Management of Biological Invasions (2016) Volume 7, Issue 3: 287–296
DOI: http://dx.doi.org/10.3391/mbi.2016.7.3.08

Research Article

Diet of the non-native spectacled caiman (*Caiman crocodilus*) in Puerto Rico

Damien R. Bontemps[1,]*, Elvira Cuevas[1], Eileen Ortiz[2], Joseph M. Wunderle, Jr.[3] and Rafael L. Joglar[1]

[1]*Department of Biology, University of Puerto Rico—Río Piedras Campus, PO Box 23360, San Juan, Puerto Rico*
[2]*Departamento de Recursos Naturales y Ambientales, PO Box 366147 San Juan, Puerto Rico*
[3]*International Institute of Tropical Forestry, USDA Forest Service, Sabana Field Research Station, HC 02, Box 6205, Luquillo, Puerto Rico*

E-mail addresses: bontempsdamien@gmail.com (DRB), epcuevas@gmail.com (EC), sygmata_pr@yahoo.com (EO), jmwunderle@gmail.com (JMW), rjoglar@gmail.com (RLJ)

**Corresponding author*

Received: 1 September 2015 / Accepted: 28 January 2016 / Published online: 18 March 2016

Handling editor: Matthew A. Barnes

Abstract

The spectacled caiman (*Caiman crocodilus*) was introduced to Puerto Rico over 50 years ago with the Tortuguero Lagoon Natural Reserve (TLNR) as its epicenter, where it is now established as an apex predator. Although concerns have been raised regarding the potential impact of this naturalized predator on Puerto Rico's native fauna, little was known of the caiman's diet on the island. Therefore this study was conducted to determine the diet of the spectacled caiman and its potential impact on island animals. For this study, measurements were obtained from 138 caimans across all life stages (12–94 cm snout–vent length; SVL) from October 2014 to May 2015 within the TLNR. Stomach contents were retrieved and analyzed based on prey category occurrence frequency. In addition, caiman muscle samples were obtained to determine their nitrogen and carbon isotopic signature. Insects were the most abundant prey items encountered with 90.7% and 68.8% in hatchling (SVL < 20 cm) and juvenile (SVL = 20–59.9 cm) stomach respectively. In adult (SVL > 60 cm) caimans, fish remains were the most significant prey items with 38.3% frequency of occurrence. Fish, insects, and gastropods were the only categories of ten designated prey categories to show significant variation among the three caiman age classes. This study provides novel information on dietary habits of spectacled caimans in Puerto Rico relevant to the design of management strategies.

Key words: diet analysis, stomach content, stable isotopes, exotic apex predator, crocodilian

Introduction

The introduction and successful establishment of apex predators has been widely documented as an important cause of biodiversity loss. Invasive top predators have been found to disrupt food webs at multiple trophic levels, modify habitats, out-compete native species for resources or to serve as vectors for disease and parasite transmission (Work et al. 2002; Levy et al. 2008; Mortensen et al. 2008; Dorcas et al. 2011). The lack of co-evolutionary history with non-native species and limited ability to geographically disperse render some native species from insular ecosystems particularly vulnerable to the effects of introduced species (D'Antonio and Dudley 1998; Simberloff 2000; Wiles et al. 2003).

Common methods to assess potential ecological impacts of introduced predators include observations of effects on prey in other geographical locations, correlative studies of predator/prey population dynamics, experimental removal, and dietary studies (Park 2004). The latter method has been widely employed by means of food extraction and stomach content analysis (SCA) across a variety of taxa (Michael Anthony et al. 2000; Pierce et al. 2004; Kidera 2008; Somaweera et al. 2011). Although these methods contribute to our understanding of a predator's diet, they do have some disadvantages. For example, the extensive sample size, labor, cost, and time required to obtain dietary information via SCA makes it a challenging technique to use, particularly when studying a predator feeding on a wide variety of prey (Pethybridge et al. 2011; Bowen and Iverson 2013). Time is of the essence when dealing with recent introductions. In spite of failure to prevent the spread of an exotic, an early detection of the potential effects can play a major role in the careful design of management strategies and establishing priorities for mitigating the threat.

Advances in the field of stable isotope analysis (SIA) have proven to be advantageous in the prediction of foraging impacts in invasive top predators (Bodey et al. 2011). Whereas stomach content analysis (SCA) reveals recently ingested prey items or a snapshot of the diet, SIA provides long-term dietary habits. It can be performed in a timely fashion in order to quickly respond to the threat. Albeit SIA is deficient in providing high taxonomic resolutions of consumed prey species, it reveals the relative diet source proportion with *a priori* knowledge of the prey species inhabiting the novel environment. Especially in the context of a generalist predator, where prey categories rather than specific prey species are to be assessed, SIA provides relevant information to predict direct dietary effects.

The spectacled caiman *Caiman crocodilus* (Linnaeus, 1758), also referred to as common caiman, is a medium-sized crocodilian considered an opportunistic omni-carnivorous species as its diet includes a wide array of invertebrates, fish, amphibians, reptiles, birds, and even mammals for larger specimens (Thorbjarnarson 1993). Less commonly known, part of their diet may include plant material such as seeds, leaves, or even fruits (Platt et al. 2013). The spectacled caiman has been introduced and is considered fully established in Florida (USA) and Isla de la Juventud (Cuba) (Ellis 1980; Estrada and Ruibal 1999). In the 1960's, it was introduced in Puerto Rico principally associated with the legal caiman pet trade during these times (Thomas and Joglar 1996). A combination of deliberate and accidental release from caiman pet owners is likely to be the cause of introduction to the natural environment. Thomas and Joglar (1996) documented the presence of *Caiman crocodilus* in the northern coastal plains of the island with the Tortuguero Lagoon Natural Reserve (TLNR) as its source of proliferation.

