

Diet of the Nile Crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana

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ABSTRACT.—The analysis of stomach contents can shed light on patterns of prey availability and foraging habits of a predator; however, recent studies have shown the potential bias in dietary studies resulting from differential digestion rates of various prey items. The stomachs of 286 Nile Crocodiles (17–166 cm snout–vent length) were lavaged over a two-year period. Taking prey residence times into account, the contents were examined for prey eaten within 24 h. *Crocodylus niloticus* has a similar ontogenetic shift in diet to that of other crocodylians. Yearlings consumed primarily aquatic insecta and arachnida. As crocodile size increased (juveniles), the diet became more diverse including crustacea, amphibia, and fish. The largest size class (subadults) consumed primarily fish. Yearlings fed consistently throughout the year; however a higher proportion of empty stomachs occurred within the juvenile and subadult size classes during the winter months. Seven species of nematodes were found within the stomachs, four of which represent new geographic records.

Although difficult to compare statistically (because of seasons, size classes, and types of analyses used), the ontogenetic trends of crocodylian diet are similar for the different species. Young crocodylians primarily consume insects and arachnids (Platt et al., 2002); these decrease in importance as crocodylians increase in size (Tucker et al., 1996). The intermediate size classes of crocodylians have the most diverse diet and feed on amphibians, small mammals, birds, reptiles, crustaceans, gastropods, and arachnids in varying proportions, as well as insects and fish (Tucker et al., 1996; Barr, 1997). Then, fish become the most important prey for the sub-adult and adult crocodylian with the occasional large mammal (Blomberg, 1976; Games, 1990). An increase in the percentage of empty or nearly empty stomachs correlates to an increase in total length (Games, 1990). These are broad generalizations, and the proportions vary with the crocodylian species, geographical location, and season; this has been documented for several species (Webb et al., 1991; Barr, 1997; Platt et al., 2006).

Bias in crocodylian dietary studies resulting from differential digestion rates of prey items, in particular slow digestion of chitinous material, was first suggested by Neill (1971) and most recently by Janes and Gutzke (2002). A few studies have also used regression formulae to predict the original mass of freshly ingested prey from recovered fragments, as well as relating the prey to its gastric residence time,

thereby reducing bias as only freshly ingested prey was used in the primary analysis (Webb et al., 1991; Barr, 1997; Hirai and Matsui, 2001).

A fundamental concept of understanding the ecology of an animal is its dietary habits (Rosenburg and Cooper, 1990), which within crocodylians affects growth, behavior, and reproduction (Lang, 1987). This study examined the diet of the Nile Crocodile with reference to size class, seasons, and differential digestion rates by analyzing prey that was eaten within 24 h of capture.

MATERIALS AND METHODS

Study Site.—The Okavango River originates in the central highlands of Angola. The Cubango and Cuito tributaries form the Okavango River which eventually enters northwestern Botswana. The upper part of the delta, the panhandle, is a 15-km broad fault-bounded, flat-bottomed valley, with a well-defined meandering channel. Two hundred kilometers later the Okavango River branches out to form the Okavango Delta, a tectonically forced alluvial fan, 22,000 km² in size, subject to annual flooding and composed of a mosaic of floodplains and islands (Andersson et al., 2003). The Okavango Delta is a flood-pulsed wetland (Wolski and Murray-Hudson, 2005) and is a recognized RAMSAR site (a wetland of international importance according to the Ramsar Convention on Wetlands, 1971).

Animal Capture and Collection of Stomach Contents.—From August 2003 to August 2005, 286 Nile Crocodiles of various size classes were

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TABLE 1. Prey age assessment criteria for food items eaten by the Nile Crocodile (*Crocodylus niloticus*).

