

**FOOD HABITS, ONTOGENETIC DIETARY PARTITIONING AND
OBSERVATIONS OF FORAGING BEHAVIOUR OF MORELET'S CROCODILE
(*CROCODYLUS MORELETII*) IN NORTHERN BELIZE**

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We studied the food habits and size-related dietary patterns of Morelet's crocodile (*Crocodylus moreletii*) in freshwater wetlands of northern Belize (1992–2000). Crocodiles ($n=420$) were classified as hatchlings, small juveniles, large juveniles, subadults or adults based on total length. Stomach contents were obtained primarily by stomach flushing. Prey items included aquatic and terrestrial insects, arachnids, aquatic gastropods, crustaceans, fish, amphibians, reptiles, birds, and mammals. Based on the percent occurrence of recovered prey items, we concluded that the smallest size classes feed largely on insects and arachnids. Large juveniles broadened their diet to include aquatic gastropods, crustaceans, fish and non-fish vertebrates. Insect and arachnid consumption declined sharply among subadults, and increasing amounts of aquatic gastropods and fish were recovered from this size class. The adult diet consisted mainly of aquatic gastropods, fish and crustaceans. Dietary diversity was greatest among large juveniles and subadults. Conversely, hatchlings and small juveniles had the most specialized (least diverse) diet owing to a reliance on insects and arachnids. Dietary overlap was greatest between adjacent size classes, and lowest between the smallest and largest size classes. We also provide field observations of prey-specific foraging behaviours.

Key words: crocodile, foraging ecology, ontogenetic dietary change, stomach flushing

INTRODUCTION

Morelet's crocodile (*Crocodylus moreletii*) is a large crocodylian (total length [TL] to 410 cm; Perez-Higareda *et al.*, 1991) that inhabits freshwater wetlands throughout much of the Atlantic lowlands of Mexico, Guatemala and Belize (Groombridge, 1987), and many aspects of its life history, including diet and foraging ecology, remain largely unknown (Platt, 1996). Platt *et al.* (2002) investigated the foraging ecology of hatchlings (<2 months old). Schmidt (1924), Shreve (1957), Alvarez del Toro (1974) and Stafford *et al.* (2003) collectively examined the stomach contents of 17 juveniles ranging from 29 to 75 cm TL, and found turtle scutes, snail opercula, fish scales, anuran bones, crustaceans and insects. Alvarez del Toro (1974) recovered the remains of fish, turtles, and an opossum (*Philander opossum*) from the stomach of an adult. Sigler & Marina (2004) documented predation by an adult on a young brocket deer (*Mazama americana*), and Perez-Higareda *et al.* (1989) compiled a checklist of vertebrate taxa consumed by a group of subadults and adults confined in a semi-natural lagoon. However, detailed field investigations have yet to be

conducted and more comprehensive dietary data for *C. moreletii* are lacking. Moreover, despite the recognition that increasing body size exerts a strong influence on diet and foraging ecology in many crocodylians (e.g. Cott, 1961; Webb *et al.*, 1982; Platt *et al.*, 1990; Thorbjarnarson, 1993b), only Tucker *et al.* (1996) have quantified intraspecific dietary niche overlap among different size classes.

Studies of diet are fundamental to understanding the ecology of an organism (Rosenberg & Cooper, 1990), and among crocodylians, diet has been demonstrated to affect body condition, growth, behaviour and reproduction (Lang, 1987; Delany *et al.*, 1999). Furthermore, behavioural patterns associated with hunting specific prey are poorly documented for most crocodylians (Lang, 1987; Gans, 1989), including *C. moreletii* (Platt, 1996). Field observation of foraging behaviour is difficult because much foraging activity is nocturnal, crocodiles are often wary, and turbidity may obscure underwater behaviour (Magnusson *et al.*, 1987; Thorbjarnarson, 1993a; Platt *et al.*, 1990). We present here the results of a dietary study of Morelet's crocodile in freshwater wetlands of northern Belize. In this study we characterize the diet of *C. moreletii*, address ontogenetic dietary differences, quantify dietary niche overlap among size classes and provide field observations of prey-specific foraging behaviours.

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STUDY AREA AND METHODS

Fieldwork was conducted from 1992 to 2000 at freshwater wetlands throughout northern Belize (Belize, Cayo, Corozal and Orange Walk Districts), a region characterized by alluvial floodplains and interfluvial swampy depressions and sinkholes (Alcala-Herrera *et al.*, 1994). Natural wetlands are estimated to occupy up to 40% of the lowlands in northern Belize (Alcala-Herrera *et al.*, 1994), and generally contain water throughout the year, although levels fluctuate (Darch, 1983). Freshwater wetlands are often heavily vegetated with *Cladium jamaicense*, *Typha domingensis*, *Eleocharis* spp. and *Nymphaea* spp. (Darch, 1983; Rejmankova *et al.*, 1995). The climate of northern Belize is considered tropical with a mean temperature every month of $>18^{\circ}\text{C}$. Annual rainfall ranges from 1,300 to 2,000 mm with a pronounced wet season occurring from mid- to late June through late November. Average monthly precipitation is variable and ranges from a maximum of 231 mm in June to a minimum of 31 mm in March (Johnson, 1983). Our study sites are described in greater detail elsewhere (Platt, 1996; Rainwater *et al.*, 1998; Platt & Thorbjarnarson, 2000).

