

**The feeding ecology of yearling, juvenile and sub-adult
Nile crocodiles, *Crocodylus niloticus*, in the
Okavango Delta, Botswana**

Kevin Michael Wallace

Thesis presented in partial fulfilment of the requirements for the degree of

Master of Science

Department of Conservation Ecology and Entomology
Faculty of AgriSciences
University of Stellenbosch

Supervisor: Dr. Alison J. Leslie

December 2006

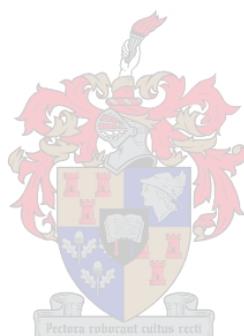
DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original
work

and that I have not previously in its entirety
or in part submitted it at any university for a degree

Signature:

Date:



ABSTRACT

The stomachs of 286 crocodiles (17 cm to 166 cm snout to vent length) were lavaged over a two year period. *Crocodylus niloticus* has a similar ontogenetic shift in diet to that of other crocodilians. Yearlings predated primarily on aquatic insecta and arachnida, as crocodile size increased (juveniles) the diet became more diverse including crustacea, amphibia and fish. The largest size class (sub-adults) consumed primarily fish. Yearlings fed consistently throughout the year, however a higher proportion of empty stomachs occurred within the juvenile and sub-adult size classes during the winter months. A captive experiment with wild caught crocodiles (0.7 kg - 20 kg) indicated a decrease in satiation rate (maximum mass of food eaten as a percentage of crocodile body mass) from 11.3 % to 6.5 % with an increase in crocodile size. Wild yearlings consumed 0.48 % of their body mass in prey per day, and juveniles, 0.23 %. The wild food conversion rates of natural prey were low, 32 % and 40 % for yearlings and juveniles respectively. This was possibly due to a high percentage of indigestible (chitinous) invertebrate mass in the diet. The percentage of stomach stone mass to crocodile body mass increased with crocodile size. Seven species of nematodes were found within the stomachs, four of which represent new geographic records.

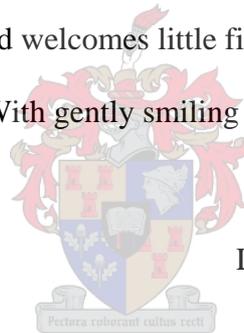
OPSOMMING

Die maaginhoud van 286 krokodille (17 cm tot 166 cm in lengte) is uitgespoel oor 'n periode van twee jaar. *Crocodylus niloticus* vertoon, in vergelyking met ander krokodilagtiges, 'n soortgelyke ontogenetiese verskuiwing in diëet. Jaaroud diere voed hoofsaaklik op akwatiese insekte en arachnida, terwyl die diëet diversifiseer om crustacea, amfibiërs en vis in te sluit soos krokodilgrootte (in jong krokodille) toeneem. Individue in die grootste grootte-klas het hoofsaaklik op vis gevoed. Jaaroud individue het konstant regdeur die jaar gevoed. Krokodille in die jong- tot sub-volwasse kategorieë, het egter 'n hoër proporsie van leë maaginhoud gehad gedurende die wintermaande. Krokodille wat uit die wild geneem is en daarna onder eksperimentele omstandighede aangehou is, het 'n afname in versadigingstempo (die maksimum massa kos wat geëet is as 'n persentasie van die individu se liggaamsmassa) vanaf 11.3 % tot 6.5 %, met 'n toename in krokodilgrootte aangetoon. Jaaroud diere wat uit die wild geneem is, het 0.48 % van hul liggaamsmassa in prooi per dag ingeneem, waarteenoor 0.23 % by jong diere. Die omsettingstempo van natuurlike prooi was laag; 32 % en 40 % vir jaaroud- en jong diere respektiewelik. Dit kan moontlik toegeskryf word aan die hoë persentasie van onverteerbare (chitineagtige) invertebraatmassa in die diëet. Die persentasie van klipmassa in die maag tot krokodilmassa, het toegeneem met 'n toename in krokodilgrootte. Sewe spesies nematode, waarvan vier nuwe geografiese rekords verteenwoordig, is in die maaginhoud van die bestudeerde krokodille gevind.

How Doth The Little Crocodile...

How doth the little crocodile
Improve his shining tail,
And pour the waters of the Nile
On every golden scale!

How cheerfully he seems to grin
How neatly spreads his claws,
And welcomes little fishes in,
With gently smiling jaws!



Lewis Carroll (2001)

Acknowledgements

This study would not have been possible without the help and encouragement of many people:

I am very grateful to Dr. Alison Leslie, my supervisor, for her constant support, advice, enthusiasm and dedication to the cause.

My parents and financial advisors, Lynda and Richard Wallace for their support and encouragement, without whom I would never have gotten this far.

My research in the Okavango Delta was made much more enjoyable and possible due to my field-work colleagues, Audrey Detoef-Boulade, Kristi Maciejewski, Georgina Thomas, Sven Bourquin and Vince Shacks for friendship, assistance and support above and beyond the call of duty. Also to Pabelelo Shone from Sepopa who helped us in our research camp.

Earthwatch Institute, USA for providing the financial support and to all the volunteers who helped both financially and physically by supporting our project.

