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DIETARY OVERLAP BETWEEN BLACK CAIMANS AND SPECTACLED CAIMANS IN THE PERUVIAN AMAZON

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ABSTRACT: The Black Caiman (*Melanosuchus niger*) experienced a dramatic population decline in the mid-20th century, becoming extinct or locally rare over most of its range due to habitat destruction and the commercial value of its hide. As the success and re-establishment of the species is now dependent on conservation efforts throughout the Amazon basin, Black Caimans require continuous monitoring despite extensive current legal protection. Although such efforts have mitigated the threat of human harvesting, a key issue facing the species today is ecological competition from sympatric Spectacled Caimans (*Caiman crocodilus*). In this study, we investigated this inferred competition by detailing the dietary overlap between Black Caimans and Spectacled Caimans in the Pacaya Samiria National Reserve in 2009. Using an adaptation of the hose-Heimlich technique, we collected and then compared the stomach contents of several individuals of each species. We found that although the proportions of prey items in their stomach contents varied seasonally, the dietary overlap between the two species remained high, suggesting intense competition for food resources. In addition to seasonal changes, the diet composition of Black Caimans also shifted ontogenetically. Young Black Caimans primarily ate insects and crustaceans, whereas larger individuals mostly preyed on fish, reducing intraspecific competition between crocodilian adults and young. Our findings suggest that Spectacled Caimans will continue to hinder the recovery of the Black Caiman population.

Key words: *Caiman crocodilus*; Conservation dependent; Diet composition; *Melanosuchus niger*; Niche partitioning; Population recovery

MANY OF the living crocodilian species are in decline across the world (Plotkin et al., 1983; Gibbons et al., 2000; Revenga et al., 2005). The primary reasons for this decrease include habitat destruction or modification (Thorbjarnarson, 1989; Brazaitis et al., 1996; Ross, 1998; Uryu et al., 2001; Revenga et al., 2005), hunting for the skin trade and for bush meat (Smith, 1980; Da Silveira and Thorbjarnarson, 1999), accidental drowning in fishing nets (Whitaker, 1987; Platt and Thorbjarnarson, 2000), and direct killing due to perceived threats to humans and domestic animals (Plotkin et al., 1983; Horna et al., 2001). Yet although many of the larger species in northern Amazonia are considered conservation dependent and are already extinct over much of their former range, several smaller species are relatively abundant and among the world's least endangered crocodilians.

The Black Caiman (*Melanosuchus niger*) is the largest Amazonian predator and by far the largest of any Neotropical crocodilian. It once

populated every Amazonian country with the exception of Venezuela and Suriname. During the last century, however, Black Caimans faced a high rate of habitat loss and considerable hunting pressures from the leather industry (Smith, 1980; Plotkin et al., 1983), precipitating a total population decrease by as much as 90% (Ross, 1998). Today, field surveys find that Black Caimans are either locally extinct or reduced in density across the Amazon basin (Rebêlo and Lugli, 2001). Recovered populations may exist in Brazil due to the complete protection of the species (Rebêlo and Magnusson, 1983; Da Silveira and Thorbjarnarson, 1999), and in Guyana (Uruena, 1990), but several ecological factors limit the overall recovery of the Black Caiman in the Amazon basin.

Black Caimans live in slow-moving, freshwater rivers, lakes, wetlands, black-water swamps, and seasonally flooded areas of the Amazon River basin. Black Caimans overlap ecologically and compete with Spectacled Caimans (*Caiman crocodilus*), which are smaller and more opportunistic (Rebêlo and Magnusson, 1983; Herron, 1991, 1994; Thorbjarnarson, 1996), with a population growth rate four times higher than that of the Black

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Caiman (Farias et al., 2004). Although Magnusson (1985) found that sympatric Black Caimans and Spectacled Caimans occupied different microhabitats, they have been found in proximity, including sightings within a meter of one another (T. Lavery, personal observation). The two species not only occur in similar habitats, but they also prey on the same food types (Magnusson et al., 1987). Therefore, the ecological competition that exists between the Black Caiman and the Spectacled Caiman may be playing an important role in slowing the Black Caiman's natural recovery in the Amazon basin (Magnusson, 1982).

Although we have a good understanding of dietary composition in Spectacled Caimans (Gorzula, 1978; Fitzgerald, 1988; Thorbjarnarson, 1993), fewer studies exist detailing the feeding behavior and diet composition of Black Caimans, especially in western Amazonia (Magnusson et al., 1987; Da Silva and Magnusson, 1999; Horna et al., 2001). The objective of this study was to analyze the dietary compositions of a population of Black Caimans and Spectacled Caimans in an area of western Amazonia with minimal human influence, and to determine the extent of interspecific dietary overlap, as well as inter- and intraspecific ontogenetic and seasonal changes in diet. We predicted that both species would experience seasonal changes in diet given the changes in prey availability, whereas the diets of younger crocodilians would differ from older individuals to minimize competition. If dietary niche separation was not pronounced between Black Caimans and Spectacled Caimans, then we expected high prey overlap despite the seasonal and ontogenetic differences.

MATERIALS AND METHODS

Study Sites

The Pacaya Samiria National Reserve (20,800 km²) is situated in the northeastern Peruvian Amazon, southwest of the city of Iquitos in the Loreto Region (5°21'S, 74°30'W, ~90 m elevation; datum = WGS84). This tropical reserve has a mean annual rainfall of over 2900 mm. Palm swamps and seasonally flooded forests along with other

wetlands compromise 90% of Pacaya Samiria's landscape in addition to several rivers, lakes, and side channels located within the reserve (González, 1999; Anderson et al., 2009). The majority of rains occur between October and May when most of the land becomes flooded. Water levels peak in March–May and are at their lowest in August–September (Soini, 1995).

The Samiria River is a black-water river system, which is characterized by low sediment loads and a brown coloration from the organic acids found in plant litter (Magnusson, 1985). Several lakes, including Atun Lake, border the Samiria River and are periodically connected to the river through seasonal channels. Caimans are found in all water bodies and in the seasonally flooded forest when water levels are high. Nocturnal surveys conducted since the 1970s have indicated some signs of Black Caiman population recovery in Pacaya Samiria National Reserve (Verdi et al., 1980; Vasquez, 1981, 1982; Street, 2003; Bodmer et al., 2005). Although the species is considered widespread today in the Samiria River basin with clear signs of recovery, Black Caiman densities remain low in most areas (Thorbjarnarson, 2010).