Crocodiles were captured at night with the aid of a headlight. Smaller animals ($\text{TL} \leq 100$ cm) were taken by hand or dip net, and a noose-pole was used to capture larger ($\text{TL} \geq 100$ cm) individuals. TL and snout-vent length (SVL; tip of snout to anterior margin of cloaca) were measured, and each crocodile was permanently marked for future identification by notching the dorsal edge of a unique series of caudal scutes (Jennings *et al.*, 1991). Crocodiles were released at the capture site within 12 to 24 hours. Crocodiles were classified as hatchlings ($\text{TL} < 30.0$ cm), small juveniles ($\text{TL} = 30.0$ – 50.0 cm), large juveniles ($\text{TL} = 50.1$ to 100.0 cm), subadults ($\text{TL} = 100.1$ – 150.0 cm) or adults ($\text{TL} > 150.0$ cm); these categories reflect size-age relationships (Platt, 1996).

Stomach contents were obtained using a modification of the stomach flushing technique of Taylor *et al.* (1978). A flexible PVC tube (exterior tube diameter = 1.4, 1.9 and 2.1 cm for crocodiles < 45 , 45–120 and > 120 cm TL, respectively) was eased down the oesophagus and into the stomach, and water was slowly poured into the tube until the abdomen became visibly distended. Gently palpating the abdomen caused a mixture of water and stomach contents to surge into the tube. The crocodile was then inverted, the contents expelled, and this mixture deposited onto a fine mesh screen. This process was repeated (usually three to four times) until only water free of stomach contents was obtained. Flushing is a safe, highly effective technique that has been demonstrated to recover $> 95\%$ of prey and most non-food items from crocodilian stomachs (Fitzgerald, 1989).

We also obtained stomach contents by dissecting a small number (< 10) of crocodiles that were killed by poachers, accidentally drowned in fishing nets, or found

dead from unknown causes. Stomach contents were sorted and prey items identified to the lowest possible taxonomic category. Each prey item was assigned to one of nine major taxonomic categories (insects, arachnids, gastropods, crustaceans, fish, anurans, reptiles, birds and mammals). The length of every snail operculum recovered from many (but not all) crocodiles was measured to the nearest 0.1 mm and used as an index of snail size (Thorbjarnarson, 1993b). Non-food items such as stones, seeds and vegetable matter were also recorded. Additionally, a few (< 5) crocodiles were captured with prey held in their jaws prior to swallowing. We assumed these prey would have been consumed had crocodiles not been captured and included them in our analysis.

We calculated the percent occurrence for each prey category by size class. Although often considered synonymous with frequency of occurrence, we follow Rosenberg & Cooper (1990) and define percent occurrence as the number of samples in which a particular prey item occurs divided by the sample size of a particular size-class of crocodile. Percent occurrence is appropriate when individual prey items cannot be quantified (Rosenberg & Cooper, 1990). Because bone, flesh and mollusc shell are rapidly digested, while chitinous remains, hair and feathers are more persistent, differential digestion of prey types is a common source of bias in studies of crocodilian diet (Jackson *et al.*, 1974; Fisher, 1981; Garnett, 1985; Magnusson *et al.*, 1987). To reduce bias from this source, we analysed ontogenetic trends within prey categories under the assumption that the remains of different prey within any one prey category persisted in the stomach for similar periods (Magnusson *et al.*, 1987; Thorbjarnarson, 1993b; Tucker *et al.*, 1996). We transformed percent occurrence data using a square root arcsine transformation (Zar, 1996) before searching for correlations in dietary composition across crocodile size classes. The association between crocodile body size and the size of snails consumed as prey was investigated by correlating the mean, minimum and maximum length of snail opercula recovered from each crocodile with crocodile SVL (Thorbjarnarson, 1993b). Results were considered significant at $P \leq 0.05$.

We used the Shannon–Wiener diversity index (H') to estimate dietary niche breadth and determine the degree of dietary specialization in each size class (Schoener, 1968). The Shannon–Wiener index is calculated as:

$$H' = - \sum p_j \log p_j$$

where p_j is the proportion of individuals using resource j (prey category). Because H' may range from 0 to infinity we standardized the index on a scale of 0 to 1 using the evenness measure J' calculated as:

$$J' = H' (\log n)^{-1}$$

where n is the number of prey categories (Krebs, 1989). The lower the value of J' , the more specialized the feeding habits of a particular size class; i.e. the lowest J'

value indicates the least diversity of prey consumed, and hence the greatest degree of specialization (Schoener, 1968; Krebs, 1989).