Prey group	24h residency criteria
Insecta	Relatively intact, most of appendages still attached
Arachnida	Main body intact
Crustacea	Main body intact
Amphibia	All were considered freshly ingested
Pisces	All unless only vertebrae was found
Mammalia	Main body intact

captured in the Okavango "Panhandle" area and stomach lavaged. The animals were allocated to one of three size classes based on snout-vent length (SVL): yearlings (17.0–38.9 cm; $N = 151$), juveniles (39.0–66.3 cm; $N = 82$) and subadults (66.4–115.8 cm; $N = 53$; Leslie, 1997).

Crocodiles were captured, either by hand or noose, from a boat at night using a spotlight. Numerous morphometric measurements were recorded, and the stomachs of the crocodiles were immediately lavaged at the site of capture. Stomach samples were obtained using a modification of a technique originally devised by Ayarzagüena (1983), modified and evaluated by Fitzgerald (1989) and Rice et al., (2006). The technique, known as the hose-heimlich technique, uses a water pump to flush out the stomach contents. A padded metal O-ring was secured between the crocodile jaws, and a lubricated pipe was inserted into the esophagus and pushed into the stomach (the distance to the stomach was estimated externally and marked on the pipe prior to insertion). Water was pumped into the stomach, which was externally hand massaged, and the contents were ejected into a collection receptacle.

Stomach samples were sorted into prey items and nonprey items. Prey item samples were then further separated into two distinct groups: (1) fresh prey items (ingested < 24 h of capture); and (2) old prey items (ingested > 24 h before capture). Prey age assessment was based on two previous studies by Games (1990) and Barr (1997; Table 1). Using museum specimens and field data, fresh prey items were regressed to their estimated original mass for the analysis (Wallace, 2006). Nonprey items consisted of parasites, stones (gastroliths), and vegetation. Prey items were digitally photographed, and a wet mass was recorded. Samples were then frozen for transport to the Department of Conservation Ecology and Entomology at the University of Stellenbosch, South Africa, for further analysis. Prey was recorded as percent occurrence (percentage of the sample that contained the particular taxon) and percent

composition (percentage of the total stomach content mass that belongs to the taxon).

Overlapping Group Analysis.—This technique was used to determine possible ontogenetic changes in diet. This involved using overlapping groups of 15 crocodiles. The first size category consisted of the 15 lightest crocodiles and the size class labeled with the mean mass for that group of 15 animals. The next size class of 15 animals incorporated the next five heaviest animals and excluded the five lightest animals, et cetera (Games, 1990). This overlapping technique gives a continuous transition of progressively heavier size classes to assist in recognition of dietary trends rather than the standard comparison of only two or three size classes (Magnusson et al., 1986).

Statistical Analysis.—A maximum-likelihood Chi-squared test was used for the ranked occurrence data and a Kruskal-Wallis analysis of variance by ranks, for nonnormally distributed prey mass and diet composition data. Arcsine-transformation was used on data converted to percentages and analyzed using a one-way ANOVA. The incidence-based coverage estimator (ICE) was used to extrapolate species richness and accumulation curves to predict the total number of different species consumed. This was calculated using EstimateS: Statistical estimation of species richness and shared species from samples (version 7.5, R. K. Colwell, <http://purl.oclc.org/estimates>). The Shannon-Wiener diversity index was used to measure the diversity of prey types eaten by the different size classes and to allow a statistical comparison among classes. All statistical analyses were performed using Statsoft, Inc., Statistica version 7.1 (SAS Institute, Cary, NC), and means are given ± 1 SE.