In 1985, after an increasing number of sightings within the TLNR and surrounding areas, the Department of Natural and Environmental Resources (DNER) implemented a management plan to eradicate the species from the island. Since then, the frequency of caiman sightings and encounters has increased far beyond the TLNR. Authorities and inhabitants of the San Juan Bay Estuary became concerned with the caiman's presence. As a result, a rapid assessment survey was performed to estimate population abundance and distribution within these areas (Joglar et al. 2010). This study revealed a drastic range expansion since its first appearance in the TLNR and presented numerous reports on caiman sightings and captures at various localities within Puerto Rico's coastal plain and its satellite island of Vieques.

Caiman crocodilus has been extensively studied in its native range including population dynamics, diet, breeding, and harvesting studies (Staton and Dixon 1977; Gorzula 1978; Ayarzagüena 1983; Thorbjarnarson 1993; Allsteadt 1994; Thorbjarnarson and Velasco 1999; Moreno-Arias et al. 2012; Laverty and Dobson 2013). In Puerto Rico, two unpublished population studies have been conducted (Santos Reyes 1988; Joglar et al. 2010). However, despite having been established on the island for over 50 years, there have been no thorough ecological studies of the caiman's effects on the native fauna. Therefore, our study was initiated to address the need for new information on the introduced caiman's foraging behavior in Puerto Rico. The objectives of our study were to use stomach content analysis to provide baseline data on caimans' diet in Puerto Rico and to make recommendations for caiman management, based on the findings of the diet analysis.

Methods

Study area

Caiman crocodilus proliferation in Puerto Rico appears to have initiated from the Tortuguero Lagoon which was designed as a natural reserve in 1971 and currently under the management of the DNER (Schwartz and Henderson 1991; Thomas and Joglar 1996). It is located between the municipalities of Vega Baja and Manatí (N 18.46328 and W -66.43962; Figure 1). The reserve contains the largest freshwater lagoon in Puerto Rico covering an approximate surface area of 2.43 km^2. The lagoon holds a water volume of approximately 2.68 million m^3 with a mean depth of 1.2 m. It is fed by subterranean, mainly fresh water sources in addition to precipitation (approx. 1,600 mm/year) and flushed about 7.5 times per year through a canal built in 1940 leading to the sea on the northeast side (Quiñones-Márquez and Fusté 1978). Other output includes the estimated evapotranspiration rate of 1,274 mm per year. Water temperatures oscillate from 24 ºC to 31 ºC in accord with seasonal changes with the absence of vertical temperature gradients. The wet and dry season occur from May to November and from December to April respectively.

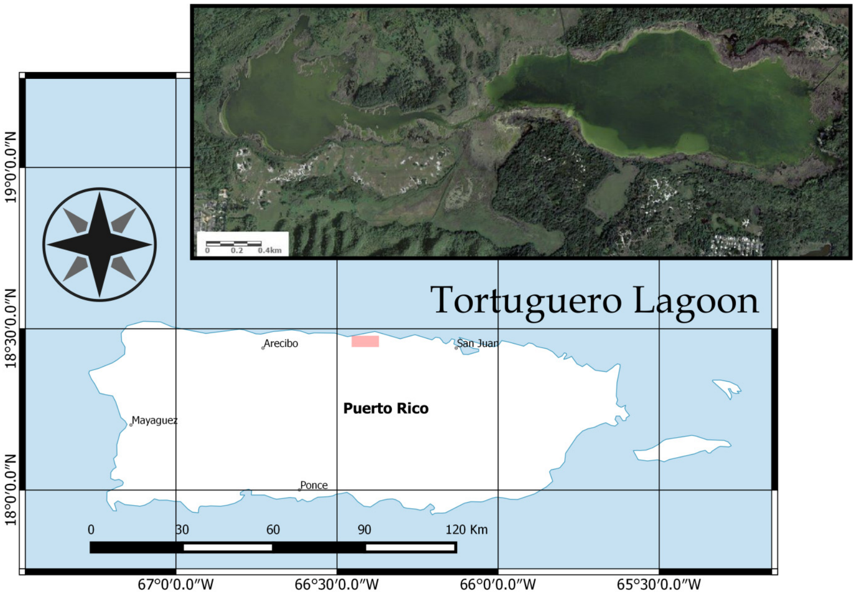

Figure 1. Map of Puerto Rico displaying the location of the Tortuguero Lagoon (in red) including a satellite photographic image.

The lagoon's surrounding habitat composition includes swamps, marshes, coastal shrubs, and hills. Among the 717 plants species recorded from the site are 144 endemic and/or endangered species. Consequently it is considered the fourth most important flora in Puerto Rico. As one of the only two natural reservoirs of the island, the Tortuguero Lagoon is of great ecological importance due to its abundant wildlife including the observed 83 bird species, 23 fish species, native reptiles, and amphibians. It represents a rich and diversified food source for opportunistic foraging by *Caiman crocodilus*.

Sample collection

Between October 2014 and May 2015, 138 recently killed caimans were obtained from the DNER as part of routine night hunts conducted within the lagoon. Typically, no more than ten hours would elapse before stomach contents were extracted except for very few cases in which carcasses were kept frozen until sampled. Total Length (TL) and Snout-to-Vent Length (SVL) were measured ventrally. Due to the presence of sexual dimorphism in which males reach greater size than females, each carcass was categorized into a respective size class based on Snout-to-Vent Length (SVL, cm) following Ayarzagüena (1983). Measured individuals were classified as hatchlings (Size Class I < 20 cm), juveniles (Size Class II = 20–59.9 cm), sub-adults/adult females (Size Class III = 60–89.9 cm), and adult males (Size Class IV ≥ 90 cm). Spring scales of 5 kg, 10 kg, and 20 kg maximums were used to record the weight of larger individuals. A Denver Instrument XL-3100D electric scale (accurate to 0.01g) was used to measure the mass of smaller caimans, mainly hatchlings. Sufficiently large individuals were sexed by finger probing through the cloacal opening. All caimans were dissected and their stomach contents stored in a 70% ethanol solution. In addition, a muscle sample from the thigh of 19 randomly selected subjects of each size class was collected to determine their nitrogen and carbon isotopic signature.