Dietary niche overlap among size classes was determined using percent overlap (P), which measures the area of overlap of the resource utilization curves of crocodile size class j and k (Krebs, 1989). P is estimated by $\Sigma (\text{minimum } p_{ij}, p_{ik}) \times 100$, where p_{ij} and p_{ik} 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).

Observations of foraging behaviour were made opportunistically while capturing crocodiles for this study and others (Platt, 1996; Rainwater, 2003; Finger, 2004), and conducting population surveys (Platt & Thorbjarnarson, 2000). We also provided apple snails (*Pomacea flagellata*) to a group of six captive *C.*

moreletii (TL c. 75 to 150 cm) in a pond at the Belize Zoo to observe prey handling behaviour.

RESULTS

We obtained stomach contents from 420 crocodiles ranging in size from 23 to 255 cm TL by stomach flushing (412) and dissection (8). Although we captured crocodiles during every month of the year, most were taken in the late dry season (March to mid-June; $n=133$) and early wet season (late June through mid-August; $n=157$). Throughout much of the wet season, crocodiles were dispersed in flooded wetlands and proved difficult to capture (Rainwater *et al.*, 1998; unpubl. data). Hatchlings ($n=71$) were collected from late August to early October, shortly after emerging from the nest (Platt *et al.*, 2002). To our knowledge no mortality resulted from capture or stomach flushing, and numerous

TABLE 1. Prey items identified in the stomach contents of 420 *Crocodylus moreletii* collected in freshwater wetlands of northern Belize (1992–2000). Includes data from Platt *et al.* (2002).

Category	Taxon	Category	Taxon
AQUATIC	Belostomatidae (giant water bugs)	AMPHIBIANS	<i>Bufo marinus</i> (marine toad)
INSECTS	Corixidae (water boatmen)		<i>Eleutherodactylus</i> spp. (rainfrog)
	Dytiscidae (predaceous diving beetles)		<i>Rana berlandieri</i> (Rio Grande leopard frog)
	Gyrinidae (whirligig beetles)	REPTILES	<i>Trachemys scripta</i> (common slider turtle)
	Hydrophiloidea (water beetles)		<i>Anolis</i> spp. (anole)
	Nepidae (water scorpions)		<i>Basiliscus vittatus</i> (basilisk lizard)
	Notonectidae (backswimmers)		<i>Ctenosaura similis</i> (spiny-tailed iguana)
	Odonata (dragonfly larvae)		<i>Iguana iguana</i> (green iguana)
	Tabanidae (horsefly larvae)		<i>Sceloporus chrysostictus</i> (spiny lizard)
TERRESTRIAL	Caelifera (grasshoppers)		<i>Coniophanes schmidtii</i> (Schmidt's striped snake)
INSECTS	Carabidae (ground beetles)	BIRDS	<i>Agelaius phoeniceus</i> (red-winged black bird)
	Embioptera (web-spinners)		<i>Butorides virescens</i> (green-backed heron)
	Ephemeroptera (mayflies)		<i>Bubulcus ibis</i> (cattle egret)
	Formicidae (ants)		<i>Egretta</i> spp. (egret)
	Lepidoptera (butterflies and moths)		<i>Phalacrocorax</i> spp. (cormorant)
	Mantidae (mantids)	MAMMALS	<i>Coendou mexicanus</i> (Mexican hairy porcupine)
	Odonata (adult dragonflies)		<i>Didelphis</i> spp. (opossum)
	Scarabaeidae (scarab beetles)		<i>Oryzomys</i> spp. (rice rat)
ARACHNIDS	Unidentified spiders		<i>Philander opossum</i> (gray four-eyed opossum)
GASTROPODS	<i>Pomacea flagellata</i> (apple snail)		<i>Rattus</i> spp. (Old World rat)
CRUSTACEANS	<i>Cardisoma</i> spp. (freshwater crab)		<i>Sigmodon hispidus</i> (cotton rat)
	<i>Procambarus</i> spp. (crayfish)		
	Decapoda (freshwater shrimp)		
FISH	<i>Astyanix fasciatus</i> (Mexican tetra)		
	<i>Belonesox belizanus</i> (alligator fish)		
	<i>Cichlasoma</i> spp. (cichlids)		
	<i>Gambusia</i> spp. (mosquito fish)		
	<i>Ophisternon aenigmaticum</i> (obscure swamp eel)		
	<i>Petenia splendida</i> (bay snook)		
	<i>Poecilia mexicana</i> (Mexican molly)		
	<i>Rhamida</i> spp. (freshwater catfish)		
	<i>Synbranchus marmoratus</i> (mud eel)		

TABLE 2. Prey items, gastroliths, empty stomachs, dietary diversity and evenness among size classes of *Crocodylus moreletii* ($n=420$) from freshwater wetlands of northern Belize. Number of crocodiles containing a specified prey followed by percent occurrence (%) within each size class in parentheses. r = correlation of percent occurrence of each prey category with size class. Size classes include hatchlings (TL<30.0 cm), small juveniles (TL=30.0–50.0 cm), large juveniles (TL=50.1–100.0 cm), subadults (TL=100.1–150.0 cm) and adults (TL>150.0 cm). Hatchling data from Platt *et al.* (2002). * $P=0.05$, ^{NS} Not significant ($P>0.05$).