Dietary Collection and Analysis

Daily 5-km transects on the Samiria River, Atun Lake, and along the channel between the two were conducted from 30 May to 15 June 2009 (high-water season), and from 25 July to 14 August 2009 (low-water season). The survey counts took place between 2000 and 0000 h in an engine-powered aluminum boat. We located caiman by using a spotlight to reflect their eyeshine at the water surface or on the riverbanks. We then captured large individuals with a steel wire noose, whereas small individuals were caught by hand. We recorded several morphological measurements for each species, including total length, snout–vent length (SVL) taken to the posterior border of the cloaca, and weight.

For caimans greater than 50 cm in total length, we used an adaptation of the hose-Heimlich technique (Fitzgerald, 1989; Platt et al., 2006; Wallace and Leslie, 2008) to collect stomach contents. For each caiman, we first

TABLE 1.—Dietary categories of Black Caimans and Spectacled Caimans from the Pacaya Samiria National Reserve on the basis of our analysis of stomach contents.

Food type	Descriptions/examples
Arachnids	Whole spiders, legs, etc.
Birds	Feathers, flesh/meat, bones, claws, etc.
Crustacean	Freshwater crabs, claws, carapace, etc.
Fish	Whole fish, flesh/meat, bones, scales, etc.
Gastropods	Freshwater snails, shell fragments, opercula, etc.
Insects	Whole insects, exoskeletons, wing cases
Mammals	Fur, flesh/meat, bones, etc.
Millipedes	Whole millipedes, fragments of millipedes, legs, etc.
Parasites	Nematode species
Reptiles	Lizard and snake bones, flesh/meat, feet, etc.
Vegetation	Leaves, sticks, bark, stems, seeds, etc.
Nonfood	Stones

opened the animal’s jaws with pliers and placed a piece of polyvinyl chloride pipe into its mouth. We then tied the mouth in place with parachute chord, so the jaws were tightly secured to the pipe but held open. The caiman was positioned vertically facing upward so that a longer, pliable plastic tube could be inserted into the mouth, past the esophagus, and down into the stomach. We lubricated the pliable tubing with water for easier insertion. Using a funnel, we poured filtered river water into the pliable tube until the caiman’s stomach was filled with water. With the funnel removed and a hand capping the pliable tube, we then massaged the caiman’s stomach. Immediately afterward, we turned the caiman headfirst towards a bucket into which we directed the water and accompanying stomach contents for collection by pulling and pushing the pliable tube a few centimeters back and forth to induce regurgitation. This method was repeated two to four times until only river water was expelled. We released each individual within 15 min of capture.

We transferred the stomach contents and accompanying river water for each individual into clean, 2-L bottles to be held overnight. The following morning, we passed the stomach contents through a filter and rinsed them with river water. Using tweezers, we then sorted the contents into piles according to 12 diet categories (Table 1) because it was not possible to identify prey animals to species.

The stomach contents were then dried for several hours under then sun and weighed by category to the nearest tenth of a gram.

Dietary analysis was performed by calculating the proportions of each prey category by dry weight for every individual’s stomach contents. To obtain a species representation, the mean of each prey category was calculated by species. We used nonparametric Mann–Whitney tests in JMP (version 9.0, SAS Institute, Inc.) to compare the mean proportions of the major prey items— crustaceans, fish, and insects—by season. The mean proportions of the minor prey items were so low that statistical comparisons by species were not appropriate.

To estimate the amount of resource overlap between species, we used Schoener’s index (1970). The Schoener’s index is calculated as:

$$PSI_{XY} = 1 - 0.5\left(\sum |p_{xi} - p_{yi}|\right)$$

where PSI is the present similarity index between species x and y , p_{xi} is the proportion of food i found in species x , and p_{yi} is the proportion of food i found in species y . A Schoener’s index value of one represents complete dietary overlap and zero signifies no overlap. Jackknifing was used to estimate a mean Schoener’s index value and variance for each season, and a nonparametric Mann–Whitney test was used in JMP to compare the index values between seasons.

To investigate the feeding diversity of each species, we used the Shannon–Wiener index (Shannon and Weaver, 1963). The Shannon–Wiener diversity index is a measure of feeding diversity rather than dietary overlap, as is described above by the Schoener’s index. The Shannon–Wiener index is calculated as:

$$H' = -\sum p_i \ln p_i$$

where p_i is the proportion of the i th resource (prey category) by mass in the stomach contents of an individual. Higher index values indicate more diverse diets. We conducted statistical tests on exponentially transformed index values as described by Jost (2006).

When testing for ontogenetic changes in diet, we used SVL because some individuals lacked complete tails. We assigned caimans to size classes for analysis as follows: I (≤ 30 cm

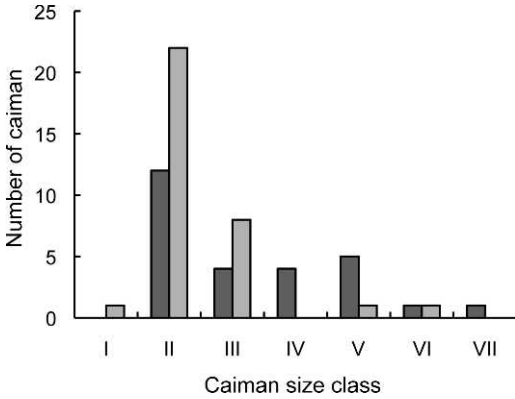


FIG. 1.—The distribution of Black Caimans (dark gray bars) and Spectacled Caimans (light gray bars) sampled in Pacaya Samiria National Reserve by size class.