I wish to thank the following members from the University of Stellenbosch, Pat Reavell, Prof. Michael Samways and Prof. Henk Geertsema (Department of Entomology) for their assistance in identifying the invertebrate fauna. Sandy Willows (Department of Botany and Zoology) for the small mammal identification. Dr. Esmé Spicer (Department Geology) for the gastrolith identification. Prof. Daan Nell (Center for statistical consultation) for the numerous and invaluable statistical consultations as well as Dr. Ken Pringle (Department of Entomology) for statistical advice and Dr. Connie Krug (Department Conservation) for statistical advice and small mammal identification.

Roger Bills (South African institute for aquatic biodiversity, Grahamstown) for the fish identification. Dr. Ansi Dippenaar-Schoeman (National Collection of Arachnids, Agricultural Research Council, Pretoria) for the arachnid identification. Prof. Joop Boomker and Kirsten Junker (Department of Veterinary Tropical Diseases, University of Pretoria, Onderspoort) for the stomach parasite identification.

The Office of the President and the Department of Wildlife and National Parks, Botswana for providing our research permits and logistic support. The Kalahari Conservation Society for logistical support and assistance in obtaining the necessary research permits in Botswana.

Phil and Kay Potter and the staff at Sepopa Swamp Stop. Jan and Eilleen Drotsky at Drotsky's Cabins. Barry and Elaine Price at Shakawe Fishing Lodge. Willy Phillips from Seronga for allowing us to build a research camp on his land. Paulie, Willamien and Braam Le Roux for support and allowing us to camp on their land. Neil and Matt at Okavango River Lodge for accommodation and pleasant conversation. Annalise and Zane Longman, Johan Boshoff and Mr. Amose at Krovango Crocodile Farm, Samochima, Botswana for assistance and allowing us to conduct the digestive study within their property.

The National Research Foundation, South Africa for financial support. Samil Motor Company for donating the much loved Unimog. Pertec International for donating the Magellan GPS units. Zero appliances for the fridges. Animal Handling and Safety Equipment for the maintenance of the capture nooses and tongs.

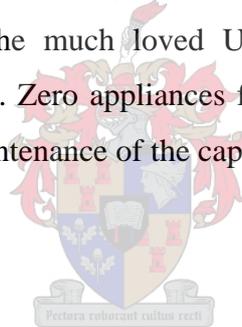


TABLE OF CONTENTS

	Page
Abstract	iii
Opsomming	iv
Acknowledgements	vi
List of Tables	xi
List of Figures	xii
CHAPTER 1 Overview of Crocodilian Diet and Digestion	
Feeding behaviour	1
Ontogenetic trends	1
Stomach content retrieval	2
Stomach content analysis	4
Rate of feeding	6
Conversion rates and digestion	7
Non-food items	8
References	10
CHAPTER 2 Study site and study animal	
Hydrology and topography	19
The fauna and flora of the region	21
The Nile crocodile, <i>Crocodylus niloticus</i>	22
References	25
CHAPTER 3 Dietary habits of the Nile crocodile, <i>Crocodylus niloticus</i>, in the Okavango Delta, Botswana	
Introduction	30
Methods	32
Crocodile capture and stomach content retrieval	32
Prey identification	32
Statistical analysis	33
Results	34
Invertebrates	48
Vertebrates	49
Prey diversity	50
Diet and skull morphometrics	51
Seasonal differences	54
Discussion	56
References	58

	Page
CHAPTER 4	
Non-food items found in stomachs of the Nile crocodile, <i>Crocodylus niloticus</i>, in the Okavango Delta, Botswana	
Introduction	62
Methods	64
Crocodile capture and stomach content retrieval	64
Stomach stones (Gastroliths)	64
Parasites	64
Statistical analysis	65
Results	66
Stomach stones (Gastroliths)	66
Parasites	67
Vegetation	68
Discussion	70
Stomach stones (Gastroliths)	70
Parasite	70
Vegetation	71
References	72
CHAPTER 5	
Digestion, nutrient assimilation and satiation level of the Nile crocodile, <i>Crocodylus niloticus</i>, in the Okavango Delta, Botswana	
Introduction	75
Methods	77
Satiation level	77
Gut passage time	77
Statistical analysis	78
Results	79
Discussion	81
References	84
CHAPTER 6	
Daily food intake and conversion rates of wild Nile crocodiles, <i>Crocodylus niloticus</i>, in the Okavango Delta, Botswana	
Introduction	87
Methods	90
Crocodile capture and stomach content retrieval	90
Stomach content analysis	90
Mark-recapture technique to estimate daily mass gain	91
Statistical analysis	92
Results	93
Yearlings	93
Juveniles	94
Sub-adults	94

		Page
	Conversion rates	94
	Discussion	97
	References	100
CHAPTER 7	Summary	
	Summary	104
	References	106
APPENDIX 1	Crocodile capture techniques	
	Night-shifts	108
	Box traps	108
APPENDIX 2	Processing	109
APPENDIX 3	Stomach content collection	110
APPENDIX 4	Prey age assessment	111
APPENDIX 5	Gastrolith identification	113
APPENDIX 6	Original prey mass	114
	Teleosti	114
	Invertebrata	117
	Mammalia	117
	Amphibia	118
APPENDIX 7	Prey species	119
APPENDIX 8	Captive digestion rate study	122