Prey category	Size class (n)					r
	Hatchlings (71)	Small juveniles (117)	Large juveniles (121)	Subadults (63)	Adults (48)	
Insects	60 (84.5)	107 (91.4)	83 (68.5)	22 (34.9)	6 (12.5)	
Arachnids	21 (29.5)	31 (26.5)	8 (6.6)	1 (1.5)	0	
Insects/arachnids (total)	69 (97.1)	112 (95.7)	84 (69.4)	23 (36.5)	6 (12.5)	-0.97*
Gastropods	2 (2.8)	6 (5.1)	25 (20.6)	26 (41.2)	34 (70.8)	0.94*
Crustaceans	0	9 (7.6)	22 (18.1)	9 (14.2)	10 (20.8)	0.90*
Fish	12 (16.9)	7 (5.9)	31 (25.6)	20 (31.7)	15 (31.2)	0.79 ^{NS}
Anurans	0	1 (0.008)	7 (0.05)	2 (0.03)	0	
Reptiles	0	0	8 (0.06)	2 (0.03)	1 (0.02)	
Birds	0	0	2 (0.01)	3 (0.04)	5 (0.10)	
Mammals	0	0	12 (0.09)	2 (0.03)	1 (0.02)	
Non-fish vertebrates (total)	0	1 (0.008)	29 (23.9)	9 (14.2)	7 (14.5)	0.65 ^{NS}
Non-food items	14 (19.7)	10 (8.5)	34 (28.0)	14 (22.2)	13 (27.0)	
Gastroliths	8 (11.2)	7 (5.9)	22 (18.1)	11 (17.6)	7 (14.5)	
Empty stomachs	0	2 (0.01)	5 (0.04)	10 (0.15)	0	
Diversity (H')	0.96	1.04	1.86	1.73	1.51	0.70 ^{NS}
Evenness (J')	0.40	0.43	0.77	0.72	0.63	0.70 ^{NS}

recaptures have since been made (Platt, 1996; Platt *et al.*, 2002; unpubl. data). Although we did not verify the effectiveness of the technique, abdominal palpation indicated that flushing resulted in complete or near-complete gastric emptying. Gastroliths that probably exceeded the tube diameter occasionally remained in stomachs despite repeated flushing.

Prey recovered from crocodile stomachs included aquatic and terrestrial insects, arachnids, aquatic gastropods, crustaceans, fish, amphibians, reptiles, birds and mammals (Table 1). Insects were the most frequently recovered prey and occurred in the stomach contents of 278 (66.1%) crocodiles of all size classes (Table 2). Although whole insects and large fragments were frequently recovered, remains generally consisted of highly macerated pieces of chitin and fleshy material that could not be identified to a particular taxonomic group. Representatives of nine insect orders (Coleoptera, Diptera, Embioptera, Ephemeroptera, Hemiptera, Hymenoptera, Lepidoptera, Odonata, Orthoptera) were found among identifiable remains (Table 1). Arachnids were recovered from 61 (14.5%) stomachs. Because insects and arachnids are functionally similar as prey, these groups were combined for analyses; insects, arachnids, or both were recovered from the stomachs of 294 (70.0%) crocodiles of all size classes. There was a significant negative correlation between size class and the percent occurrence of insects/arachnids (Table 2). Hatchlings and small juveniles feed almost exclusively on insects/arachnids. With the exception of three large ants recovered from a stomach

that also contained fresh anuran remains, we found nothing to suggest that insects or arachnids were secondarily ingested.

Gastropods were found in the stomach contents of 93 (22.1%) crocodiles from all size classes (Table 2). *Pomacea flagellata*, a large (ca. 60–70 g) ampullarid snail abundant in freshwater wetlands of northern Belize (Covich, 1983) was the only gastropod recovered. There was a significant positive correlation between size class and the percent occurrence of gastropods (Table 2). In a sample of 72 crocodiles (containing 1–618 opercula) there were significant positive correlations between crocodile SVL and mean ($r=0.84$), minimum ($r=0.69$) and maximum ($r=0.87$) operculum length.

Crustaceans were a relatively minor component of the diet and occurred in only 50 stomachs (11.9%) from all size classes except hatchlings (Table 2). There was a significant positive correlation between the percent occurrence of crustaceans and size class (Table 2).