SVL), II (30.1–40 cm SVL), III (40.1–50 cm SVL), IV (50.1–60 cm SVL), V (60.1–70 cm SVL), VI (70.1–80 cm SVL), and VII (80.1–90 cm SVL). Most of the captured Spectacled Caimans were found in the classes II–III (Fig. 1), namely juveniles of a SVL of 30 cm to 45 cm, with only two larger individuals of SVLs of 68.5 cm and 78.9 cm. Because of the lack of sufficient SVL variation for Spectacled Caimans, we only analyzed Black Caiman diets for ontogenetic changes. We used nonparametric Spearman’s ρ correlations in JMP to test how the Shannon–Wiener diversity index values, the total dry mass of stomach contents, and the proportions of specific prey items varied with SVL. A nonparametric mechanis-

tic growth model was applied to find the mean dry mass of stomach contents against SVL and nonparametric logistic (2p) models to fit the prey proportion data using JMP. We used nonparametric Kruskal–Wallis tests in JMP to check for changes in the dietary proportions of major prey items and in the exponentially transformed Shannon–Wiener index values across caiman size classes.

RESULTS

Dietary Composition

Overall, 28 Black Caimans and 33 Spectacled Caimans were captured for dietary analyses. One Black Caiman had an empty stomach and therefore was excluded in the results.

The proportions of prey items in the diet differed between the two seasons of data collection for both species (Table 2). During the high-water season, diets primarily consisted of insects and crustaceans. Fish, however, made up the majority of caiman diets during the low-water season. For Black Caimans, the proportion of fish in the stomach contents increased by 702% from high-water season to low-water season, whereas the proportions of crustaceans and insects decreased by 62% and 93%, respectively (Mann–Whitney test, crustaceans: $U = 1.46$, $P = 0.15$; fish: $U = 3.80$, $P = 0.0001$; insects: $U = 3.87$, $P = 0.0001$, $n_{\text{Highwater}} = 11$, $n_{\text{Lowwater}} = 16$; Fig. 2a). The results for Spectacled Caimans mirrored those of Black

TABLE 2.—The mean dietary compositions of Black Caimans and Spectacled Caimans by prey proportions collected during late May to early June, 2009 (high-water season, $n_{\text{BC}} = 11$, $n_{\text{SC}} = 13$) and late July to early August, 2009 (low-water season, $n_{\text{BC}} = 16$, $n_{\text{SC}} = 20$). The error values represent the standard error of the mean. The asterisks indicate statistically significant ($P \leq 0.05$) seasonal differences in prey item content for each species.

Food type	Black Caiman		Spectacled Caiman	
	High water	Low water	High water	Low water
Arachnids	0 \pm 0	0 \pm 0	0 \pm 0	0.003 \pm 0.003
Birds	0 \pm 0	0 \pm 0	0 \pm 0	0.04 \pm 0.04
Crustacean	0.35 \pm 0.11	0.13 \pm 0.06	0.25 \pm 0.09	0.06 \pm 0.03
Fish	0.08 \pm 0.06	0.67 \pm 0.08*	0.09 \pm 0.04	0.59 \pm 0.07*
Gastropods	0.006 \pm 0.01	0.001 \pm 0	0.05 \pm 0.04	0.001 \pm 0.001
Insects	0.47 \pm 0.12	0.03 \pm 0.02*	0.56 \pm 0.10	0.08 \pm 0.03*
Mammals	0.07 \pm 0.07	0.06 \pm 0.06	0 \pm 0	0 \pm 0
Millipedes	0 \pm 0	0 \pm 0	0 \pm 0	0.001 \pm 0.001
Parasites	0.01 \pm 0.002	0.01 \pm 0.002	0.001 \pm 0.001	0.01 \pm 0.003
Reptiles	0 \pm 0	0 \pm 0	0 \pm 0	0.03 \pm 0.03
Vegetation	0.02 \pm 0.007	0.12 \pm 0.04	0.05 \pm 0.03	0.18 \pm 0.05
Nonfood	0.001 \pm 0.001	0 \pm 0	0 \pm 0	0 \pm 0

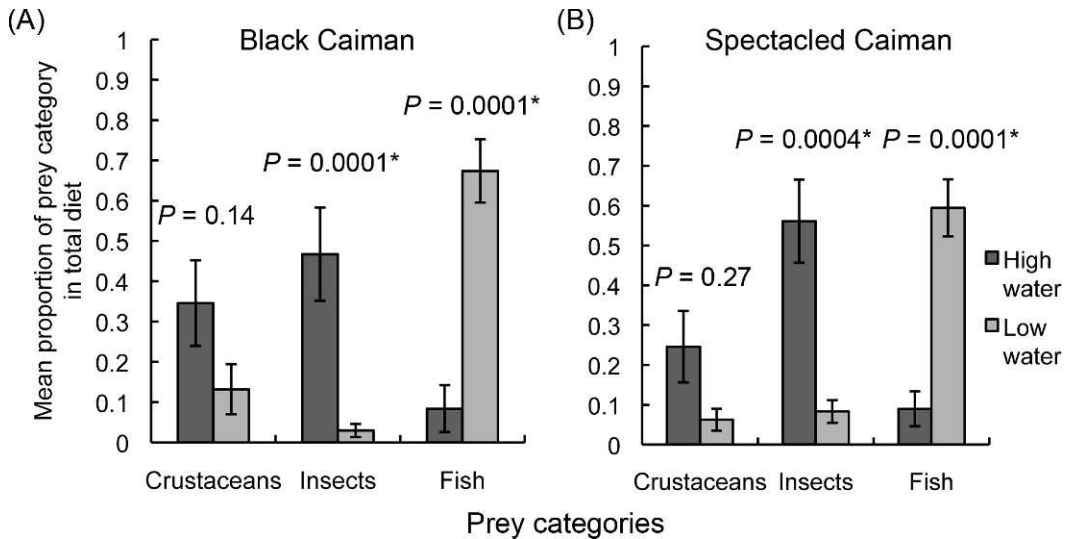


FIG. 2.—(A) The mean proportions of crustaceans, fish, and insects in a Black Caiman diet for the high-water season ($n = 11$) and the low-water season ($n = 16$) in 2009. (B) The mean proportions of crustaceans, fish, and insects in a Spectacled Caiman diet for the high-water season ($n = 13$) and the low-water season ($n = 20$) in 2009. The error bars represent the standard error of the mean. The asterisks adjacent to P values indicate statistical significance.