LIST OF TABLES

Table	Page
1.0 Summary of stomach content retrieval techniques	3
1.1 Factors affecting stomach content analysis	5
3.0 Type and mass of all prey remnants found in stomachs	40
3.1 Type and mass of recently ingested prey found in stomachs	43
3.2 Shannon-Wiener diversity index indicating species richness of the diet between the three size classes	51
3.3 Mean monthly crocodile body, air and water temperatures (⁰ C) during night-shifts between August 2003 and August 2005	54
4.0 Occurrence of parasites in stomachs	67
4.1 Number and percentage infestation of crocodiles that contained stomach parasites	68
5.0 Digestive and satiation rates for the three size classes of crocodiles ..	80
5.1 Comparative digestive studies	82
6.0 Prey mass and daily food intake (DFI) for two size classes of crocodile ...	95
6.1 Mean conversion rates for yearlings and juveniles based on recapture data and DFI	96
A.7.0 Identified prey species recovered from stomachs and estimated original mass	119
A.8.0 Number and dimensions of crocodile holding cages	122

LIST OF FIGURES

Figure	Page
2.0 Panhandle study area, Okavango Delta, Botswana	20
3.0 Proportion of stomachs containing fresh prey items	34
3.1 Overlapping analysis showing mean percentage of stomachs containing fresh prey relative to crocodile size (SVL)	35
3.2 Variation in proportion of stomachs containing fresh prey items between the sexes	36
3.3 Mean mass of fresh prey (regressed to original mass) found in stomachs of the three size classes	37
3.4 Mean percentage of fresh prey (regressed to original mass) found in stomachs relative to crocodile mean body mass	37
3.5 Number and percentage of fresh prey items found in the sample of yearlings that had predated prey < 24 hours previously	38
3.6 Number and percentage of fresh prey items found in the sample of juveniles that had predated prey < 24 hours previously	39
3.7 Number and percentage of fresh prey items found in the sample of sub-adults that had predated prey < 24 hours previously	39
3.8A Percent occurrence of the main prey groups for yearlings	46
3.8B Percent occurrence of the main prey groups for juveniles	46
3.8C Percent occurrence of the main prey groups for sub-adults	46
3.9A Percentage composition of the main prey groups for yearlings	47
3.9B Percentage composition of the main prey groups for juveniles	47
3.9C Percentage composition of the main prey groups for sub-adults	47
3.10 Species accumulation curve for fresh prey species recovered from all crocodile stomachs combined	51
3.11 Percent occurrence of stomachs containing all remnants of the main invertebrate prey groups using ‘overlapping group analysis’	52
3.12 Percent occurrence of stomachs containing all remnants of the main vertebrate prey groups using ‘overlapping group analysis’	52

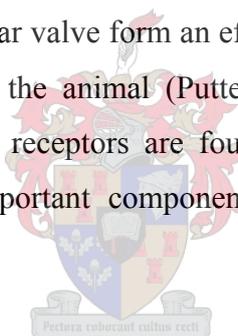
Figure	Page
3.13 Ratio of head length / head width relative to snout to vent length	53
3.14 Ratio of head length / head depth relative to snout to vent length	53
3.15 Seasonal differences in the proportion of stomachs with fresh prey	55
4.0 Proportion of all stomachs lavaged that contained gastroliths	66
4.1 Gastolith mass as a percentage of mean crocodile body mass	67
4.2 Proportion of all stomachs lavaged that contained vegetation	69
5.0 Mass of food eaten by crocodiles in a given time period expressed as a percentage of body mass (satiation level)	79
A.6.1. Relationship between standard length and mass for <i>Hepsetus odoe</i> (African Pike)	114
A.6.2. Relationship between standard length and mass for <i>Tilapia rendalli</i> (Redbreast tilapia)	115
A.6.3. Relationship between standard length and mass for <i>Tilapia sparrmanii</i> (Banded tilapia)	115
A.6.4. Relationship between head width and mass for <i>Synodontis sp.</i> (Squeaker)	116
A.6.5. Relationship between head width and mass for <i>Siloriformes sp.</i> (Catfish)	116
A.6.6. Relationship between total length and mass for <i>Dytascidae sp.</i> (Water beetles)	117

CHAPTER 1

Overview of Crocodilian Diet and Digestion

Feeding behaviour

Crocodilians are adept predators. Terrestrial prey capture utilises binocular vision, aerial focusing (Fleishman *et al.* 1988) and acceleration provided by the tail and hind limbs from a cryptic floating posture (Davenport, 1990; Busbey, 2005). Aquatic prey capture employs tactile senses which trigger a snapping behaviour (Davenport, 1990) with rapid lateral movements of the head (Busbey, 2005) concurring with the crocodilian inability to focus underwater (Fleishman *et al.* 1988). Crocodilians swallow prey by means of inertial feeding (Gans, 1969; Busbey, 2005). This can puncture the integumentary envelope of the prey (Davenport, 1990) and may help with digestion (Jackson and Ryan, 1986). The dorsal and ventral components of the gular valve form an efficient seal consistent with the natural behaviour and feeding habits of the animal (Putteril and Soley, 2006). In *Crocodylus niloticus* both pressure and taste receptors are found throughout the epithelium of the palate and gingivae and are important components in monitoring taste and pressure (Putteril and Soley, 2003).