Fish were the most frequently recovered vertebrate prey, and occurred in the stomachs of 85 (20.2%) crocodiles of all size classes (Table 2). With the exception of an anuran recovered from a small juvenile, fish were the only vertebrates consumed by hatchlings and small juveniles. Although the percent occurrence of fish remains was positively correlated with size class, this relationship was not significant (Table 2). However, the recovery of scales from an adult *Petenia splendida*, undoubtedly consumed as carrion by six hatchlings in a single pod (Platt *et al.*, 2002), inflated the percent occurrence of fish among this size class. If these six

TABLE 3. Percentage of dietary overlap (%) among size classes of *Crocodylus moreletii* from freshwater wetlands in northern Belize. Size classes include hatchlings (TL<30.0 cm), small juveniles (TL=30.0–50.0 cm), large juveniles (TL=50.1–100.0 cm), subadults (TL=100.1–150.0 cm) and adults (TL>150.0 cm).

Size class	Hatchlings	Small juveniles	Large juveniles	Subadults	Adults
Hatchlings	100.0				
Small juveniles	89.0	100.0			
Large juveniles	59.8	58.1	100.0		
Subadults	41.6	38.7	68.4	100.0	
Adults	23.1	18.3	45.1	71.0	100.0

hatchlings are removed from the analysis, the correlation between the percent occurrence of fish and size class becomes significant ($r=0.90$).

Vertebrates other than fish were poorly represented in the diet and occurred in only 46 (10.9%) crocodiles (Table 2). Amphibians, reptiles, birds and mammals were recovered from 10 (2.3%), 11 (2.6%), 10 (2.3%) and 15 (3.5%) crocodiles, respectively. The percent occurrence of non-fish vertebrates was positively correlated with size class, although this relationship was not significant (Table 2). Non-fish vertebrates were most frequently recovered from large juveniles; these consisted primarily of rice rats (*Oryzomys* spp.). Few subadults or adults contained non-fish vertebrates and with one exception, non-fish vertebrates were lacking from the stomach contents of hatchlings and small juveniles.

Non-food items were present in the stomach contents of 85 (20.2%) crocodiles of all size classes and included fragments of vegetation, hard seeds, pieces of wood, stones and parasites. Gastroliths (stones and hard seeds) were recovered from 55 (13.0%) crocodiles of all size classes. Empty stomachs were rarely encountered among any size class (Table 2).

Dietary diversity (H') and evenness (J') values were not significantly correlated with size class (Table 2). Dietary diversity was greatest among large juveniles and subadults, intermediate in adults, and lowest among hatchlings and small juveniles. Conversely, dietary specialization (evenness) was greatest among hatchlings and small juveniles owing to a reliance upon a limited selection of prey, primarily insects and arachnids. Large juveniles and subadults consumed insects and arachnids in addition to increasing amounts of crustaceans, gastropods and vertebrate prey, and consequently had the most generalized diet of any size class. Dietary specialization was intermediate in adults, due to the high occurrence of snails.

To summarize the general ontogenetic trend based on the percent occurrence of prey items recovered from *C. moreletii*, the diet of hatchlings and small juveniles comprises largely insects and arachnids. Large juveniles likewise rely heavily on insects and arachnids, but broaden the diet to include gastropods, crustaceans, fish and non-fish vertebrates. Consumption of insects and arachnids appears to decline greatly among subadults, and increasing amounts of gastropods and fish were found among the stomach contents; crustaceans and

non-fish vertebrates were recovered less often from this size class. Gastropods were the prey most frequently recovered from adults, and although fish and crustaceans were found less often, these are nonetheless important prey for this size class. Insects and non-fish vertebrates appear to be a minor component of the adult diet.

Dietary overlap was greatest among adjacent size classes (Table 3). Near complete overlap occurred between hatchlings and small juveniles. High overlap (>60%) occurred between large juveniles and subadults, and subadults and adults, while moderate overlap (50–60%) was found between hatchlings and large juveniles, and small and large juveniles. Overlap was low (30–50%) between adults and large juveniles, as well as between subadults and hatchlings and small juveniles. The lowest (<30%) overlap occurred between adults, and hatchlings and small juveniles.

DISCUSSION

Our study is the first to examine stomach contents from a large sample of *C. moreletii* ranging in size from hatchlings to mature adults. It should be noted that several factors may confound dietary analyses based on stomach contents in crocodilians. Firstly, differing gut retention times of various prey species may bias results (Garnett, 1985; Janes & Gutkze, 2002), but because we analysed ontogenetic trends within prey categories, bias from this source is probably minimal (Magnusson *et al.*, 1987; Thorbjarnarson, 1993b); i.e., any digestibility bias was consistent within prey types regardless of variation among prey types (Tucker *et al.*, 1996).