Caimans. The proportion of fish in the stomach contents of Spectacled Caimans increased by 560% from high-water season to low-water season, whereas the proportions of crustaceans and insects in the diet decreased by 74% and 85%, respectively (Mann–Whitney test, crustaceans: $U = 1.11$, $P = 0.27$; fish: $U = -3.54$, $P = 0.0004$; insects: $U = -3.82$, $P = 0.0001$, $n_{\text{Highwater}} = 13$, $n_{\text{Lowwater}} = 20$; Fig. 2b).

Dietary Overlap

We analyzed the dietary overlap between Black Caimans and Spectacled Caimans by season. The relationship between the diets of Black Caimans and Spectacled Caimans produced Schoener's index values of 0.82 ± 0.008 during the high-water season and 0.81 ± 0.004 during the low-water season. Therefore, dietary overlap not only remained unchanged across the two seasons (Mann–Whitney test, $U = 1.49$, $P = 0.14$), but was also very high between the two species, approaching a Schoener's index value of 1.0.

Diet Diversity and Ontogenetic Changes

We calculated the index values for each species by season and then exponentially transformed the values for analysis. Black

Caimans had a mean exponentially transformed Shannon–Wiener index value of 1.91 ± 0.20 during the high-water season ($n = 11$) and 1.81 ± 0.14 during the low-water season ($n = 16$). Spectacled Caimans had mean values of 1.91 ± 0.21 during the high-water season ($n = 13$) and 2.14 ± 0.15 during the low-water season ($n = 20$). The mean Shannon–Wiener index values for Black Caimans and Spectacled Caimans did not differ significantly by species (Mann–Whitney test, $U = -1.04$, $P = 0.30$), by season (Mann–Whitney test, $U = -0.53$, $P = 0.60$), or by species and season (Mann–Whitney test, Black Caiman: $U = 0.47$, $P = 0.64$; Spectacled Caiman: $U = -1.03$, $P = 0.30$).

For Black Caimans, we also investigated how the Shannon–Wiener diversity index values varied with SVL and SVL size classes and found no difference (Spearman's ρ correlation, $\rho = -0.08$, $P = 0.69$; Kruskal–Wallis, $W = 3.31$, $P = 0.65$; Fig. 3a; Table 3), indicating no role of caiman size on feeding diversity.

Despite a lack of change in feeding diversity, the diets of Black Caimans did vary with SVL. First, the mass of prey consumed significantly increased with SVL (Spearman's