Stomach content analysis

Collected stomach contents were placed in a fine sieve and rinsed out with water to remove mucous substances and gastric juices following the procedure of Thorbjarnarson (1993). Retrieved prey remains were identified to the lowest taxonomic level possible using a dissecting microscope, when necessary, and placed into one of the ten designated prey categories (i.e. birds, mammals, reptiles, amphibians, fish, gastropods, crustaceans, insects, myriapods, arachnids). Some prey parts may remain in the stomach of crocodilians for a much longer period of time than others (e.g. chitinous exoskeleton of insects, keratinized scutes of reptiles) (Garnett 1985; Barr 1997; Janes and Gutzke 2002; Nifong et al. 2012). To reduce some of the bias associated with different rates of digestibility for different prey items, only prey categories presenting substantial evidence of consumption (e.g. recently ingested or partially digested) were recorded. To further minimize this bias, the analysis was performed based on prey category frequency of occurrence (%) rather than quantifying stomach contents' volume or weight. This represents a convenient technique and the most robust and interpretable approach when quantification of individual prey items is difficult (Rosenberg and Cooper 1990, Baker et al. 2014). Another potential bias may occur due to secondary ingestion (e.g. invertebrates consumed by fish consumed by caimans). An overestimation of the importance of a prey category caused by secondarily ingested prey can occur and must be considered when making inferences on foraging habits of larger caimans (Jackson et al. 1974).

A Mann-Whitney U test and a Kruskal–Wallis analysis of variance by ranks were used to determine the level of statistical significance of differences in prey category utilization between sexes and across ontogenetic stages respectively, based on nonnormally distributed dietary data. Furthermore, a Spearman rank correlation test was used to evaluate potential correlation between prey category utilization and caiman size (SVL). These statistical analyses were conducted using R Studio software (R Core Team 2014, version 3.1.2).

Nitrogen and carbon stable isotopes determination

We supplemented the SCA, which provides only a "snapshot" observation of the caiman diet, with nitrogen and carbon isotopic values. The temporal scale of the diet revealed by stable isotopes depends on the type of tissue used such as scutes, teeth, muscles, or blood (Dalerum and Angerbjörn 2005; Lecomte et al. 2011). Moreover, biases associated with different rates of digestion present in SCA are less relevant when using SIA since food is assimilated rather than ingested (Vander Zanden et al. 1997).

Stable carbon isotopes ($\delta^{13}C$) can determine different sources of primary productivity (i.e. the consumer's food source ecosystem or biome) (DeNiro and Epstein 1978; Bodey et al. 2011) whereas stable nitrogen isotopes ($\delta^{15}N$) can be used to identify the trophic positions of both predators and prey revealing a 3–5 ‰ stepwise enrichment with each rise in trophic level (DeNiro and Epstein 1981; Hobson and Clark 1992; Pierce et al. 2004). The delta (δ) notation represents the isotope composition as the ratio of the heavy to the light isotopes (i.e. ^{13}C:^{12}C and ^{15}N:^{14}N). Carbon isotopes are typically compared to the standard reference materials from Vienna PeeDee Belemite (VPDB) whereas nitrogen isotopes are measured relative to ambient air nitrogen. Isotopic values are expressed in parts per thousand (‰) such that:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3 \text{ where,}$$
$$X = {}^{13}C \text{ or } {}^{15}N$$
$$R = {}^{13}C{:}{}^{12}C \text{ or } {}^{15}N{:}{}^{14}N$$

For this study, hind leg muscle samples were collected from caimans of all life stages. These caimans were selected based on stratified random sampling. Samples were dried at 60 ºC (Shellab oven) for 72 hours. They were then reduced to a fine powder processed through the Retsch MM200 grinder for one minute at 27 revolutions per second. Between 0.9 mg and 1.2 mg for each muscle sample was weighed using an electronic scale (Metller Toledo Classic Plus; last calibrated on October 7, 2013) and placed into tin capsules pressed for micro analysis. Capsules were sent to the Stable Isotope Laboratory of Miami University, Florida to determine nitrogen and carbon isotopic compositions.

Potential differences of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopic composition between sexes and life stages were evaluated using MANOVA. When significances were found, ANOVA was then used to enhance the resolution on the contribution of each isotope to the results obtained with MANOVA. Spearman's correlation analysis was used to determine the relationship of nitrogen isotopic compositions and size (SVL).

Results

A total of 138 caimans representing four size classes were captured and sampled. Because only two large males were sufficiently large for inclusion in size class IV (≥ 90 cm SVL), we merged size class IV into size class III. As a result size class III included all adults regardless of their sex or size. The sex of 81 (29 females and 52 males) individuals was successfully determined. Although remains of birds, mammals, and amphibians were only recorded in male caiman stomachs, the Mann-Whitney U Test revealed no significant difference in the consumption of any of the established prey categories between males and females ($P > 0.05$).

Table 1. Prey category, plant material, gastroliths, human refuse, and empty stomachs based on occurrence frequency from spectacled caimans collected in Tortuguero Lagoon, Puerto Rico. n = number of caiman stomachs analyzed in size class I, II, and III (i.e. hatchlings, juveniles, and adults). No. = number of stomachs containing substantial evidence of indicated category.

	Size Class (n)					
	I (43)		II (48)		III (47)	
Prey category	No.	%	No.	%	No.	%
Insects	39	90.7	33	68.8	7	14.9
Fish	0	0.0	9	18.8	18	38.3
Gastropods	1	2.3	12	25.0	10	21.3
Crustaceans	5	11.6	5	10.4	4	8.5
Birds	0	0.0	0	0.0	2	4.3
Mammals	0	0.0	3	6.3	2	4.3
Reptiles	0	0.0	5	10.4	3	6.4
Amphibians	0	0.0	2	4.2	0	0.0
Myriapods	2	4.7	2	4.2	2	4.3
Arachnids	5	11.6	5	10.4	1	2.1
Plant Material	6	14.0	22	45.8	26	55.3
Gastroliths	0	0.0	4	8.3	3	6.4
Human Refuse	0	0.0	2	4.2	6	12.8
Empty	3	7.0	3	6.3	8	17.0