Secondly, some authors have suggested that insect remains found in crocodilian stomachs were acquired secondarily from anurans consumed as prey (Neill, 1971; Jackson *et al.*, 1974; Wolfe *et al.*, 1987). However, we found nothing to suggest that secondary ingestion is a significant source of insects for *C. moreletii*. Anurans were poorly represented in the stomach contents of all size classes, particularly so among smaller crocodiles in which the occurrence of insects was greatest. Dietary studies of other crocodilians have likewise concluded that consumption of anurans is rare (Webb *et al.*, 1982; Delany & Abercrombie, 1986; Delany, 1990; Platt *et al.*, 1990; Webb *et al.*, 1991; Thorbjarnarson, 1993b; Tucker *et al.*, 1996). Moreover, in the single case where we recovered insect and anuran remains from the same crocodile, both were similar in size, suggesting consumption of the insects by

the co-occurring anuran was unlikely. Finally, because prey movement is important in eliciting a feeding response in crocodylians (Fleishman & Rand, 1989), ambush predators such as most anurans (Duellman & Trueb, 1986), which remain motionless for long periods, are likely to escape detection by foraging crocodiles. However, our conclusions and those of others regarding the consumption of anurans should be interpreted with caution owing to the rapid digestion of amphibians in the crocodylian stomach. Delany & Abercrombie (1986) note that sirens (*Siren lacertina*) fed to captive *A. mississippiensis* were completely digested within 24 hours and suggested that this may result in amphibians being under-represented in studies of crocodylian stomach contents.

The results of our study and others (Schmidt, 1924; Alvarez del Toro, 1974; Stafford *et al.*, 2003) indicate that insects and arachnids are especially important prey for the smaller size classes of *C. moreletii*. These results are not unexpected as studies of most crocodylians suggest that insects are the primary food for smaller size classes (e.g. Cott, 1961; Staton & Dixon, 1975; Webb *et al.*, 1982; Delany, 1990; Platt *et al.*, 1990; Thorbjarnarson, 1993b). Both aquatic and terrestrial insects are consumed by small *C. moreletii* suggesting that a variety of foraging modes are employed. Terrestrial insects are probably captured when crocodiles forage at the land/water ecotone and among emergent vegetation, or when insects fall into the water (Palis, 1989; Platt *et al.*, 1990).

Ampullarid snails are abundant in freshwater wetlands of northern Belize (Covich, 1983), and have previously been reported as prey for juvenile and subadult *C. moreletii* (Schmidt, 1924; Alvarez del Toro, 1974; Stafford *et al.*, 2003). Alvarez del Toro (1974) considered aquatic snails especially important food for "small" crocodiles. However, snail consumption was not reported in the only previous study of adult *C. moreletii* diet (Perez-Higareda *et al.*, 1989). In contrast to other studies of *C. moreletii* diet, our results indicate that while snails are consumed by all size classes, consumption increases with increasing crocodile body size, and is greatest among the two largest size classes. Schmidt (1924) speculated that the blunt posterior teeth of *C. moreletii* are well adapted for crushing molluscs.

The positive correlations of mean, minimum and maximum snail operculum lengths with crocodile SVL suggests that as *C. moreletii* grow larger they consume increasingly larger snails while excluding smaller snails from their diet. Optimal foraging theory predicts such an ontogenetic shift in the lower size limit of prey when the energy content of individual prey is small in relation to the energetic cost of capture and ingestion (Stephens & Krebs, 1986; Arnold, 1993). Because crocodiles are gape-limited predators (Schmidt & Holbrook, 1984), mechanical constraints undoubtedly define the upper size limit of snails that can be consumed.

It is unclear how *C. moreletii* detect and locate snails underwater, but tactile and chemical cues are probably

important. We observed wild *C. moreletii* capturing snails underwater while crawling along the bottom and making frequent lateral head sweeps; contact with a snail elicited snapping behaviour. Specialized sensory organs on the jaws (Soares, 2002) probably facilitate underwater prey capture by functioning as mechanoreceptors that locate prey by touch (Thorbjarnarson, 1993a). Because *Pomacea* are known to release alarm pheromones in the presence of crocodylians (Snyder & Snyder, 1971), it is also possible that waterborne chemical cues play a role in locating snails. Waterborne chemicals are detected by taste buds on the tongue and posterior palate of the American alligator (*Alligator mississippiensis*) and stimulate head sweeping behaviour (Weldon *et al.*, 1990) similar to that observed among *C. moreletii*. The importance of visual cues in underwater prey capture is probably minimal as the crocodylian eye is severely hyperopic (farsighted) and usually covered by opaque membranes when submerged (Fleishman *et al.*, 1988; Platt & Brantley, 1991).

Diefenbach (1979) reported that *Caiman latirostris* swallowed intact snails either underwater or after raising the head above the surface, but we observed *C. moreletii* at the Belize Zoo crushing snails prior to swallowing. Snails were seized, held between the jaws, and then crushed in a series of rapid mandibular contractions with the head held at or slightly above the water surface. This was followed by several slow, lateral head sweeps with the jaws slightly agape and just below the surface that appeared to flush shell fragments from the mouth. The head was then tilted upwards and the crushed snail swallowed.