Ontogenetic trends

Although difficult to compare statistically (due to seasons, size classes and the types of analyses used), the ontogenetic trends of crocodilian diet are similar for the different species. Young crocodilians primarily predate on insects (Coleoptera, Orthoptera and Odonata) and arachnids. These decrease in importance as the crocodilian increases in size. The intermediate size classes of crocodilians feed on amphibians, small mammals, birds, reptiles, crustaceans, gastropods and arachnids in varying proportions as well as insects and fish. Fish then become the most important prey for the sub-adult and adult crocodiles with an occasional large mammal. An increase in the percentage of empty or nearly empty stomachs correlates to an increase in total length (TL). The mean percentage of prey mass relative to crocodile body mass decreases with an increase in crocodile TL. The percentage of stomachs with stones (gastroliths) present increases with crocodile size, although gastroliths are found less often in Caiman than in other species. These are broad generalisations and the proportions of prey and prey items vary with the crocodilian

species, geographical location and season and this has been documented for several species by the following authors:

American alligator, *Alligator mississippiensis* (Valentine *et al.* 1972; McNease and Joanen, 1973; Delany and Abercrombie, 1986; Wolfe *et al.* 1987; Delany, 1990; Barr 1997)

American crocodile, *Crocodylus acutus* (Thorbjarnarson, 1988; Platt *et al.* 2002b)

Dwarf crocodile, *Osteolaemus tetraspis osborni* (Riley and Huchzermeyer, 2000)

Johnston's crocodile, *Crocodylus johnstoni* (Webb *et al.* 1982; Tucker, *et al.* 1996)

Morelet's crocodile, *Crocodylus moreletii* (Platt *et al.* 2002a)

Nile crocodile, *Crocodylus niloticus* (Cott, 1954, 1961; Corbett, 1959a, 1959b; Taylor, 1973; Pooley and Gans, 1976; Blomberg, 1976; Whitfield and Blaber, 1979; Pooley, 1982; Hutton, 1984, 1987; Leslie, 1997; Games, 1990)

Saltwater crocodile, *Crocodylus porosus* (Taylor, 1979; Webb *et al.* 1991)

Spectacled caiman, *Caiman crocodilus* (Magnusson *et al.* 1987; Thorbjarnarson, 1993)

Stomach content retrieval

Unlike studies of terrestrial predators that can involve the analysis of scat or faeces (Anoop and Hussain, 2005; Lenain *et al.* 2004) or with direct observation of aquatic predators feeding (Born *et al.* 2003) or use of signature lipid analysis to identify the natural prey (Jeffs *et al.* 2004), the most accurate way of obtaining dietary data from crocodylians is via a post-mortem. The studies by Corbett (1959a, b), Taylor (1973), Blomberg (1976), Games (1990) and Thorbjarnarson (1993) involved the analysis of stomach contents from harvested crocodiles which also allowed complete recovery of stomach and oesophageal parasites.

Non-lethal methods (Table 1.0) have also been employed to retrieve stomach contents: (i) the scoop and pump method devised by Taylor *et al.* (1978) and later revised by Webb *et al.* (1982); (ii) the garden hose method designed by Ayarzagüena (1983) and a modification of this technique by Fitzgerald (1989), and (iii) the hose-heimlich technique (Barr, 1997). However, none of these techniques remove all the embedded stomach and oesophageal parasites. The effectiveness of the scoop and pump method and the hose-heimlich techniques were 69 % and 100 % (respectively) for removing prey items and 50 % and 83 % for gastroliths. Both methods were thus more reliable than the original garden hose method (Fitzgerald, 1989).

Table 1.0 Summary of stomach content retrieval techniques

Source	Species	Common name	Technique
Barr (1997)	<i>A. mississippiensis</i>	American alligator	Hose-heimlich
Blomberg (1976)	<i>C. niloticus</i>	Nile crocodile	Post-mortem
Corbett (1959a)	<i>C. niloticus</i>	Nile crocodile	Post-mortem
Delany (1990)	<i>A. mississippiensis</i>	American alligator	Post-mortem
Delany and Abercrombie (1986)	<i>A. mississippiensis</i>	American alligator	Post-mortem
Games (1990)	<i>C. niloticus</i>	Nile crocodile	Scoop and pump; Post-mortem
Graham (1968)	<i>C. niloticus</i>	Nile crocodile	Post-mortem
Hutton (1987)	<i>C. niloticus</i>	Nile crocodile	Scoop and pump
Leslie (1997)	<i>C. niloticus</i>	Nile crocodile	Scoop and pump
Magnusson <i>et. al.</i> (1986)	<i>C. crocodilus</i>	Spectacled caiman	Scoop and pump
	<i>P. trigonatus</i>	Smooth fronted caiman	Scoop and pump
	<i>P. palpebrosus</i>	Dwarf caiman	Scoop and pump
	<i>M. niger</i>	Black caiman	Scoop and pump
Platt (2002)	<i>C. moreletti</i>	Morelet's crocodile	Hose-heimlich Observation;
Pooley (1982)	<i>C. niloticus</i>	Nile crocodile	Post-mortem
Rice (2004)	<i>A. mississippiensis</i>	American alligator	Hose-heimlich
Riley and Huchzermeyer (2000)	<i>O. tetraspis</i>	Dwarf crocodile	Post-mortem
Taylor (1979)	<i>C. porosus</i>	Saltwater crocodile	Scoop and pump
Thorbjarnarson (1993)	<i>C. crocodilus</i>	Spectacled caiman	Post-mortem
Tucker <i>et al.</i> (1996)	<i>C. johnstoni</i>	Freshwater crocodile	Scoop and pump
Valentine (1972)	<i>A. mississippiensis</i>	American alligator	Post-mortem
Webb <i>et al.</i> (1982)	<i>C. porosus</i>	Saltwater crocodile	Scoop and pump
Webb <i>et al.</i> (1991)	<i>C. porosus</i>	Saltwater crocodile	Scoop and pump
Wolfe (1987)	<i>A. mississippiensis</i>	American alligator	Post-mortem