Prey category occurrence frequency

Aquatic insects were the most frequently recovered prey from stomachs (Table 1). Members of the genus *Belostoma* made up the greatest percentage of consumed insects followed by larva of the family Stratiomyidae (Table 2). Fish were another commonly found prey item, especially in adults. Yet only two were successfully identified as *Eleotris* sp. and *Oreochromis* sp. Unlike the fish category, aquatic gastropods were found across all life stages with a higher occurrence frequency of *Melanoides tuberculata* (Müller, 1774) and *Tarebia granifera* (Lamarck, 1822). Members of the genus *Macrobrachium* comprised the majority of the identified crustaceans. Of the arachnids encountered, the majority (81.8%) belonged to the family Pisauridae. Prey from other categories did not represent a substantial component of stomach contents. Gastroliths were recovered only from juvenile (n= 4) and adult (n= 3) stomachs. Plant material, mainly seeds and grass, were found in hatchling (13.4%), juvenile (45.8%), and adult (55.3%) stomachs. Human refuse (e.g. glass, rubber, metal, and plastic material) was found in juvenile (n= 2) and adult (n= 6) stomachs. Empty stomachs were encountered in hatchlings (n= 3), juveniles (n= 3), and adults (n= 8).

Ontogenetic variation of prey category utilization

The frequency of the three most abundant prey categories (i.e. insects, fish, and gastropods) significantly varied across life stages (Figure 2). The consumption of insects decreased as caiman size increased (Spearman r = -0.626, df = 2, $P < 0.001$) whereas consumption of fish increased as caiman size increased (Spearman r = 0.448, df = 2, $P < 0.001$). Gastropod consumption was very low in hatchlings, peaked in juveniles, and slightly decreased in adult caimans (Spearman r = 0.448, df = 2, $P < 0.001$).

Carbon and nitrogen isotopic values

A total of 19 caimans from different life stages were used to obtain carbon and nitrogen isotopic values (Table 3). δ^{13}C and δ^{15}N isotope composition did not differ significantly ($P > 0.05$) between male and female caimans. However, stable isotope composition did show significant variation across ontogenetic stages (MANOVA: $F_{2,16} = 5.35$; $P = 0.002$). A separate analysis revealed that δ^{13}C was statistically indistinguishable among life stages (ANOVA: $F_{2,16} = 51.62$; $P = 0.228$) whereas δ^{15}N differed significantly (ANOVA: $F_{2,16} = 13.71$; $P < 0.001$) among life stages. The Tukey's test revealed a significant ($P < 0.05$) difference in δ^{15}N values among all stages except between hatchlings and juveniles. A significant positive relationship was found between δ^{15}N and SVL when hatchlings were excluded (Spearman r = 0.539, df = 13, $P < 0.047$; Figure 3).

Discussion

The findings of the stomach contents analysis were, to some extent, similar to those reported from native *Caiman crocodilus* in regions of the Amazon (Magnusson et al. 1987; Laverty and

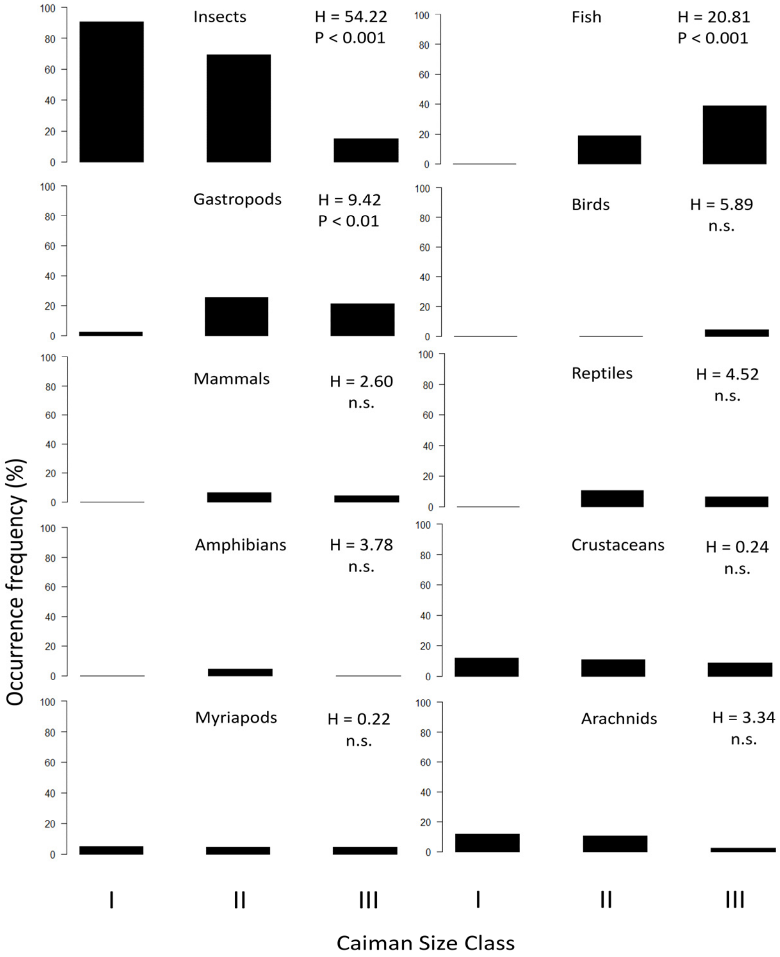

Figure 2. Variation in prey category occurrence frequency across spectacled caiman size classes I, II, and III (i.e. hatchlings, juveniles, and adults) with respective level of significance (P-value) from stomachs of 138 caimans collected in the Tortuguero Lagoon, Puerto Rico. The Kruskal-Wallis statistic (H) shows the degree of discrepancy among rank sums (i.e. a higher H value represents a higher discrepancy among size classes).