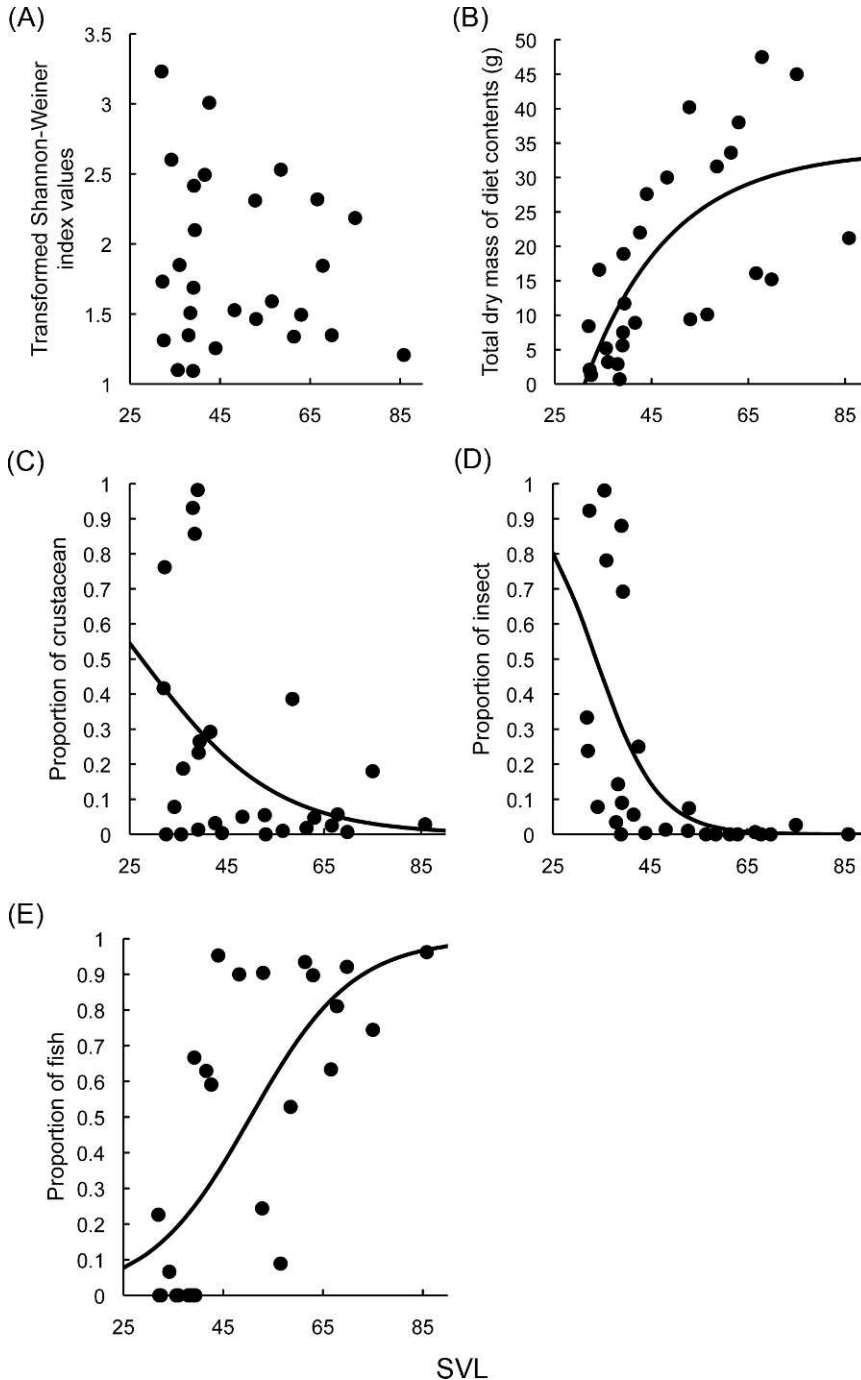


FIG. 3.—(A) Relationship between exponentially transformed Shannon–Wiener diversity index values for each Black Caiman individual and SVL (Shannon–Wiener index = $2.15 - 0.01 \text{ (SVL)}$, $r^2 = 0.02$, $n = 27$). (B) Relationship between the dry mass of food in the stomach contents of Black Caimans and SVL (mass = $34.04 [1 - 5.86 \times 10^{-0.06 \text{ (SVL)}]}$, $r^2 = 0.49$, $n = 27$). (C) Relationship between the proportion of crustaceans in each Black Caiman’s stomach contents and SVL (crustaceans = $1 / [1 + 0.14 \times 10^{0.07 \text{ (SVL)}}]$, $r^2 = 0.18$, $n = 27$). (D) Relationship between the proportion of insects in each Black Caiman’s stomach contents and SVL (insects = $1 / [1 + 0.01 \times 10^{0.16 \text{ (SVL)}}]$, $r^2 = 0.38$, $n = 27$). (E) Relationship between the proportion of fish in each Black Caiman’s stomach contents and SVL (fish = $1 / [1 + 137.46 \times 10^{-0.10 \text{ (SVL)}}]$, $r^2 = 0.51$, $n = 27$).

TABLE 3.—The mean prey proportions of crustaceans, insects, and fish in the diet of Black Caimans, as well as the exponentially transformed Shannon–Wiener diversity index values for Black Caimans by size class. The error values represent the standard error of the mean.

Size class	n	Dietary proportions			Shannon–Wiener diversity index
		Crustaceans	Insects	Fish	
II	12	0.39 ± 0.11	0.43 ± 0.11	0.08 ± 0.06	1.83 ± 0.12
III	4	0.09 ± 0.07	0.08 ± 0.06	0.77 ± 0.09	2.07 ± 0.41
IV	4	0.11 ± 0.09	0.02 ± 0.02	0.44 ± 0.18	1.97 ± 0.26
V	5	0.03 ± 0.01	0.001 ± 0.001	0.84 ± 0.06	1.67 ± 0.19
VI	1	0.18	0.03	0.74	2.19
VII	1	0.03	0	0.96	1.21

ρ correlation, $\rho = 0.74$, $P < 0.0001$; Fig. 3b). Additionally, the proportion of crustaceans in the diet decreased by 97.71% as SVL increased from 30 cm to 85 cm (Spearman’s ρ correlation, $\rho = -0.32$, $P = 0.10$; Fig. 3c), whereas the proportion of insects in the diet also decreased by 99.98% over the same change in SVL (Spearman’s ρ correlation, $\rho = -0.75$, $P < 0.0001$; Fig. 3d). However, the proportion of fish in the diet of Black Caimans increased by 720% as caiman SVL increased from 30 cm to 85 cm (Spearman’s ρ correlation, $\rho = 0.77$, $P < 0.0001$; Fig. 3e). When considering the proportions of the major prey items in the diet against size class of Black Caimans (Table 3), the results mirrored what was found above. As SVL increased, the proportion of crustaceans in the diet decreased (Kruskal–Wallis, $W = 4.79$, $P = 0.44$), the proportion of insects significantly decreased (Kruskal–Wallis, $W = 15.81$, $P = 0.0074$), and the proportion of fish significantly increased ($W = 19.45$, $P = 0.0016$).

DISCUSSION

Whereas previous studies have found both seasonal and ontogenetic shifts in crocodilian diets (Magnusson et al., 1987; Tucker et al., 1996; Da Silveira et al., 1997; Da Silveira and Magnusson, 1999; Horna et al., 2001; Platt et al., 2006; Wallace and Leslie, 2008), this study focused on the extent of dietary overlap between the sympatric Black Caimans and Spectacled Caimans. To better understand the extent of the species’ dietary overlap, changes in the diet composition of one species were compared with those of the other. In Pacaya Samiria, we found high overlap in the diets of Black Caimans and Spectacled

Caimans, despite significant seasonal changes in diet composition.

Magnusson et al. (1987) mentioned five important points to consider when interpreting data on crocodilian stomach contents:

- (1) Different prey types digest at different rates, so slower rates of digestion will positively influence the frequency of occurrence of a prey type in stomach samples.
- (2) Prey size matters. Larger prey items require more time to digest than smaller items.
- (3) Some prey have indigestible parts, such as the operculae of mollusks, and accumulate in the crocodilian’s stomach contents.
- (4) The amount of food eaten affects the rate at which indigestible items are retained.
- (5) Prey items of different mass, volume, or area can have different nutritive values for a carnivore.

Secondary ingestion of invertebrates by fish was discounted as a substantial source of bias after previous studies on the Nile Crocodile (Cott, 1961), the American Alligator (Jackson et al., 1974), and the Australian Freshwater Crocodile (Webb et al., 1982), which concluded that varying retention times of prey items were a more substantial limitation. We did not distinguish between old and fresh prey, but we limited our analysis within prey categories to minimize the bias of varying retention times (Magnusson et al., 1987; Thorbjarnarson, 1993). Digestion rate, however, is faster in smaller crocodilians because of higher metabolic rates (Coulson and Hernandez, 1983), so total prey consumption was likely underestimated for smaller caimans.

As Tucker et al. (1996) found, the dietary shifts from invertebrate to primarily vertebrate-based diets remained distinct even after accounting for this bias. Because multiple collections of dietary samples were not possible for a specific caiman, we could not determine the average diet of individuals. Therefore, we were unable to see if caimans individually behave opportunistically or actively seek out certain prey items. By averaging out the diet proportions over a small period of time, however, we gained insight on what the species as a whole were eating. Small sample sizes limited our statistical analysis to identifying trends for each species. Unfortunately, we were unable to test for ontogenetic partitioning in diets of Spectacled Caimans because of a small sample of adults. Interestingly, however, the diets of Black Caimans and Spectacled Caimans remained similar with a high Schoener's index value of dietary overlap in Pacaya Samiria despite significant seasonal differences in diet for each species. This suggests that both species take advantage of prey opportunities. Therefore, to resist periods of food scarcity, caimans may adjust their feeding behavior according to changes in prey abundance and occurrence (Horna et al., 2001).