Stomach content analysis

The analysis of stomach contents may shed light on patterns of prey availability and foraging habits of the predator (Stafford, 2005). However, stomach content data has to be used carefully due to different rates of prey evacuation and diurnal feeding habits of the predator (Jackson and Ryan, 1986; Games, 1990; Barr, 1997; Andersen, 2001). Bias in dietary studies can be caused by differential digestion rates of prey items, especially those that contain chitinous structures (Neill, 1971; Jackson and Campbell, 1974; Garnett, 1985; Barr, 1997). In crocodylians, tissue fluids from prey items can dilute the stomach pH. However, the resulting level still allows the digestion of bone. The optimum pH level for chitinase is 3.5. Although it is still effective at a pH of 1.5, the enzyme's activity is reduced (Dandrifosse, 1974). Allowances must be made for hard and soft-bodied prey (Jackson and Ryan, 1986; Games, 1990; Barr, 1997; Andersen, 2001), although bearing in mind that damage to the prey item during capture may allow for entry sites for digestive enzymes (Jackson and Ryan, 1986).

Most dietary studies use numerical traits (% occurrence) and prey mass (% composition). However, the composition of prey in the final analysis is often the semi-digested mass of the prey from the stomach, not the original prey mass, which would be a more accurate representation. A few studies have used regression methods or measurements of the whole prey to estimate the original morphometric size and mass of the whole prey item from recovered fragments (Valentine *et al.* 1972; Taylor, 1979; Wolfe *et al.* 1987). However, these studies did not take prey gastric residence time into account and so may have overestimated the importance of certain prey items that have a long gastric residence time. More recently, studies have used regression formulae to predict the original mass of recently ingested prey from recovered fragments (Games, 1990; Webb *et al.* 1991; Barr, 1997; Hirai and Matsui, 2001; Aanoop and Hussain, 2005).

Only a few studies to date have analysed stomach contents, taking prey gastric residence time into account. Corbett (1959a, b) noted that the condition of prey items found in the stomach could provide information on when it was caught, which could be used in determining the rate of feeding and adopted a scoring system taking into account the volume of the food. The use of a pre reference series derived from captive feeding experiments allowed Games (1990) to analyse prey items that were digested within 24 hours in *C. niloticus* and Barr (1997) analysed items digested up to 48 hours previously in

A. mississippiensis. Analysis of these ‘fresh’ items would have eliminated the bias encountered in previous studies, that over or under-represented certain prey items. Only a few studies have included gastric residence times with analysis of stomach contents (*Carcharhinus plumbeus*: Medved *et al.* 1988; *A. mississippiensis*: Delaney and Abercrombie, 1986; Barr, 1994, 1997; *C. niloticus*: Games, 1990; *C. porosus*: Webb *et al.* 1991).

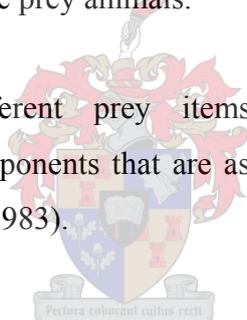
There are many additional factors that can affect the analysis of stomach contents (Table 1.1). In order to understand dietary habits of crocodylians, it is important to relate the prey items found to the actual species found in that particular system. Estimates of prey abundance are important to detect possible differences in prey abundance due to annual prey fluctuations (Bush, 2003).

Table 1.1 Factors affecting stomach content analysis

FACTOR	DESCRIPTION
Prey composition	Protective coverings such as hair or scales may slow diffusion of the gastric secretions (Delany and Abercrombie, 1986) and chitinous material persists longer than flesh or bone (Garnett, 1985).
Prey surface area	Larger prey items with a low surface area to volume ration will take longer to digest (Diefenbach, 1975b).
Crocodile size	Small crocodiles with a high metabolic rate will digest equivalent prey items at a faster rate than larger crocodiles (Coulson and Hernandez, 1983).
Season / diurnal fluctuations	Temperature variations will affect digestion, the lower the temperature from the optimum, the longer it may take to digest (Diefenbach, 1975a).

Table 1.1 continued Factors affecting stomach content analysis

FACTOR	DESCRIPTION
Amount of prey consumed	Food retention in the stomach may depend on the amount of additional food eaten (Ruggerone, 1989).
Secondary ingestion	Consumption of predacious prey, frogs and fish, which may have recently ingested prey (Jackson and Campbell, 1974; Neill, 1971; Tucker <i>et al.</i> 1996).
Prey representation	Difficulty in recognising if prey fragments come from one or more prey animals.
Nutritional value	Different prey items may have different nutritional components that are assimilated at different rates (Lance <i>et al.</i> 1983).



Rate of feeding

It is important to determine what crocodilians are feeding upon, but also how often they predate various prey items. An experiment using captive animals showed a maximum possible predation rate of *C. niloticus* on *Mugil cephalus* (Striped mullet) in the St. Lucia estuary (Whitfield and Blaber, 1979). Games (1990) and Medved *et al.* (1988) estimated rates of feeding using a formula based on the proportion of empty stomachs within the sample (Diana, 1979). However a model fitted to the observed data that includes empty stomachs will be biased due to the gastric evacuation relationship (Bromley, 1994). Recent fishery studies (Anderson, 2001; Rindorf, 2004) have presented models that utilise the estimation of field gastric evacuation rates to predict feeding frequencies. Feeding frequency is directly related to stomach clearance times in fish (Elliot and Persson, 1978; Pennington, 1985; Ruggerone, 1989).