RESULTS

Stomach Contents.—The proportion of stomachs containing fresh prey decreased with an increase in crocodile size. Fresh prey remnants were found in 41.3% of the combined sample. There was a gradual decrease in the occurrence of stomachs that contained fresh prey with an increase in crocodile size (Fig. 1; $154.112 - 70.4218 \times \log_{10}(x)$, $r = -0.65$, $P < 0.05$). Fresh prey items were more frequently found within yearlings stomachs (55.6%) than those of either juveniles (29.8%) or subadults (18.9%; $\chi^2 = 15.21$, $P < 0.01$). There was no significant difference between the frequencies of fresh stomach contents between the sexes. Fresh stomach contents were recovered from 57.9% of male and 48.8% of female yearlings ($F_{1,51} = 0.01$, $P > 0.05$), 31.7% of male and 21.0% of female juveniles ($F_{1,80} = 0.79$, $P > 0.05$), and 19% of male

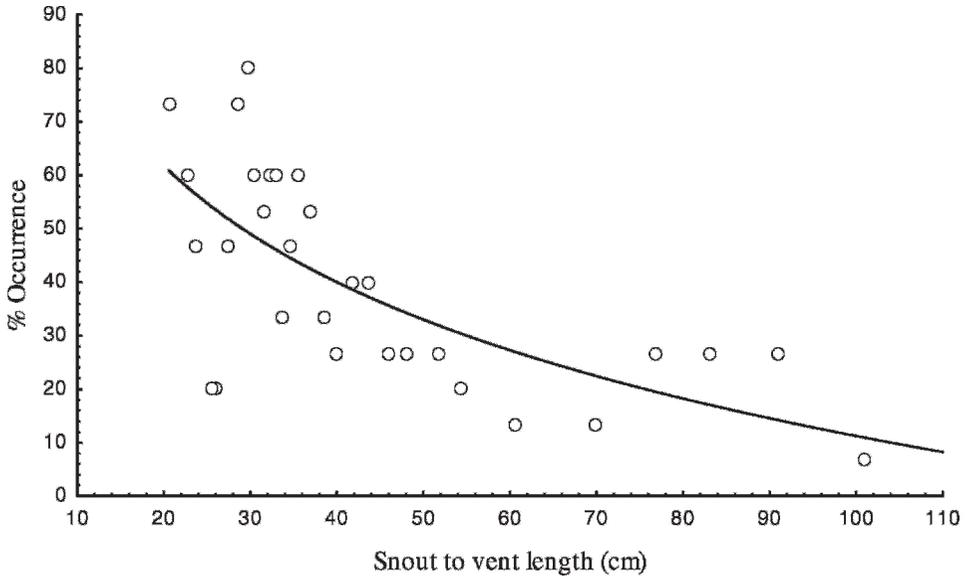


FIG. 1. Overlapping analysis showing mean percentage of Nile Crocodile (*Crocodylus niloticus*) stomachs containing fresh prey relative to crocodile size (SVL).

and 18.8% of female subadults ($F_{1,51} = 0.01, P > 0.05$).

The mass of fresh prey relative to body mass decreased with an increase in crocodile size (Fig. 2; $H_2 = 31.02, P < 0.05$). Stomachs of yearlings contained a significantly higher mass of fresh prey relative to body mass ($0.4\% \pm 0.1$) than juveniles ($0.3\% \pm 0.1; F_{1,234} = 4.32, P <$

0.05) and subadults ($0.1\% \pm 0.03; F_{1,203} = 6.68, P < 0.05$). Juveniles ($0.3\% \pm 0.1$) did not differ significantly to subadults ($F_{1,135} = 2.84, P > 0.05$).

The average number of fresh prey items found decreased with an increase in crocodile size ($F_{2,117} = 0.87, P < 0.05$). Yearling stomachs contained 1.7 (± 0.3) fresh prey items on

