least consumed item. For hatchlings we found 1D = 3.58 (≈ 4 items) which indicates that all prey types are equally important; same as for sub-adults with 1D = 4.58 (≈ 5 items). However, this last value is unreliable because of the small sample size and because prey frequencies are very similar among individuals. No significant differences were found between diversity among the 3 size classes (Fig. 2). This suggests that the hatchlings, juveniles and sub-adults of *C. c. chiapasius* compete for the same prey. The possible strong competition for food with *Crocodylus acutus* may also limit food resources for caimans.

It is difficult to compare true diversity values (1D) with the entropy index of Shannon (H'), used in former studies. The pattern shown by both indexes may not be the same. Laverty and Dobson (2013), and Wallace and Leslie (2008) reported no important changes in the niche breadth of hatchlings juveniles, sub-adults and adults in *C. c. crocodilus* in Peru, and *Crocodylus niloticus* in Angola (as estimated by H'); however, these authors did not present any statistics to test differences. Other studies based in H' index reported that juvenile and sub-adult crocodilians behave as generalists, but hatchlings and adults as specialists (Platt, Thorbjarnarson et al., 2013; Tucker et al., 1996). Studies based on Shannon H' entropy index do not represent prey type numbers that are truly important in crocodilian diet, ignoring that some preys may be incidental encounters. Based on current knowledge, it is impossible to establish the level of specialization of any kind according to Shannon's diversity index. If the H' indexes are weighted with respect the abundance of each prey type (true diversity, 1D value), it is likely that different conclusions would have been reached.

As expected (e.g., in Platt et al., 2006; Platt, Thorbjarnarson et al., 2013; Tucker et al., 1996), we found higher niche overlap in adjacent size classes as reported in other studies of crocodilians. Also, as expected, the diet overlap between hatchlings and sub-adults is the lowest (75.6%); however, this overlap is quite high compared to what Tucker et al. (1996) and Platt et al. (2006, 2013a) in *C. johnstoni*, and *C. moreletii* and *C. acutus* in Australia and Belize, respectively. These authors found a 64.0% overlap between specimens of 10 to 20 cm and 60 to 70 cm SVL, and 41.6% and 45.7% of overlap between specimens of 15 to 20 cm and 60 to 90 cm of SVL. The high overlap between 3 size classes of *C. c. chiapasius* indicates that there is strong interspecific competition for food resources within the Hueyate estuary.

We found no statistical differences neither in prey type composition ($Q = 2.0$, $p = 0.3678$) or in prey type abundance ($X^2 = 1.9756$, $p = 0.3759$) between size classes of the Chiapas caiman. This result differs from reports by Thorbjarnarson (1993), Seijas and Ramos (1980) and Laverty and Dobson (2013) in *C. c. crocodilus* in Venezuela and Peru, *C. johnstoni* in Australia (Tucker et al., 1996), and *C. acutus* and *C. moreletii* in Belize (Platt et al., 2006, 2013a), which, without a proper statistical test, suggest that the composition and abundance of prey types differs from one size class to another. To make these affirmations more objective, all reports need to be statistically tested. In our study, we also found that there are numerically clear diet changes in *C. c. chiapasius*: hatchlings and juveniles feed mainly on invertebrates (insects, arachnids and crustaceans), while sub-adults add vertebrates to their diet (i.e., fish and birds) (Fig. 3). This agrees with diet ontogenetic changes documented for *C. c. crocodilus* in Venezuela, Brazil and Peru (Da Silveira & Magnusson et al., 1999; Laverty & Dobson, 2013; Thorbjarnarson, 1993), *Melanosuchus niger* in Peru (Horna et al., 2003), and some other crocodilians (Borteiro et al., 2009; Platt et al., 2006, 2013a; Tucker et al., 1996; Wallace & Leslie, 2008). Shift to a vertebrate diet reflects an increase of energy requirements as well as the ability to capture larger prey because of their larger size (Webb et al., 1991).

Finally, we found that the largest proportion of stomach remains in most specimens is vegetable matter that cannot be considered as food. Agreeing with other reports (Casas-Andreu & Barrios-Quiroz, 2003; Seijas & Ramos, 1980; Thorbjarnarson, 1993), vegetable remains in crocodilian stomach contents are accidental during foraging (Platt, Elsey et al., 2013; Platt, Thorbjarnarson et al., 2013; Wallace & Leslie, 2008; Webb et al., 1991). Casas-Andreu and Barrios-Quiroz (2003) considered that crocodilians may function as incidental secondary seed dispersers; however, recent experiments in *Alligator mississippiensis* and *C. acutus* found that seeds recovered from the stomach of these species have very low or no viability (González-Solórzano et al., 2016; Rosenblatt et al., 2014). These facts indicate that it is unlikely that as other crocodilians, *C. c. chiapasius* is an effective seed disperser.

It is striking that we did not found gastroliths in any of the stomach contents of *C. c. chiapasius*. Gastroliths are common in *C. c. crocodilus* (Seijas & Ramos, 1980; Thorbjarnarson, 1993) and other crocodilians (Borteiro et al., 2009; Platt et al., 2006, 2013a; Tucker et al., 1996; Wallace & Leslie, 2008; Webb et al., 1991) when using stomach washing techniques (Taylor et al., 1978). We believe that the lack of gastrolithes in Hueyate estuary caimans is an effect of the geology of the area. The site is dominated by fine grains clay and/or muddy soil, with abundant organic material (Carabias et al., 1999), and small stones are rarely found. It is possible that remains as vegetation may help the digestion process in crocodilians as suggested by Garnett (1985).

This work represents the first effort to study the diet of *C. c. chiapasius* in Mexico and not only through direct observations (e.g., Álvarez-del Toro, 1974). Insects and crustaceans are the most important prey types in the diet of these caimans. Feeding change pattern associated to size class in the Chiapas caiman is similar to that found in other crocodilians; although no statistical differences were found in the composition, abundance and true diversity between hatchlings, juveniles and sub-adults. It is recommended to analyze diet changes through the year, diet variation in different habitats throughout the distribution of the species, increasing the number of sub-adults and adults in the sample, and to compare the diet with the sympatric *C. acutus*. We suggest to use the 1 true diversity index (1D) to

evaluate food intake diversity, and niche breath (specialists vs. generalists) instead of Shannon entropy index H'. We also suggest the use of the statistical test of hypothesis to support numerically different findings in order to drive a more objective conclusion.

Acknowledgments

This work was funded by the Crocodile Specialist Group (CSG) (07/15/2014) to GS. Alicia Rojas (Facultad de Ciencias, UNAM) identified many of the invertebrate food remains. Giovany González Desales, Didier Labarre and Fernando Soria assisted in the field work. Uncle Abel (Humberto Yee) and his family provided field facilities.

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