Conversion rates and digestion rates

In crocodylians, the rate of digestion is proportional to their metabolic rate. Animals need to absorb the osmotically active particles at the rate at which they are released. Absorption rates are a function of the amount of blood flowing through the villi. The rate of removal of solutes from the body fluids will be proportional to the blood flow through the tissues that utilise these solutes for energy or growth (Coulson *et al.* 1990). The assimilation of nutrients in captive juvenile *C. porosus* has been shown to occur not only in the small intestine, but also in the large intestine, and possibly also in the rectum with rates of assimilation for protein at 97.4 %, for energy at 85.2 % and for dry mass at 77.5 % [Davenport *et al.* 1990]. These are higher than assimilation rates found in the spectacled caiman for protein (91.8 %), for energy (68.2 %) and for dry mass (62 %) [Davenport *et al.* 1992].

Hatchling *A. mississippiensis* have a metabolic rate twenty-five times higher than an adult and so require twenty-five times the amount of food per unit of body mass for maintenance and growth. They therefore digest food at a much faster rate (Coulson and Hernandez, 1983). Captive *A. mississippiensis* have a food conversion rate of 40 % within the first year, but this is reduced to 25 % by 1 – 3 years of age (Coulson *et al.* 1973). Under controlled-environmental conditions, hatchling *C. porosus* fed daily, had lower conversion rates (28 %) than those fed every two days (40 %) [Webb *et al.* 1990]. Garnett & Murray [1986] estimated captive *C. porosus* juveniles to convert 17 – 37 % of food under a variety of feeding regimes.

Carnivorous reptiles can digest between 80 and 90% of the prey item they consume (Bennett and Dawson, 1976; Skoczylas, 1978; Harwood, 1979). Webb *et al.* [1991] showed the wild conversion rates for *C. porosus* based on daily food intake and weight gain over time and estimated a mean conversion rate of 82.4 %. Games [1990] approximated the conversion rates of juvenile wild Nile crocodiles at a mean of 63 %. The reliability of this method depends on accurate data of daily feeding regimes and daily estimates of growth (Medved *et al.* 1988). These estimates show wild crocodiles as being more efficient at converting food than their captive counterparts. These higher conversion rates could be attributed to the fact that wild animals feed less frequently. Therefore, their physiological digestive and assimilation mechanisms may be more efficient than that of captive animals that routinely have full stomachs.

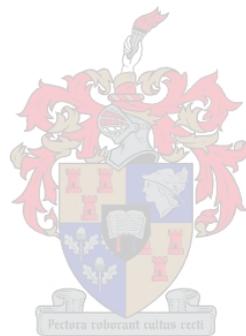
Non-food items

Deliberate lithography has been observed in several species of lizards and turtles as well as in crocodylians (Sokol, 1971). Gastroliths may account for up to 1 % of total crocodile mass (Brazaitis, 1969). The reason for these accumulated stones is still under speculation. One possibility is that they have a hydrostatic function such as ballast, to achieve negative buoyancy to assist diving (Cott, 1961). The gastroliths would also lie directly below the lungs, the area of most positive buoyancy and may assist the control of longitudinal posture and rolling (Taylor, 1994). However, Henderson (2003) produced a model showing that relatively small quantities of gastroliths (<2 % of the total body mass) found in aquatic tetrapods, are considered inconsequential for buoyancy and stability and that the lungs are the principle agent for hydrostatic buoyancy control.

The second possibility is an aid to digestion (Sokol, 1971; Diefenbach, 1975a; Davenport *et al.* 1990), however gastroliths have been observed in the stomach of *C. niloticus* with fragile and yet uncrushed prey (Cott, 1961). Chitinous particles may also act in the same way as stones in young wild crocodiles (Garnett, 1985). Davenport *et al.* (1990) found that young salt-water crocodiles deliberately ingest small stones and other hard material. X-rays and X-radiographs showed that this inorganic material is retained within the stomach and is moved around during digestion, suggesting involvement in the breakdown of ingested prey, possibly assisting in squeezing fluids from arthropods. However, Taylor (1993) suggests that the stone's movement may be a consequence of normal digestive contractions and there is no proof that it helps process the food more efficiently.

A number of parasites have been found associated with crocodylians. Leeches have been found on *C. niloticus* from the Kruger National Park (*Placobdella multistriata*, *Parabdella aspera*), as well as the nematode worm, *Dujardinascrais dujardini* (Pienaar, 1966). The larvae of *Trichinella zimbabwensis* were found in skeletal muscle and mature parasites were also found in the small intestine of *C. niloticus* in Zimbabwe. (Pozio, 2002). Tightly spiralled nematodes and large infestations of ascarids can form large ulcers in the stomach wall (Taylor, 1973). Nematodes (*Multicaecum agile*, *Dujardinascrais dujardini* and *Contraecum* sp.) were found in the stomach of *C. niloticus* from Uganda. The later species was most probably derived from fish and the former two parasites are specific to crocodiles (Cott, 1961). Parasites specific to certain prey items, such as catfish, may be transferred to crocodiles (Reed, 2003).

Studies have shown that the frequency of plant remains in stomachs increases with crocodile size (Taylor, 1973; Blomberg 1976). Taylor (1973) suggested that plant material has a nutritional value although crocodilians are unable to digest either vegetable proteins or polysaccharides (Coulson and Hernandez, 1983).