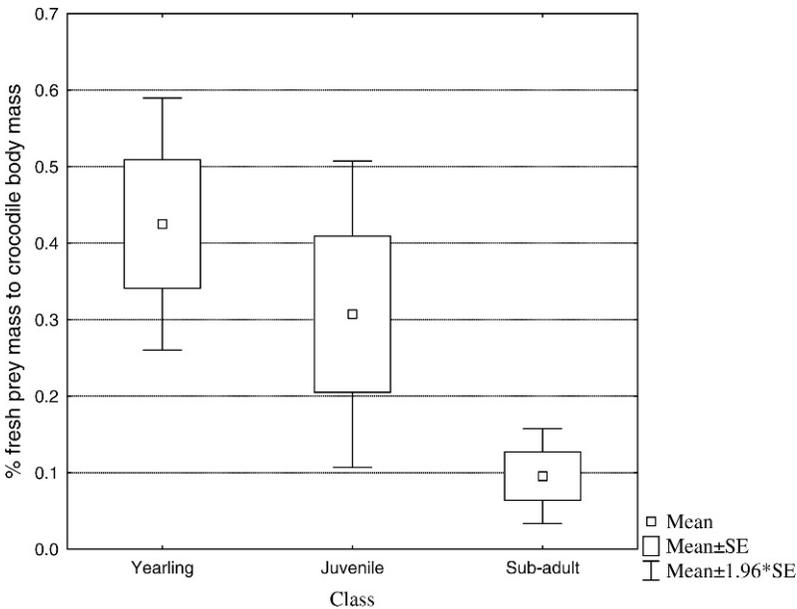


FIG. 2. Mean percentage of fresh prey (regressed to original mass) found in Nile Crocodile (*Crocodylus niloticus*) stomachs relative to crocodile mean body mass (mean, standard error, and 95% confidence limits).

TABLE 2. Type and mass of recently ingested prey found in stomachs of the Nile Crocodile (*Crocodylus niloticus*). Percent composition (% of the total prey mass that belongs to that taxon) and percent occurrence (% of the sample that contained the particular taxon).

Prey group	% Composition			% Occurrence		
	Yearling	Juvenile	Subadult	Yearling	Juvenile	Subadult
INVERTEBRATA	45.6	44.1	1.2	86.9	83.3	30
Crustacea		17.2			8.3	
Decapoda		17.2			8.3	
Arachnida	7.6	1.6	0.1	57.1	41.7	10
Pisauridae	3.5	1		27.4	29.2	
Araneidae	0.1	0.2		1.2	8.3	
Lycosidae	0.4			2.4		
Tetragnathidae	0.9			7.1		
Unidentified Arachnida	2.8	0.3	0.1	20	8.3	10
Insecta	38	25.3	1.1	57.1	45.8	20
Dermaptera	0.2			2.4		
Orthoptera	5.6	3.1		7.1	4.2	
Tettigonidae	4.3			6		
Gryllotalpidae	1.3	3.1		1.2	4.2	
Hymenoptera	0.1	0		2.4		
Coleoptera	18.2	18	0.8	11.9	20.8	10
Terrestrial Coleoptera	0.3	0.1		2.4	4.2	
Hydrophilid	6	9.3	0.8	4.8	12.5	10
Dytiscidae	11.9	8.2		9.5	12.5	
Gyrinidae		0.3			4.2	
Lepidoptera	1.5	0.7		7.1	4.2	
Unidentified Lepidoptera	0.2	0.7		2.4	4.2	
Noctuidae	1.3			3.6		
Diptera	0.2	0.1		2.4	4.2	
Odonata	3.8		0.2	2.4		10
Libellulidae	3.8			2.4		
Unidentified Odonata			0.2			10
Hemiptera	9.9	4		29.8	8.3	
Nepidae	0.1			2.4		
Belostomatidae	8.4	4		23.8	8.3	
Gerridae	1.4			13.1		
VERTEBRATA	51	51.6	77	25	25	90
Teleosti	11.6	35	68	10.7	12.5	80
Hepsetidae		26.2	27		4.2	10
Siluriformes			12.6			20
Cichlidae	3.1	7.3	6.9	1.2	4.2	10
Mochokiae			7.2			10
Momyridae		1.5	4.2		4.2	10
Poecillidae	3.8			7.1		
Characin	2			2.4		
Cyprinidae	0.9			1.2		
Unidentified Teleosti	1.8		10.2	3.5		20
Mammalia	30.8	11.2	9	3.6	4.2	10
Muroidea		11.2	9		4.2	10
Soricidae	12.3			2.4		
Unidentified Mammalia	18.5	11.2	9	1.2	4.2	10
Amphibia	8.6	0.9		7.1	4.2	
Hyperolidae	2.2	0.9		3.5	4.2	
Unidentified Amphibia	6.4			3.5		
Reptilia		4.5			4.2	
Unidentified Squamata		4.5			4.2	
OTHER	3.4	4.3	21.8	50	66.7	80
Stones	0.4	0.3	20.8	3.6	20.8	50
Parasites	0.6	0.7	0.7	40.5	45.8	30
Vegetation	2.5	3.4	0.3	22.6	29.2	25