In contrast to our results, previous studies found few fish among the stomach contents of *C. moreletii*, probably owing to the small number of crocodiles examined and the preponderance of juveniles in this sample (Schmidt, 1924; Shreve, 1957; Alvarez del Toro, 1974; Stafford *et al.*, 2003). Perez-Higareda *et al.* (1989) included *Cichlasoma* sp. and *Anguilla* sp. on a checklist of prey consumed by *C. moreletii*, but did not quantify percent occurrence in the diet. Tactile, visual and auditory cues appear important in fish capture by *C. moreletii*. We frequently observed *C. moreletii* snapping at surface disturbance when among dense schools of *Astyanix fasciatus*, *Poecillia mexicana* and *Gambusia* spp., surface-swimming fish that create considerable disturbance when feeding. Crocodiles floated slowly in a "cross-posture position" (Olmos & Sazima, 1990) among schools of fish, making occasional forward lunges or lateral head swipes directed at surface disturbances. Crocodylians are sensitive to vibrations on the water's surface, and anecdotal accounts exist of crocodylians snapping at splashing or dripping water (Hartley & Hartley, 1977; Lazell & Spitzer, 1977). Others have commented on the importance of surface disturbance in fish capture (Whitfield & Blaber, 1979; Schaller & Crawshaw, 1982; Olmos & Sazima, 1990; Soares, 2002), and Platt *et al.* (1990) found that while

surface-swimming fish were a significant component in the diet of juvenile *A. mississippiensis*, fish inhabiting the mid-littoral zone were rarely consumed. Success rates of surface fishing are typically low (Olmos & Sazima, 1990; Thorbjarnarson, 1993a) and therefore this behaviour is probably energetically worthwhile only when fish are present in high densities. Although we never observed *C. moreletii* capturing bottom-dwelling fish (e.g. catfish and eels), these occurred in the diet and are probably taken in a manner similar to that described for snails that relies heavily on tactile cues.

Previous studies found non-fish vertebrates among the stomach contents of a limited number of juvenile, subadult and adult *C. moreletii* (Schmidt, 1924; Shreve, 1957; Alvarez del Toro, 1974; Stafford *et al.*, 2003). According to Perez-Higareda *et al.* (1989), wading birds were the principal food of 48 semi-captive subadult and adult *C. moreletii*, but wild and domestic mammals, amphibians and reptiles were also consumed; however, because frequencies of individual taxa in the diet were not reported, comparisons with our results must remain qualitative. Despite their low percent occurrence in the stomachs we examined, some non-fish vertebrates, particularly mammals and birds, may be important prey for *C. moreletii*. As noted by Rosenberg & Cooper (1990), measures of percent occurrence tend to minimize the importance of infrequently consumed larger prey that may nonetheless make significant energetic contributions to the diet.

While avian remains were rarely found among the stomach contents of *C. moreletii*, we observed two instances of crocodile predation on birds during this study. The first occurred when an adult (TL c. 180 cm) crocodile made two near-vertical lunges to snap at grey-breasted martins (*Progne chalybea*) skimming above the surface of a pond. These lunges began with the head resting on the surface, and propelled the crocodile far enough out of the water to expose the forefeet to view; one lunge resulted in prey capture. *Crocodylus niloticus* have likewise been reported to capture small, low-flying birds (Atwell, 1954). We also observed a subadult crocodile (TL c. 120 cm) swimming from a rookery with a freshly killed adult green-backed heron (*Butorides virescens*) in its mouth. Additionally, although predation was not observed, concentrations of crocodiles were frequently encountered at cormorant (*Phalacrocorax* spp.) roosts during spotlight surveys. Predation of adult and juvenile wading birds at rookeries and nocturnal roosts by *A. mississippiensis* is well documented in the literature (McIlhenny, 1935; Hopkins, 1968; Ruckdeschel & Shoop, 1987).

Plant material, small stones and hard seeds are frequently reported among stomach contents in studies of crocodilian diet (Cott, 1961; Webb *et al.*, 1982; Platt *et al.*, 1990; Webb *et al.*, 1991; Thorbjarnarson, 1993b; Tucker *et al.*, 1996). Although deliberate frugivory by captive crocodilians has been observed (Brueggen, 2002; Brito *et al.*, 2002), it is generally assumed that plant material is ingested incidental to prey capture and

has no nutritional value (Coulson & Hernandez, 1983). Small stones and other hard objects are purposefully consumed and serve as gastroliths (Davenport *et al.*, 1990; Fitch-Snyder & Lance, 1993). While not essential for digestion, gastroliths are thought to facilitate the breakdown of ingested prey in a manner similar to grit in the avian gizzard, and may be especially important for smaller size classes that consume chitin-rich diets (Sokol, 1971; Platt *et al.*, 1990; Fitch-Snyder & Lance, 1993). Davenport *et al.* (1990) found that gastroliths enhance digestion by squeezing fluids from punctured arthropods, but Taylor (1993, 1994) discounted this role and speculated that gastroliths serve primarily as ballast for buoyancy control. More recently, Henderson (2003) used a mathematical and computational model to convincingly demonstrate that the relatively small mass of gastroliths occurring in crocodilian stomachs is inconsequential for maintaining stability and buoyancy in the water column.