REFERENCES

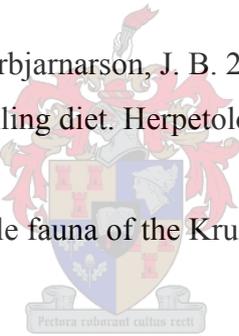
- Andersen, N.G. 2001. A gastric evacuation model for three predatory gadoids and implications of using pooled field data of stomach contents to estimate food rations. *Journal of Fish Biology*. 59: 1198 - 1217
- Anoop, K.R. and Hussain, S.A. 2005. Food and feeding habits of smooth-coated otters (*Lutra perspicillata*) and their significance to the fish population of Kerala, India. *Journal of Zoology London*. 266: 15 - 23
- Ayarzagüena, S. J. 1983. Ecología del caiman de anteojos en los llanos de Apure Venezuela. *Donana Acta Vertebrata numero especial*. 10: 1 - 136
- Barr, B. 1994. Dietary studies on the American alligator, *Alligator mississippiensis*, in Southern Florida, Unpublished MSc Thesis, University of Miami, Coral Gables
- Barr, B. 1997. Food habits of the American alligator, *Alligator mississippiensis*, in the Southern Everglades. Unpublished PhD. Thesis, University of Miami
- Bennet, A. F. and Dawson, W. R. 1976. Metabolism. In: *Biology of the Reptilia* (Edited by Gans C., and Dawson, W. R.), Vol. 5, pp 127 - 233. Academic Press, New York
- Blomberg, G. E. D. 1976. Feeding and nesting ecology and habitat preferences of Okavango crocodiles. *Proceedings of the Symposium: Okavango Delta and its future utilisation*, Botswana Society, Gaborone, Botswana
- Born, E.W., Rysgaard, S., Ehlme, G., Sejr, M., Acquarone, M. and Levermann, N. 2003. Underwater observations of foraging free-living Atlantic walrus (*Odobenus rosmarus rosmarus*) and estimates of their food consumption. *Polar Biology*. 26: 348 - 357
- Brazaitis, P. 1969. The occurrence and ingestion of gastroliths in two captive crocodilians. *Herpetologica*. 25 (1): 63 - 64

- Bromley, P.J. 1994. The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. *Reviews in Fish Biology and Fisheries*, 4: 36 - 66
- Busbey III, A. B. 2005. Form and function of the feeding apparatus of *Alligator mississippiensis*. *Journal of Morphology*. 202 (1): 99 - 127
- Bush, A, 2003. Diet and diel feeding periodicity of juvenile scalloped hammerhead sharks, *Sphyrna lewini*, in Kāne'ōhe Bay, Ō'ahu, Hawai'i. *Environmental Biology of Fishes*. 67: 1 - 11
- Corbett. P. S. 1959a. The food of a sample of crocodiles (*Crocodylus niloticus* L.) from Lake Victoria. *Proceedings of the Zoological Society of London*. 133 (4): 561 - 572
- Corbett, P. S. 1959b. Notes on the insect food of the Nile crocodile in Uganda. *Proceedings of the Royal Entomological Society of London. Series A. Gen* 34: 17 - 22
- Cott. H. B. 1954. The status of the Nile crocodile in Uganda. *Uganda Journal* 18 (1): 1 - 12
- Cott, H. B. 1961. Scientific results of an enquiry 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, T. D., Coulson, R. A. and Hernandez, T. 1973. Some observations on the growth of captive alligators. *Zoologica*. 58: 47 - 52
- Coulson, R. A., Coulson, T. D. and Herbert, J. D. 1990. How do digestion and assimilation rates in alligators vary with temperature? *Comparative Biochemistry and Physiology*. 96A (4): 441 - 449
- Coulson, R.A. and Hernandez T. 1983. Alligator metabolism: studies on chemical reactions in vivo. *Comparative Biochemistry and Physiology*. 74B:1 - 182

- Dandrifosse, G. 1974. Digestion in reptiles. *In*: M. Florkin and B. T. Scheer (eds.), Chemical Zoology. pp. 249 - 270. Academic Press, New York.
- Davenport, J., Andrews T. J. and Hudson G. 1992. Assimilation of energy, protein and fatty acids by the Spectacled Caiman *Caiman crocodilus crocodilus* L. Herpetological Journal. 2: 72 - 76
- Davenport, J., Grove, D. J., Cannon, J., Ellis, T. R. and Stables, R. 1990. Food capture, appetite, digestion rate and efficiency in hatchling and juvenile *Crocodylus porosus*. Journal of Zoology London. 220: 569 - 592
- Delaney, M. F. 1990. Late summer diet of juvenile American alligators. Florida Game and Fresh Water Fish Commission, Wildlife Research Laboratory, Florida
- Delaney, M. F. and Abercrombie, C. L. 1986. American alligator food habits in North Central Florida. Journal of Wildlife Management. 50 (2): 348 - 353
- Diana, J. S. 1979. The feeding pattern and daily ration of a top carnivore, the northern Pike (*Esox lucius*). Canadian Journal of Zoology. 57: 2121 - 2127
- Diefenbach, C. O. Da C. 1975a. Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia) - I. Rate of gastric digestion and gastric motility as a function of temperature. Comparative Biochemistry and Physiology. 51A: 259 - 265.
- Diefenbach, C. O. Da C. 1975b. Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia) - II. Effects of temperature on pH and proteolysis. Comparative Biochemistry and Physiology. 51A: 267 - 274.
- Elliot, J. M. and Persson, L. 1978. The estimation of daily rates of food consumption for fish. Journal of Animal Ecology. 47: 977 - 991
- Fitzgerald, L. A. 1989. An evaluation of stomach flushing techniques for crocodylians. Journal of Herpetology. 23 (2): 170 - 172