TABLE 3. Shannon-Wiener diversity index indicating species richness of the diet between the three size classes of the Nile Crocodile (*Crocodylus niloticus*). Species richness = total number of species predated. Total abundance = total number of individuals predated.

	Yearling	Juvenile	Subadult
Shannon-Wiener			
Diversity index	2.6	2.7	1.7
Species richness (S)	32	18	8
Total abundance	175	32	17
Evenness	0.74	0.92	0.81

average, a significantly higher number than juveniles that contained $0.5 (\pm 0.1)$ and subadults that contained $0.4 (\pm 0.2)$. This indicated that yearlings consumed prey items more frequently than either juveniles or subadults.

Invertebrates occurred in 86.9% and 83.3% of the yearling and juvenile stomachs, respectively (Table 2). Fish were found more frequently with an increase in crocodile size and constituted a higher percentage of the total dietary mass. Juveniles contained the only evidence of freshly ingested crustaceans, although evidence of old remnants was found in the stomachs of all three classes. The juvenile class was the only size class with old bird and turtle remains present. The diet of the subadults consisted primarily of fish, occurring in 80.0% of the stomachs and constituting 68.0% of the diet. Old remnants of bivalves were found in juvenile (3.7%) and subadult (17.0%) stomachs. The occurrence of

vegetable matter (primarily papyrus with grasses and seeds) in stomachs remained relatively constant ($\chi^2 = 0.59, P > 0.05$). Vegetation was found in the stomachs of 22.6% of yearling, 29.2% of juvenile, and 25.0% of subadult crocodiles. Vegetation constituted 0.08% (± 0.02) of yearling, 0.05% (± 0.02) of juvenile and 0.07% (± 0.04) of subadult body mass, respectively.

Prey Diversity.—Using the ICE as an estimate of species richness of the diet of all three size classes of crocodiles combined, a total of 75 different prey species was predicted. An estimated total of 53 different species was predicted within the yearling size class alone. ICE was not calculated for the juvenile or subadult size classes because the sample sizes were not adequate for reliable estimates. The Shannon-Wiener diversity index (Table 3) indicates that the two smaller size classes consumed a similar diversity of prey, both significantly higher than that of the subadult size class ($F_{2,288} = 14.11, P < 0.01$).

Diet Shift.—The transition to different prey types occurs at the upper end of the juvenile size class. The occurrence of both insects and arachnids declined with increasing crocodile size (Fig. 3). There was a marked change in the diet as fish became more dominant and mammals were consumed less often when crocodiles exceeded a SVL of 40 cm (Fig. 4).

Seasonal Differences.—The proportion of yearlings with fresh prey items present did not differ significantly between summer (59.5%) and winter (51.4%; $F_{1,149} = 1.00, P > 0.05$).