Effects of Seasonality on Diet

Caiman diets are influenced by the seasonal change in water levels. During periods of high water levels, caimans might not only change their foraging techniques, but might opt to stop eating altogether (Da Silveira et al., 1997). In Pacaya Samiria, caimans avoided the seasonally deep river waters during the high-water season by entering the shallow waters of the flooded forest. During periods of low water levels, food availability changes as does caiman density. As water levels dropped, caimans and other aquatic organisms, such as fish, withdrew from the seasonally flooded forest habitats. The lesser depths and smaller overall area in the rivers, channels, and lakes increased prey vulnerability to crocodilians, particularly for fish (Da Silveira et al., 1997; Da Silveira and Magnusson, 1999). This increased vulnerability could easily explain the significant seasonal differences in diets found in Pacaya Samiria, as more fish were

found in the stomach contents of both species of caiman over the low-water season. Further work should concentrate on seasonal prey availability and the corresponding diet compositions of caimans to address the reasons for change in proportions of prey items between the high-water and the low-water seasons. Additionally, it would be interesting to know whether these seasonal changes in diet are accompanied by changes in body condition or growth rate for the two species.

Influence of Caiman Size on Diet

Gorzula (1978) found that Spectacled Caimans in Venezuela had a more diverse diet during a period of high water levels than during the low-water-level season. However, with a larger sample size, our Shannon-Wiener diversity index results indicated no seasonal change in diet diversity despite changes in diet composition. Above-average water levels in Pacaya Samiria in 2009 may have affected that result by increasing prey availability during the low-water season. As suggested by the high Schoener's index values for dietary overlap, diet diversity was not significantly different between the two species. Additionally, diet diversity did not change significantly with size in Black Caimans.

Several components of the dietary composition of Black Caimans shifted ontogenetically. Although Da Silveira and Magnusson (1999) found no relationship between the size class of Black Caimans and the mean mass of food or the mean proportion of prey categories other than molluscs, the Pacaya Samiria data suggest the contrary. As expected, larger Black Caimans ate more food. Additionally, the dietary composition of Black Caimans shifted with size class. Young caimans specialized on insects and crustaceans, whereas the stomach contents of larger individuals were mostly composed of fish. Previous studies have confirmed that a majority of young crocodilians feed primarily on insects and crustaceans in addition to small proportions of other prey items (Cott, 1961; Medem, 1981, 1983; Webb et al., 1982; Magnusson et al., 1987; Delany, 1990; Platt et al., 1990; Thorbjarnarson, 1993; Tucker et al., 1996). By predominantly feeding on insects and

invertebrates rather than fish and terrestrial vertebrates, crocodilian young minimize competition with adults (Horna et al., 2001). Although prey size for young crocodilians is largely dictated by head size and gape capacity, larger individuals continue eating insects and crustaceans, but choose to supplement their diets with fish, terrestrial vertebrates, and snails when available, maintaining a diverse diet (Magnusson et al., 1987). Therefore, although the Black Caiman is a top predator in the Amazon basin, even adults depend on both invertebrates and vertebrates to satisfy their energetic needs (Horna et al., 2001).

Further studies on caiman feeding ecology could help clarify the relationship between Black Caimans and Spectacled Caimans. Given that the largest individuals of Black Caimans are much greater in size and mass than the largest Spectacled Caimans, the competition between the two species may differ at different size classes. Obtaining the stomach contents of the larger individuals of both species would provide greater insight on the ontogenetic shift in caiman diets and the extent of dietary overlap of the larger individuals.

Reasons for Concern

Human exploitation previously decimated the populations of sexually mature Black Caimans. Although Black Caimans do not reach sexual maturity until an approximate total length of 200 cm (Brazaitis, 1973), Spectacled Caimans mature at a total length of less than 130 cm (Staton and Dixon, 1977). The smaller size at sexual maturity made Spectacled Caimans more resilient than Black Caimans to the hunting pressures of man because Spectacled Caimans, but not Black Caimans, were likely given the chance to reproduce before being captured (Magnusson, 1982; Rebêlo and Magnusson, 1983). Studies detailing the overlap and the type of interaction—whether competitive, mutualistic, or both—between the two species provide further information for their management as populations of Black Caimans recover across the Amazon basin.

Although the Black Caiman is currently listed as lower risk on the International Union

for Conservation of Nature Red List (Ross, 2000), its population recovery is dependent on conservation efforts across the Amazonian countries. The purpose of this study was to analyze the extent of competition that the species receives from a sympatric crocodilian in an area without significant human influence. The Spectacled Caiman is an extremely adaptable species, invading all open habitats including those created by humans and those previously vacated by the decline in the Black Caiman population (Ross and Magnusson, 1989). Individuals of both species prefer open, quiet waters and are sympatric in rivers, lakes, and channels throughout the Amazon River basin (Medem, 1971; Magnusson, 1985). Magnusson (1982) speculated that the Spectacled Caiman behaves as a colonizing species, only to be replaced again by the Black Caiman. Now, with reduced numbers of Black Caimans, individuals likely compete on some level with Spectacled Caimans. Bodmer et al. (2007) found that the density of Spectacled Caimans in Pacaya Samiria has been depleted since 1981 as the population of Black Caimans slowly recovers, indicating a level of competition in which Black Caimans triumph over Spectacled Caimans despite diet similarities found in this study.

Densities of Black Caimans remain far below their numbers from a century ago, making continued monitoring of its population necessary (Plotkin et al., 1983). Magnusson (1982) suggested that the number of Spectacled Caimans in an area is inversely proportional to the level of protection given to Black Caimans. Further research should address the roles of both Black Caimans and the Spectacled Caimans in areas with varying levels of protection to better understand the niche overlap between the two species. A potential study could monitor individual or population growth rates of Black Caimans in matched oxbow lakes from which Spectacled Caimans have or have not been experimentally removed to see the extent to which Spectacled Caimans affect the recovery of Black Caimans. Although competition plays a role in the establishment of caiman species, it is possible that Black Caimans and Spectacled Caimans are capable of living together to the same extent as they are now in Pacaya Samiria.