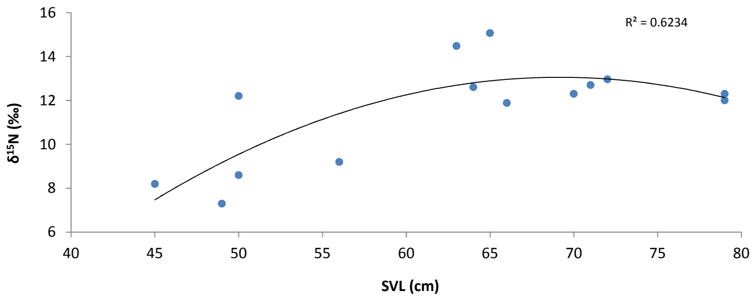

Figure 3. Relationship between stable isotope compositions of $\delta^{15}N$ and SVL of sampled spectacled caimans in the Tortuguero Lagoon. The trend line represents a significant ($P < 0.047$) positive relationship between δ15N and SVL when excluding hatchlings from the analysis.

Dobson 2013) and in the central Venezuelan Llanos (Thorbjarnarson 1993). For instance, the increase in consumption of fish and the decrease in that of insects with size occurred in spectacled caiman native and introduced ranges. Such patterns have been previously reported in many dietary studies of crocodilians and occur presumably as a mean to reduce intraspecific competition among life stages along with the ability to consume larger prey as crocodilians gape size increases (Horna et al. 2001). Our findings were similar to those of Thorbjarnarson 1993 where some of the most frequently consumed invertebrates were aquatic aquatic coleopterans and hemipterans (predominantly Belostomatidae). However, in caimans from the central Venezuelan Llanos, no dipterans were reported

Table 2. Identified taxa with percentage contribution of the respective prey category (e.g. Larva species of the Order Diptera were found in 54.4% of the stomachs containing the insect category) from stomach contents of spectacled caimans collected in Tortuguero Lagoon, Puerto Rico.

Prey Item	Composition (%)
Insects	
Diptera (Larva)	54.4
Belostoma sp.	43.0
Phyllophaga sp.	27.8
Dytiscidae	27.8
Odonata (Larva)	10.2
Unid. Coleoptera	6.4
Gerridae	6.3
Ephemeroptera	3.8
Hymenoptera	3.8
Hydrophilidae	1.3
Fish	
Eleotris sp.	3.7
Oreochromis sp.	3.7
Unidentified	96.3
Gastropods	
Melanoides tuberculata	47.8
Tarebia granifera	39.1
Marisa cornuarietis	13.0
Neritina sp.	8.6
Bulimulus guadalupensis	4.3
Birds	
Gallus gallus domesticus	100.0
Mammals	
Mus musculus	60.0
Unidentified	40.0
Reptiles	
Trachemys scripta elegans	50.0
Trachemys stejnegeri stejnegeri	25.0
Caiman crocodilus	25.0
Amphibians	
Lithobates catesbeianus	50.0
Unidentified Anuran	50.0
Crustaceans	
Macrobrachium sp.	28.5
Palaemon pandaliformis	14.3
Unidentified	64.3
Myriapods	
Diplopoda	100.0
Arachnids	
Pisauridae	90.9
Hydrachnidiae	9.1

in the diet whereas in the non-native caiman, larva from the families Stratiomyidae, Syrphidae, and Tabanidae combined represented the major component (54.4%) of the ingested insects. In some of the smaller caiman stomachs, as many as 6 to 8 individual dipteran larvae were observed, but recorded only as a single entry for the presence of insects based on the occurrence frequency analysis. Freshwater prawns of the genus *Macrobrachium* and shrimps constituted the majority of identified crustaceans in our study with the exception of a fragment of a crab's claw recovered from a single stomach. This is, in contrast to the Llanos caimans (Thorbjarnarson 1993) where the freshwater crab, *Dilocarcinus dentatus* (Randall, 1839) was the only crustacean species reported in the diet.

In spite of high dietary similarities, it was not surprising to find some differences in composition of ingested prey given the opportunistic and generalist nature of the spectacled caiman's foraging behavior. Its diet is expected to reflect the prey composition of its environment (Magnusson et al. 1987), thus, explaining the variation in the occurrence frequency of some taxa. As in many other crocodilian species, results indicated a much higher consumption of aquatic than terrestrial prey. The two most commonly encountered terrestrial prey were beetles of the genus *Phyllophaga* (Scarabaeidae) and mice *Mus musculus* (Linnaeus, 1758). The former was frequently observed (pers. obs., D.R.B.) clinging to surrounding aquatic vegetation (mainly *Typha domingensis*). These nocturnal beetles are known to be attracted to light and are considered to be poor flyers compared to other flying insects. It is possible that their attraction to the reflection of the moon in the lagoon or other light sources accounts for their presence in the water (P. Gutiérrez, pers. comm. 2015). *Mus musculus* is a capable swimmer particularly in still water bodies (Hiadlovská et al. 2012) and may have been captured while swimming on the water surface. The only evidence of bird consumption included parts of a chicken (*Gallus gallus domesticus*) found in two adult males, one of them containing a curled up metal wire possibly used for restraining live bait. The absence of some of the largest vertebrates of the area (e.g. domestic mammals, iguanas, aquatic birds) in caiman stomachs may have resulted from the scarcity of size class IV caimans in the study site. The lack of this size class is most likely due to human persecution of these larger caimans.

Although caimans are known to be territorial (especially adult males), heavy hunting activities in these areas may be responsible for a constant immigration flow from nearby areas as unattended territories become available. To support this speculation, during every night when collecting samples at the lagoon, 20–30 caiman were sighted regardless of the number removed. Their seemingly rapid dispersal behavior and ability to fill empty territories undoubtedly contributed to their successful establishment in Puerto Rico.

Nitrogen isotopic values significantly varied across ontogenetic stages representing food assimilated

Table 3. Mean (±SD) $\delta^{15}N$ and $\delta^{13}C$ values for spectacled caiman muscle samples collected from the Tortuguero Lagoon, Puerto Rico. Sample size (n) and snout-vent length (SVL) are also displayed.