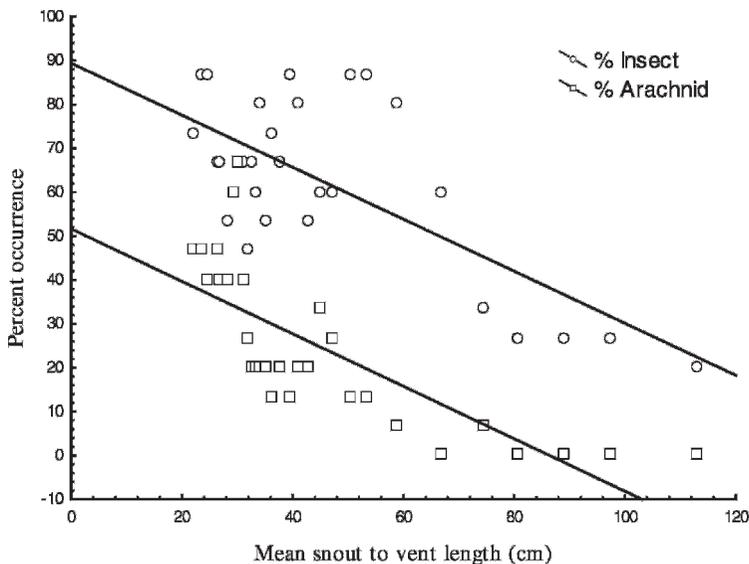


FIG. 3. Percent occurrence of Nile Crocodile (*Crocodylus niloticus*) stomachs containing all remnants of the main invertebrate prey groups using an overlapping group analysis.

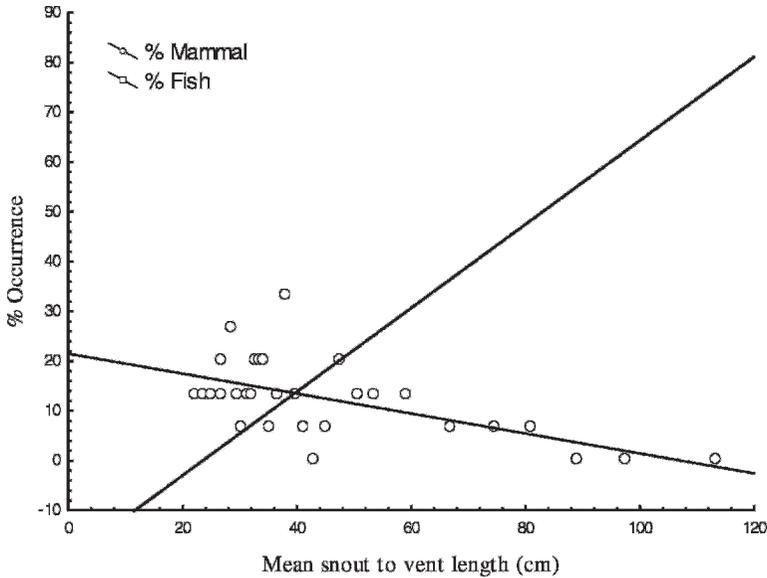


FIG. 4. Percent occurrence of Nile Crocodile (*Crocodylus niloticus*) stomachs containing all remnants of the main vertebrate prey groups using an overlapping group analysis.

However, the proportion of juveniles with fresh stomach contents present was significantly higher in summer (37.3%) than in winter (16.1%; $F_{1,80} = 4.27$, $P < 0.05$). None of the 15 subadult crocodiles caught during the winter months had any fresh prey items present when compared to 23.7% of stomachs with fresh prey items during the summer months ($F_{1,51} = 5.16$, $P < 0.05$).

Stomach Stones (Gastroliths).—Gastroliths occurred with increasing frequency with an increase in crocodile size ($\chi^2 = 24.96$, $P < 0.01$). Total gastrolith mass relative to crocodile body mass increased with crocodile size but not significantly ($F_{2,29} = 0.35$, $P > 0.05$). Four percent of yearling, 20.8% of juvenile, and 26.4% of subadult stomachs contained gastroliths. Yearling stomachs contained gastroliths that constituted 0.13% (± 0.05) of total crocodile body mass; juvenile stomachs contained gastroliths that constituted 0.18% (± 0.1); and the stomachs of subadults contained gastroliths that constituted 0.26% (± 0.11).