Spectacled Caimans could even be a potential food source for large Black Caimans, and therefore benefit the recovery of the latter species. However, if populations of Black Caimans continue to face the threats of human exploitation, a different approach to caiman conservation, such as translocations, may be appropriate.

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LITERATURE CITED

- Anderson, J.T., J.S. Rojas, and A.S. Flecker. 2009. High-quality seed dispersal by fruit-eating fishes in Amazonian floodplain habitats. *Oecologia* 161:279–290.
- Bodmer, R., P. Puertas, P. Pérez, A. Escobedo, F. Arévalo, M. Recharte, and C. Ríos. 2005. Estado actual de las especies paisajísticas de fauna silvestre y del monitoreo a grupos de manejo de la cuenca del Samiria, RNPS. Reporte Técnico. Unpublished Report to WCS, Iquitos, Peru.
- Bodmer, R., T. Fang, and P. Puertas. 2007. Wildlife populations in the Pacaya-Samiria National Reserve, Peru. Unpublished Report to WCS, Iquitos, Peru.
- Brazaitis, P. 1973. The identification of living crocodilians. *Zoologica* 58:59–101.
- Brazaitis, P., G.H. Rebêlo, C. Yamashita, E.A. Odierna, and M.E. Watanabe. 1996. Threats to Brazilian crocodilian populations. *Oryx* 30:275–284.
- Cott, H.B. 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.
- Coulson, R.A., and T. Hernandez. 1983. Alligator Metabolism: Studies on Chemical Reactions in vivo. Pergamon Press, USA.
- Da Silveira, R., and W.E. Magnusson. 1999. Diets of Spectacled and Black Caiman in the Anavilhanas Archipelago, Central Amazonia, Brazil. *Journal of Herpetology* 33:181–192.
- Da Silveira, R., and J.B. Thorbjarnarson. 1999. Conservation implications of commercial hunting of black and spectacled caimans in the Mamiraua sustainable development reserve, Brazil. *Biological Conservation* 88:103–109.
- Da Silveira, R., W.E. Magnusson, and Z. Campos. 1997. Monitoring the distribution, abundance and breeding areas of *Caiman crocodilus crocodilus* and *Melanosuchus niger* in the Anavilhanas Archipelago, Central Amazonia, Brazil. *Journal of Herpetology* 31:514–520.
- Delany, M.F. 1990. Late summer food habits of juvenile American alligators. *Journal of Herpetology* 24:418–421.
- Farias, I.P., R. Da Silveira, B. de Thoisy, L.A. Monjeló, J. Thorbjarnarson, and T. Hrbek. 2004. Genetic diversity and population structure of Amazonian crocodilians. *Animal Conservation* 7:1–8.
- Fitzgerald, L. 1988. Dietary patterns of *Caiman crocodilus* in the Venezuelan Llanos. Master thesis, University of New Mexico, USA.
- Fitzgerald, L.A. 1989. An evaluation of stomach flushing techniques for crocodilians. *Journal of Herpetology* 23:170–172.
- Gibbons, J.W., D.E. Scottt, T.J. Ryan, K.A. Buhlmann, T.D. Tuberville, B.S. Metts, J.L. Greene, T. Mills, Y. Leiden, S. Poppy, and C.T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. *Bioscience* 50:653–666.
- González, J.A. 1999. Effects of harvesting of waterbirds and their eggs by native people in the northeastern Peruvian Amazon. *Waterbirds* 22:217–224.
- Gorzula, S. 1978. An ecological study of *Caiman crocodilus* inhabiting savanna lagoons in the Venezuelan Guayana. *Oecologia* 35:21–24.
- Herron, J.C. 1991. Growth rates of Black caiman *Melanosuchus niger* and spectacled caiman *Caiman crocodilus*, and the recruitment of breeders in hunted caiman populations. *Biological Conservation* 55:103–113.
- Herron, J.C. 1994. Body size, spatial distribution, and microhabitat use in the caimans, *Melanosuchus niger* and *Caiman crocodilus*, in a Peruvian lake. *Journal of Herpetology* 28:508–513.
- Horna, J.V., R. Cintra, and P.V. Ruesta. 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, J.F., H.W. Campbell, and K.E. Campbell. 1974. The feeding habits of crocodilians: Validity of the evidence from stomach contents. *Journal of Herpetology* 8:78–381.
- Jost, L. 2006. Entropy and diversity. *Oikos* 113:363–375.
- Magnusson, W.E. 1982. Biological aspects of the conservation of Amazonian crocodilians. Pp. 108–116 in *Crocodiles: Proceedings of the 5th Working Group of the Crocodile Specialist Group*. IUCN, Switzerland.
- Magnusson, W.E. 1985. Habitat selection, parasites, and injuries in Amazonian crocodilians. *Amazoniana* 9:193–204.
- Magnusson, W.E., E.V. Da Silva, and A.P. Lima. 1987. Diets of Amazonian crocodilians. *Journal of Herpetology* 21:85–95.
- Medem, F. 1971. Biological isolation of sympatric species of South American crocodilia. Pp. 152–158. In *Crocodiles: Proceedings of the 1st Working Meeting of the Crocodile Specialist Group of the Species Survival Commission of the IUCN*. Switzerland.
- Medem, F. 1981. Los Crocodylia de Sur America, Volume 1. Los Crocodylia de Colombia. Colciencias, Colombia.
- Medem, F. 1983. Los Crocodylia de Sur America, Volume 2. Venezuela–Trinidad–Tobago–Guyana–Suriname–Guyana Francesa–Ecuador–Peru–Bolivia–Brasil–Paraguay–Argentina–Uruguay. Colciencias, Colombia.
- Platt, S.G., and J.B. Thorbjarnarson. 2000. Status and conservation of the American crocodile, *Crocodylus acutus*, in Belize. *Biological Conservation* 96:13–20.