Sampling Source	n	SVL (cm)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Adult Males	5	72.60 ± 6.43	12.38 ± 0.28	-26.56 ± 1.44
Adult Females	4	66.50 ± 3.87	13.60 ± 1.45	-26.11 ± 2.42
Juveniles	5	50.00 ± 3.94	9.10 ± 1.86	-26.74 ± 1.50
Hatchlings	5	14.38 ± 0.70	10.98 ± 1.05	-25.17 ± 2.11

from different trophic levels for all except between hatchlings and juveniles (Table 3). In fact, the mean nitrogen values were found to be higher in hatchlings than juveniles. Such results are seemingly contradictory to the expectation that nitrogen isotope composition increases with trophic level and size (Hobson and Clark 1992; Pierce et al. 2004). However, hatchlings may have assimilated higher nitrogen values through the yolk sac content maternally provided as observed in a previous study of Nile crocodiles (Radloff et al. 2011). A subsequent decrease in nitrogen signature could have occurred as the maternal signature faded and recently hatched caimans started foraging on prey with lower nitrogen levels. Consequently, we excluded hatchlings from the analysis of the relationship between caiman SVL and nitrogen isotopic values.

A determination of the foraging habits of spectacled caimans in Puerto Rico would be better performed using a combination of SCA and SIA rather than any one method alone. This study represents a baseline, the first study conducted on dietary habits of this exotic predator since its introduction over 50 years ago. Appropriate introduced population management is a delicate task and one that must be carefully carried out, especially when dealing with an established exotic predator, as their removal can have undesired consequences on ecosystems (Prugh et al. 2009; Courchamp et al. 2011). Meckstroth et al. (2007) advise resource managers to obtain comprehensive knowledge of an introduced predator's diet before implementing removal protocols. In this study, we have documented that predation on vertebrate native species was rare and included only two hatchling Puerto Rican sliders (*Trachemys stejnegeri stejnegeri*) and a single spinycheek sleeper (*Eleotris* sp.). We found no evidence of predation on endangered species. In contrast, we detected a much higher percentage of non-native prey including some considered as invasive species in the stomach samples.

To date, there is no substantial evidence that the spectacled caiman has a significant direct impact at multiple trophic levels or is the cause of major food web disruption on the island. The caiman's diversified diet as opposed to a selective one may minimize its predation pressure on any specific prey population. Likewise, it could be responsible for mesopredator population control providing some predator release at lower trophic levels. To further our understanding of its foraging behavior, similar dietary studies combining stomach content and stable isotope analysis should be performed in areas where larger caimans (size class IV) are more common as their diet may include vertebrate species larger than those found in our study. Aquatic bird species are of particular concern as they share a common environment with caimans and are likely to be included in the diet of larger individuals. For example, Thorbjarnarson (1993) identified 28.6% of all birds found in spectacled caiman stomachs as *Porphyrula martinica*. In the Tortuguero Lagoon natural reserve, 35 species of aquatic birds have been reported, of which, 22 species are native and the rest are resident to Puerto Rico. Despite an active population management program, changes in bird population dynamics in or outside the Tortuguero Lagoon natural reserve remain virtually unmonitored, an essential but often omitted step required to effectively assess this exotic species' effect on the ecosystem. Based on the results of this diet analysis, we recommend that natural resource managers locate hot spots for concentration of size class IV caimans on the island, especially where aquatic birds are highly abundant and diversified. We further recommend thorough monitoring of both predator and concerned prey population in these zones before and after initiating caiman population control plans. This former step may provide clarity on the degree of impact, if any, on specific prey population with respect to locality. Furthermore, we encourage managers and scientists alike to collaborate in providing exotic caiman population estimates, current distribution, and growth rates as essential parameters in the management of this species.

Acknowledgements

This study was partially financed by the Center for Applied Tropical Ecology and Conservation (CATEC) and by the Proyecto Coquí. Permits to access the Tortuguero Lagoon Natural Reserve were obtained from the Department of Natural and Environmental Resources (DNER). We thank those that provided valuable support and feedback throughout the development of the project: R. Thomas, M. Garcia, T. Giray, P. Burrowes, and S. Vega. Two anonymous reviewers and the editor provide helpful comments. We also thank the members of the Puerto Rico Joint Forces of Rapid Action (FURA) of Vega Baja for their considerable efforts in securing research equipment and ensuring a safe working environment throughout the completion of this study. A. Cotto and the official vehicle maintenance university workshop staff made a generous contribution enabling ground and aquatic transportation. We benefited and are grateful for the many other services provided by the University of Puerto Rico, Río Piedras. We extend our sincere gratitude to the many research assistants and volunteers that participated in the field and laboratory data collection and analysis: A. Figueroa, J. Gutierrez, J. Morales, F. Rodriguez, P. Gonell, A. Rosado, V. Couvas, S. Furumo, O. Torres, D. David, L. Santiago, P. Furumo, B. Van Schooten, P. Caligari, G. Castro, L. Pacheco, D. Cruz, B. Garcia, T. Hernandez, Y. Figueroa, P. Oneil, D. Fontanez, and J. Santiago. Furthermore, A. Ramírez, P. Gutiérrez, S. Kelly, J. Ackerman, M. Aboukheir, and O. Acevedo kindly provided the resources or/and spent the time to identify some of the prey species found in caimans' stomach. This study complied with guidelines and recommendations provided by the university's Institutional Animal Care and Use Committee (IACUC).