Ontogenetic dietary changes have not been previously reported for *C. moreletii*, but are well documented in many species of crocodilians (Lang, 1987), and presumably reflect energetic advantages and the ability of larger individuals to capture larger prey (Webb *et al.*, 1991). In general, smaller size classes subsist primarily on insects and crustaceans, with a pronounced increase in the consumption of vertebrates as individuals mature (Lang, 1987). *Crocodylus moreletii* appears to follow this general pattern except that as crocodiles mature, the diet includes increasing amounts of aquatic snails rather than vertebrates. This trend is undoubtedly exaggerated by the tendency of snail opercula to accumulate in the stomach (Barr, 1997), over-emphasizing the percent occurrence of this item in the diet. However, other vertebrate remains such as fish scales, turtle scutes, bird feathers and mammal hair that are likewise resistant to digestion (Delany & Abercrombie, 1986; Janes & Gutzke, 2002) would also accumulate and be over-represented in the diet if crocodiles were consuming significant numbers of these taxa.

We found high dietary overlap between adjacent size classes of *C. moreletii*, with decreasing overlap as size differences increased; the lowest overlap occurred between the largest and smallest size classes. This is not unexpected in a species such as *C. moreletii* that undergoes an almost 500-fold increase in body size from hatching to adulthood. Similar findings were reported by Tucker *et al.* (1996) for *C. johnstoni* in the only previous study to quantify intraspecific dietary overlap in crocodilians. Despite high dietary overlap between similar-sized *C. moreletii*, niche overlap alone does not necessarily indicate that competition is occurring (Pianka, 1988). Although habitat use by *C. moreletii* has yet to be investigated, intraspecific size-related ecological separation appears commonplace among crocodilians (Lang, 1987) and may function to reduce competition for food (Tucker *et al.*, 1996).

The magnitude of dietary overlap between the largest (adult) and smallest (hatchling and small juvenile) size classes of *C. moreletii* is within the range of differences

typically found between species (MacArthur, 1972; Polis, 1984). If different size classes use sufficiently different resources, they may function as different ecological entities (see review by Polis, 1984). These entities were described by Enders (1976) and Maiorana (1978) as 'ecological species', and defined as intraspecific units whose differences in resource use approximate those of taxonomic species. Because intraspecific competition between 'ecological species' is minimal, interspecific rather than intraspecific interactions may be more important in defining patterns of resource use for these size classes (Polis, 1984). However, these potentially complex community interactions have not been investigated in any crocodilian.

Finally, although we did not investigate seasonal patterns of prey consumption by *C. moreletii* in northern Belize, seasonal changes in diet have been reported in other crocodilians (Valentine *et al.*, 1972; Gorzula, 1978; Hutton, 1987; Thorbjarnarson, 1993b; Tucker *et al.*, 1996). Prey availability is often influenced by seasonal fluctuations in water levels that function to concentrate or disperse prey (Valentine *et al.*, 1972; Platt *et al.*, 1990; Thorbjarnarson, 1993b). For example, during dry periods crustaceans are often unavailable when aestivating, while fish become concentrated in shallow pools and are readily captured by foraging crocodiles (Thorbjarnarson, 1993b). On the other hand, fish are less available when dispersed by rising water levels, while terrestrial insects become accessible in partially flooded vegetation (Platt *et al.*, 1990). Given the pronounced wet-dry seasonality of northern Belize, seasonal differences in the diet of *C. moreletii* are likely and warrant future investigation.

ACKNOWLEDGEMENTS

We wish to express our gratitude to Robert Noonan and the staff of Gold Button Ranch, and Mark, Monique and Colin Howells of Lamanai Outpost Lodge, for providing essential logistical support during this study. SGP was supported by grants from Wildlife Conservation Society and Clemson University. TRR, AGF, STM and TAA were supported by Lamanai Field Research Center, U. S. EPA (Grant no. R826310 to STM), and an ARCS Foundation (Lubbock, Texas Chapter) scholarship to TRR. Additional support was provided by the Royal Geographical Society, Richard and Carol Foster, Monkey Bay Wildlife Sanctuary and Cheers Restaurant. Sharon Matola and Tony Garel provided access to crocodiles at the Belize Zoo. We thank Jan Meerman, Hannibal Smith, B. A. Barachus and Christine Tupper for field assistance, and Karen McGlothlin for invertebrate identification. Research permits were issued by Rafael Manzanero and Emil Cano of the Conservation Division, Forest Department, Belmopan, Belize. Comments by Richard Montanucci, David Tonkyn, Edward Pivorun, Thomas Lacher, Peter Stafford and two anonymous reviewers improved earlier drafts of this manuscript.

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