- Platt, S.G., C.G. Brantley, and R.H. Hastings. 1990. Food habits of juvenile American alligators in the upper Lake Pontchartrain Estuary. *Northeast Gulf Science* 11:120–130.
- Platt, S.G., T.R. Rainwater, A.G. Finger, J.B. Thorbjarnarson, T.A. Anderson, and S.T. McMurtry. 2006. Food habits, ontogenetic dietary partitioning, and observations of foraging behaviour of Morelet's crocodile (*Crocodylus moreletii*) in northern Belize. *Herpetological Journal* 16:281–290.
- Plotkin, M.J., F. Medem, R.A. Mittermeier, and I.A. Constable. 1983. Distribution and conservation of the black caiman (*Melanosuchus niger*). Pp. 695–705 in A. Rhodin and K. Mitaya (Eds.), *Advances in Herpetology and Evolutionary Biology*. Museum of Comparative Zoology, UK.
- Rebêlo, G.H., and L. Lugli. 2001. Distribution and abundance of four caiman species (Crocodylia: Alligatoridae) in Jau National Park, Amazonas, Brazil. *Revista de Biologia Tropical* 49:1095–1109.
- Rebêlo, G.H., and W.E. Magnusson. 1983. An analysis of the effect of hunting on *Caiman crocodilus* and *Melanosuchus niger* based on the sizes of confiscated skins. *Biological Conservation* 26:95–104.
- Revenge, C., I. Campbell, R. Abell, P. de Villiers, and M. Bryer. 2005. Prospects for monitoring freshwater ecosystems towards the 2010 targets. *Philosophical Transactions of the Royal Society B* 360:397–413.
- Ross, C.A., and W.E. Magnusson. 1989. Living crocodilians. Pp. 58–73 in C.A. Ross, and S. Garnett (Eds.), *Crocodiles and alligators*. Merehurst Press, UK.
- Ross, J.P. 2000. *Melanosuchus niger*. In IUCN 2011. IUCN Red List of Threatened Species, Version 2011.2. IUCN, Switzerland.
- Ross, P. (Ed.). 1998. *Crocodiles: An action plan for their conservation*. IUCN, Switzerland.
- Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418.
- Shannon, C.E., and W. Weaver. 1963. *The mathematical theory of communication*. University of Illinois Press, USA.
- Smith, N.J.H. 1980. Caimans, capybaras, otters, manatees and man in Amazônia. *Biological Conservation* 19:177–187.
- Soini, P. 1995. Características climáticas: Un resumen de cinco años de registros de la temperatura, pluviosidad y fluviometría en Cahuana, río Pacaya. Pp. 207–209 in P. Soini, A. Tovar, and U. Valdez (Eds.), *Reporte Pacaya-Samiria, Centro de Datos para la Conservación*, Universidad Nacional Agraria La Molina, Peru.
- Staton, M.A., and J.R. Dixon. 1977. Breeding biology of the spectacled caiman, *Caiman crocodilus crocodilus* in the Venezuelan Llanos. U.S. Fish and Wildlife Service, Wildlife Research Report 5:1–21.
- Street, K. 2003. The diet and abundance of three caiman species (*Caiman crocodilus*, *Melanosuchus niger*, and *Paleosuchus trigonatus*) along the Rio Samiria, Peru. Master thesis, University of Kent, UK.
- Thorbjarnarson, J. 1989. Ecology of the American crocodile (*Crocodylus acutus*). Pp. 228–258 in P.M. Hall (Ed.), *Crocodiles: Their Ecology, Management, and Conservation*. IUCN, Switzerland.
- Thorbjarnarson, J.B. 1993. Diet of the Spectacled Caiman (*Caiman crocodilus*) in the central Venezuelan Llanos. *Herpetologica* 49:108–117.
- Thorbjarnarson, J.B. 1996. Reproductive characteristics of the order Crocodylia. *Herpetologica* 52:8–28.
- Thorbjarnarson, J.B. 2010. Black Caiman *Melanosuchus niger*. Pp. 29–39 in S.C. Manolis, and C. Stevenson (Eds.), *Crocodiles. Status Survey and Conservation Action Plan*, 3rd Ed. Crocodile Specialist Group: Darwin. IUCN, Switzerland.
- Tucker, A.D., C.J. Limpus, H.I. McCallum, and K.R. McDonald. 1996. Ontogenetic dietary partitioning by *Crocodylus johnstoni* during the dry season. *Copeia* 1996:978–988.
- Uruena, E. 1990. Black caiman in Guyana. *Crocodile Specialist Group Newsletter* 9:24.
- Uryu, Y., O. Malm, I. Thornton, I. Paynes, and D. Cleary. 2001. Mercury contamination of fish and its implications for other wildlife of the Tapajós basin, Brazilian Amazon. *Conservation Biology* 15:38–446.
- Vasquez, R.P.G. 1981. Bases bio-ecológicas para el manejo de los Alligatoridae en Jenaro Herrera (Requena-Peru). Universidad Nacional Agraria, Peru.
- Vasquez, R.P.G. 1982. Análisis de la situación actual de los caimanes y del cocodrilo de Tumbes en el Peru. *Revista Forestal del Peru* 1–2:171–194.
- Verdi, L., L. Moya, and R. Pezo. 1980. Observaciones preliminares sobre la bioecología del lagarto blanco *Caiman crocodilus* (Linnaeus, 1758; Alligatoridae) en la Cuenca del Rio Samiria, Loreto-Perú. Seminario sobre los Proyectos de Investigación ecología para el manejo de los recursos naturales renovables del bosque tropical húmedo del 12 al 18 de octubre 1980. UNAP-Cooperación Técnica del Gobierno Suizo (COTESU)-ORDELORETO, Peru.
- Wallace, K.M., and A.J. Leslie. 2008. Diet of the Nile crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *Journal of Herpetology* 42:361–368.
- Webb, G.J.W., S.C. Manolis, and R. Buckworth. 1982. *Crocodylus johnstoni* in the McKinlay River area, N.T. 1. Variation in the diet, and a new method of assessing the relative importance of prey. *Australian Journal of Zoology* 30:877–899.
- Whitaker, R. 1987. The management of crocodilians in India. Pp. 63–72 in G.J.W. Webb, S.C. Manolis, and P.J. Whitehead (Eds.), *Wildlife Management: Crocodiles and Alligators*. Surrey Beatty and Sons, Australia.

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