References

Allsteadt J (1994) Nesting ecology of *Caiman crocodilus* in Caño Negro, Costa Rica. *Journal of Herpetology* 28: 12–19, http://dx.doi.org/10.2307/1564674

Ayarzagüena J (1983) Ecología del Caimán de anteojos o baba (*Caiman crocodilus* L.) en los llanos de Apure (Venezuela). *Doñana Act. vert. N° especiall*, 10–3: 136

Baker R, Buckland A, Sheaves M (2014) Fish gut content analysis: robust measures of diet composition. *Fish and Fisheries* 15: 170–177, http://dx.doi.org/10.1111/faf.12026

Barr B (1997) Food habits of the American alligator, *Alligator mississippiensis*, in the Southern Everglades. Ph.D. Dissertation. University of Miami, Coral Gables, FL, 243 pp

Bodey TW, Bearhop S, McDonald RA (2011) Invasions and stable isotope analysis – informing ecology and management. In: Veitch CR, Clout MN, Towns DR (eds), Island invasives: eradication and management, IUCN, Gland, Switzerland, pp 148–151

Bowen WD, Iverson SJ (2013) Methods of estimating marine mammal diets: a review of validation experiments and sources of bias and uncertainty. *Marine Mammal Science* 29: 719–754, http://dx.doi.org/10.1111/j.1748-7692.2012.00604.x

Cott HB (1961) Scientific Results of an Inquiry into the Ecology and Economic Status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *Transactions of the Zoological Society of London* 29: 211–357, http://dx.doi.org/10.1111/j.1096-3642.1961.tb00220.x

Courchamp F, Caut S, Bonnaud E, Bourgeois K, Angulo E, Watari Y (2011) Eradication of alien invasive species: surprise effects and conservation successes. In: Veitch CR, Clout MN, Towns DR (eds), Island invasives: eradication and management. IUCN, Gland, Switzerland, pp 285–289

Dalerum F, Angerbjörn A (2005) Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. *Oecologia* 144: 647–658, http://dx.doi.org/10.1007/s00442-005-0118-0

D'Antonio CM, Dudley TL (1998) Biological invasions as agents of change on islands versus mainlands. In: Vitousek PM, Loope LL, Adsersen H (eds), Islands: Biological Diversity and Ecosystem Function. Springer, Berlin, pp 103–121, http://dx.doi.org/10.1007/978-3-642-78963-2_9

DeNiro M, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42: 495–506, http://dx.doi.org/10.1016/0016-7037(78)90199-0

DeNiro M, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* 45: 341–351

Dorcas ME, Willson JD, Reed RN, Snow RW, Rochford MR, Miller MA, Meshaka Jr. WE, Andreadis PT, Mazzotti FJ, Romagosa CM, Hart KM (2011) Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proceedings of the National Academy of Sciences of the United States of America* 109: 2418–2422, http://dx.doi.org/10.1073/pnas.1115226109

Ellis TM (1980) *Caiman crocodilus*: An Established Exotic in South Florida. *Copeia* 1: 152–154, http://dx.doi.org/10.2307/1444148

Estrada A, Ruibal R (1999) A Review of Cuban Herpetology. In: Crother BI (ed), Caribbean Amphibians and Reptiles. Academic Press, San Diego, 495 pp, http://dx.doi.org/10.1016/B978-012197955-3/50014-8

Garnett S (1985) The consequences of slow chitin digestion on crocodilian diet analyses. *Journal of Herpetology* 19: 303–304, http://dx.doi.org/10.2307/1564189

Gorzula SJ (1978) An Ecological Study of *Caiman crocodilus crocodilus* Inhabiting Savanna Lagoons in the Venezuelan Guayana. *Oecologia* 35: 21–34, http://dx.doi.org/10.1007/BF00345539

Hiadlovská Z, Strnadová M, Macholán M, Vošlajerová Bímová B (2012) Is water really a barrier for the house mouse? A comparative study of two mouse subspecies. *Folia Zoologica* 61(3–4): 319–329

Hobson KA, Clark RG (1992) Assessing Avian Diets Using Stable Isotopes 1. Turnover of ^{13}C in Tissues. *The Condor* 94: 181–188, http://dx.doi.org/10.2307/1368807

Horna JV, Cintra R, Vasquez Ruesta P (2001) Feeding ecology of black caiman *Melanosuchus niger* in a western Amazonian forest: The effects of ontogeny and seasonality on diet composition. *Ecotropica* 7: 1–11

Jackson JF, Campbell HW, Campbell KE (1974) The Feeding Habits of Crocodilians: Validity of the Evidence from Stomach Contents. *Journal of Herpetology* 8: 78–381, http://dx.doi.org/10.2307/1562912

Janes D, Gutzke WHN (2002) Factors Affecting Retention Time of Turtle Scutes in Stomachs of American Alligators, *Alligator mississippiensis*. *American Midland Naturalist* 148: 115–119, http://dx.doi.org/10.1674/0003-0031(2002)148[0115:FARTOT]2.0.CO;2

Joglar RL, Soler Figueroa WE, Santiago L, Vélez N (2010) A Rapid Assessment Survey of the Distribution and Abundance of the Spectacled Caiman (*Caiman crocodilus*) in the San Juan Bay Estuary, Puerto Rico. Unpublished report to the San Juan Bay Estuary Program, pp 23–25

Kidera N, Tandavanitj N, Oh D, Nakanishi N, Satoh A, Denda T, Izawa M, Ota H (2008) Dietary Habits of the Introduced Cane Toad *Bufo marinus* (Amphibia: Bufonidae) on Ishigakijima, Southern Ryukyus, Japan. *Pacific Science* 62: 423–430, http://dx.doi.org/10.2984/1534-6188(2008)62[423:DHOTIC]2.0.CO;2

Laverty TM, Dobson AP (2013) Dietary Overlap between Black Caimans and Spectacled Caimans in the Peruvian Amazon. *Herpetologica* 69: 91–101, http://dx.doi.org/10.1655/HERPETOLOGICA-D-12-00031

Lecomte N, Ahlstrøm Ø, Ehrich D, Fuglei E, Ims RA, Yoccoz NG (2011) Intrapopulation Variability Shaping Isotope Discrimination and Turnover: Experimental Evidence in Artic Foxes. *PLoS ONE* 6(6): e21357, http://dx.doi.org/10.1371/journal.pone.0021357

Levy JK, Crawford PC, Lappin MR, Dubovi EJ, Levy MG, Alleman R, Tucker SJ, Clifford EL (2008) Infectious Diseases of Dogs and Cats on Isabela Island, Galapagos. *Journal of Veterinary Internal Medicine* 22: 60–65, http://dx.doi.org/10.1111/j.1939-1676.2007.0034.x.