DISCUSSION

The diet of the Okavango crocodiles was almost entirely from within the river itself. Pisuridae spiders (the main arachnid prey) spend most of their time on or very close to the water surface. The family, Lycosidae, is able to traverse the water surface and often live close to water (Corbett, 1959). The invertebrate portion of the diet consisted primarily of predacious water bugs, water beetles, and fish-

eating spiders, which prey upon fish fry. The remaining invertebrate prey is almost exclusively aquatic, primarily hemipterans and coleopterans. Small mammals occasionally traverse the main channel (pers. obs.). A very small proportion of the diet was truly terrestrial, such as some of the arachnids, coleopterans, and orthopterans. In addition to prey items, several nonfood items were also retrieved from stomachs. All gastroliths recovered from the stomachs of the Okavango crocodiles were quartz, although one crocodile contained a single feldspar stone among other quartz stones. The porous nature of some of the quartz stones indicate that they may have formed within the stomach caused by calcium precipitation from the bones of prey (E. Spicer, pers. comm.).

The smaller crocodiles relied primarily on surface and subsurface feeding at the littoral vegetated fringe of the river as indicated by the range of insects eaten (P. Reavell, pers. comm.). With an increase in body length, crocodile diet shifted away from insect prey toward small mammals and then fish, concurring with the observations of Tucker et al. (1996), who stated a similar ontogenetic diet shift in *C. johnstoni* as body size increased and the cranium broadened. A broadening of the head allows for the capture of larger prey and a relative gain in energy and growth (Webb et al., 1978).

The proportion of empty stomachs was not significantly different between seasons for the yearlings, possibly because of a higher metabolic demand (Coulson et al., 1973) that requires continuous feeding. Seasonal differences be-

tween feeding were apparent with an increase in size, as empty stomachs were more frequently encountered during the winter months. However, the yearlings and juveniles that fed during the winter months still consumed a similar total prey mass when compared to the mass consumed in the summer months.

Gastrolith mass in relation to crocodile mass did not increase significantly with an increase in crocodile size. The percentage of body mass that the gastroliths accounted for was relatively low, 0.13–0.26%, when compared to other crocodilians where gastroliths can account for up to 1.0% of body mass (Brazaitis, 1969). Gastroliths occurred at a higher frequency within juvenile and subadults stomachs than in the stomachs of yearlings. Data from this study indicate a relatively low occurrence of stomach gastroliths possibly because of the geology of the area. In general, stones are seldom encountered in the panhandle area, the substrate of which is dominated by Kalahari sand. The technique used in this study for stomach-content retrieval was evaluated by Fitzgerald (1989) as 83% effective for the recovery of stones. Cott (1961) found stomach stones in all shot adult *C. niloticus*; however, his postmortem analysis would have been a more effective technique for stone retrieval than the method used in this study.

All parasites recovered from the crocodiles have previously been documented parasitizing crocodilians (Yamaguti, 1961). However, the stomach lavage technique used in this study may not give an accurate estimate of parasitic load, because embedded and oesophageal parasites are not entirely removed (Fitzgerald, 1989).

Plant remains increasing in frequency with an increase in crocodile size have been reported from several studies (Blomberg, 1976; Taylor, 1979), and data from this study show a similar trend. Taylor (1979) suggested that plant material has a nutritional value, although crocodilians are unable to digest either vegetable proteins or polysaccharides (Coulson and Hernandez, 1983).

The Okavango crocodiles are highly dependent on aquatic prey, and although many crocodilians have a similar ontogenetic shift in diet, there is local variation within the diet and between populations. This highlights the importance of dietary studies in the compilation of management plans. However, to fully use dietary data, it is important to use it within the context of the predator population and prey abundance, more so if the prey has a commercial value, such as Tilapia in the Okavango system, and where there is also an open access

fishery regime. There is scope for future studies that can incorporate these factors.

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