Magnusson WE, Vieira da Silva E, Lima AP (1987) Diets of Amazonian Crocodilians. *Journal of Herpetology* 21: 85–95, http://dx.doi.org/10.2307/1564468

Meckstroth AM, Miles AK, Chandra S (2007) Diets of Introduced Predators Using Stable Isotopes and Stomach Contents. *Journal of Wildlife Management* 71: 2387–2392, http://dx.doi.org/10.2193/2005-527

Michael Anthony R, Barten NL, Seiser PE (2000) Foods of Artic Foxes (*Alopex lagopus*) During Winter and Spring in Western Alaska. *Journal of Mammalogy* 81: 820-828, http://dx.doi.org/10.1644/1545-1542(2000)081<0820:FOAFAL>2.3.CO;2

Moreno-Arias RA, Ardila-Robayo MC, Martínez-Barreto W, Suárez-Daza RM (2012) Population ecology of spectacled caiman (*Caiman crocodilus fuscus*) in Magdalena River Valley (Cundinamarca, Colombia). *Caldasia* 35(1): 25 – 36

Mortensen HS, Dupont YL, Olesen JM (2008) A snake in paradise: Disturbance of plant reproduction following extirpation of bird flower-visitors on Guam. *Biological Conservation* 141: 2146–2154, http://dx.doi.org/10.1016/j.biocon.2008.06.014

Nifong J, Rosenblatt AE, Johnson NA, Barichivich W, Silliman BR, Heithaus MR (2012) American alligator digestion rate of blue crabs and its implications for stomach contents analysis. *Copeia* 2012 (3): 419–423, http://dx.doi.org/10.1643/ce-11-177

Park K (2004) Assessment and management of invasive alien predators. *Ecology and Society* 9(2): 12

Pethybridge H, Daley RK, Nichols PD (2011) Diet of demersal sharks and chimaeras inferred by fatty acid profiles and stomach content analysis. *Journal of Experimental Marine Biology and Ecology* 409(1–2): 290–299, http://dx.doi.org/10.1016/j.jembe.2011.09.009

Pierce GJ, Santos MB, Learmonth JA, Mente E, Stowasser G (2004) Methods for Dietary Studies on Marine Mammals. In: Understanding the Role of Cetaceans in the Marine Ecosystem. CIESM Workshop Monograph, Commission Internationale pour l'exploration Scientifique de la mer Méditerranée, Monaco

Platt S, Elsey RM, Liu H, Rainwater TR, Nifong JC, Rosenblatt AE, Heithaus MR, Mazzotti FJ (2013) Frugivory and seed dispersal by crocodilians: an overlooked form of saurochory? *Journal of Zoology* 291: 87–99, http://dx.doi.org/10.1111/jzo.12052

Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS (2009) The Rise of the Mesopredator. *BioScience* 59: 779–791, http://dx.doi.org/10.1525/bio.2009.59.9.9

Quiñones-Márquez F, Fusté LA (1978) Limnology of Laguna Tortuguero, Puerto Rico. Unpublished report for the U.S. Geological Survey, Water Resources Division

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/ (accessed June 14, 2015)

Radloff FGT, Hobson KA, Leslie AJ (2011) Characterising ontogenetic niche shifts in Nile crocodile using stable isotope ($\delta^{13}C$, $\delta^{15}N$) analyses of scute keratin. *Isotopes in Environmental and Health Studies* 48: 439–456, http://dx.doi.org/10.1080/10256016.2012.667808

Rosenberg KV, Cooper RJ (1990) Approaches to Avian Diet Analysis. *Studies of Avian Biology* 13: 80–90

Santos Reyes R (1988) Programa de control poblacional de caimans (*Caiman crocodilus fuscus*) en Laguna Tortuguero. Unpublished Report: XIV Simposio de Recursos Naturales, 123 pp

Schwartz A, Henderson RW (1991) Amphibians and Reptiles of the West Indies:Descriptions, Distributions, and Natural History. University of Florida Press, Gainesville, 720 pp

Simberloff D (2000) Extinction-proneness of Island Species – Causes and Management Implications. *The Raffles Bulletin of Zoology* 48(1): 1–9

Somaweera R, Webb JK, Shine R (2011) Determinants of Habitat Selection by Hatchling Australian Freshwater Crocodiles. *PLoS ONE* 6: e28533, http://dx.doi.org/10.1371/journal.pone.0028533

Staton MA, Dixon JR (1977) Breeding Biology of the Spectacled Caiman, *Caiman crocodilus crocodilus*, in the Venezuelan Llanos. Fish and Wildlife Service Wildlife Research Report 5, Washington D.C.

Thomas R, Joglar R (1996) The herpetology of Puerto Rico, past, present and future. In: Figueroa Colón JC (ed), The Scientific Survey of Puerto Rico and Virgin Islands. An Eighty-Year Reassessment of the Island's Natural History. Annals of the New York Academy of Sciences, 766, 264 pp, http://dx.doi.org/10.1111/j.1749-6632.1996.tb17420.x

Thorbjarnarson JB (1993) Diet of the Spectacled Caiman (*Caiman crocodilus*) in The Central Venezuelan Llanos. *Herpetologica* 59(1): 108–117

Thorbjarnarson JB, Velasco A (1999) Economic Incentives for Management of Venezuelan Caiman. *Conservation Biology* 13: 397–406, http://dx.doi.org/10.1046/j.1523-1739.1999.013002397.x

Vander Zanden MJ, Cabana G, Rasmussen JB (1997) Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (δ15N) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Sciences* 54(5): 1142–1158, http://dx.doi.org/10.1139/cjfas-54-5-1142

Wiles GJ, Bart J, Beck Jr. RE, Aguon CF (2003) Impacts of the Brown Tree Snake: Patterns of Decline and Species Persistence in Guam's Avifauna. *Conservation Biology* 17: 1350–1360, http://dx.doi.org/10.1046/j.1523-1739.2003.01526.x

Work TM, Massey JG, Lindsay DS, Dubey JP (2002) Toxoplasmosis in three species of native and introduced Hawaiian birds. *Journal of Parasitology* 88: 1040–1042, http://dx.doi.org/10.1645/0022-3395(2002)088[1040:TITSON]2.0.CO;2