- Fleishman, L. J., Howland, H. C., Howland, M. J., Rand, A. S. & Davenport, M. L. 1988. Crocodiles don't focus underwater. *Journal of Comparative Physiology*. 163 A: 441 - 443
- Games, I. 1990. The feeding ecology of two Nile crocodile populations in the Zambezi valley. Unpublished PhD Thesis, University of Zimbabwe
- Gans, C. 1969. Comments on inertial feeding. *Copeia*. 855 - 857
- Garnett, S. T. 1985. The consequences of slow chitin digestion on crocodilian diet analyses. *Journal of Herpetology*. 19: 303 - 304
- Garnett, S.T. and Murray, R.M. 1986. Parameters affecting the growth of the estuarine Crocodile, *Crocodylus porosus* in captivity. *Australian Journal of Zoology*. 34: 211 - 223
- Graham, A. 1968. The Lake Rudolf crocodile (*Crocodylus niloticus* Laurenti) population. Mimeographed report to Kenya Game Department, Nairobi.
- Harwood, R. H. 1979. The effect of temperature on digestive efficiency of three species of lizards, *Cnemidophorus tigris*, *Gerrhonotus multicaratus* and *Sceloporus occidentalis*. *Comparative Biochemistry and Physiology*. 63A: 417 - 433
- Henderson, D.M. 2003. Effects of stomach stones on the buoyancy and equilibrium of a floating crocodilian: a computational analysis. *Canadian Journal of Zoology* 81: 1346 - 1357
- Hirai, T. and Matsui, M. 2001. Attempts to estimate the original size of partly digested prey recovered from stomachs of Japanese anurans. *Herpetological Review*. 32 (1): 14 - 16
- Hutton, J. M. 1984. Population ecology of the Nile crocodile, *Crocodylus niloticus* Laurenti, 1768, at Ngezi, Zimbabwe. Unpublished PhD Thesis, University of Zimbabwe

- Hutton, J. M. 1987. Growth and feeding ecology of the Nile crocodile, *Crocodylus niloticus* at Ngezi, Zimbabwe. *Journal of Animal Ecology*. 56: 25 - 38
- Jackson, J. F. and Campbell, H. W. 1974. The feeding habits of crocodilians: Validity of evidence from stomach contents. *Journal of Herpetology*. 8 (4): 378 - 381
- Jackson, S. and Ryan, P. G. 1986. Differential digestion rates of prey by White-chinned Petrels (*Procellaria aequinoctialis*). *Auk*. 103: 617 - 619
- Jeffs, A.G., Nichols, P.D., Mooney, B.D., Phillips, K.L. and Phleger, C.F. 2004. Identifying potential prey of the pelagic larvae of the spiny lobster, *Jasus edwardsii* using signature lipids. *Comparitive Biochemistry and Physiology B*. 137: 487 - 507
- Lance, V., Joanen, T. and McNease L. 1983. Selenium, vitamin E, and trace elements in the plasma of wild and farm-reared alligators during the reproductive cycle. *Canadian Journal of Zoology*. 61: 1744 - 1751
- Lenain, D.M., Olfermann, E. and Warrington, S. 2004. Ecology, diet and behaviour of fox species in a large, fenced protected area in central Saudi Arabia. *Journal of Arid Environments*. 57: 45 - 60
- Leslie A. J., 1997. The ecology and physiology of the Nile crocodile, *Crocodylus niloticus*, in Lake St Lucia, Kwazulu/Natal, South Africa. PhD Thesis. Drexel University, USA
- Magnusson, W.E., Da Silva, E.V. and Lima, A.P., 1987. Diets of Amazonian crocodiles. *Journal of Herpetology*. 21 (2): 85 - 95
- McNease, L. and Joanen, T. 1973. Alligator diets in relation to marsh salinity. *Proceedings of the Annual Conference South Eastern Association of Fish and Wildlife Agencies*. 31: 36 - 40

- Medved, R.J., Stillwell, C.E. and Casey J.G. 1988. The rate of food consumption of young sandbar sharks (*Carcharhinus plumbeus*) in Chincoteague Bay, Virginia. *Copeia*. 4: 956 - 963
- Neill, W. T. 1971. *In*: The last of the ruling reptiles: alligators, crocodiles and their kin. Columbia Univ. Press, Ithaca. p 486
- Pennington, M. 1985. Estimating the average food consumption by fish in the field from stomach content data. *Dana*. 5: 81 - 86
- Platt, S. G., Rainwater, T. R. and McMurry, S. T. 2002a. Diet, gastrolith acquisition and initial feeding among hatchling Morelet's crocodiles in Belize. *Herpetological Journal*, Vol.12, pp 81 - 84
- Platt, S. G., Rainwater T.R. & Thorbjarnarson, J. B. 2002b. *Crocodylus acutus* (American crocodile) hatchling diet. *Herpetological Review*. 33 (3): 202 - 203
- Pienaar, U. De V. 1966. The Reptile fauna of the Kruger National Park. National Parks Board, Pretoria
- 
- Pooley, A.C. 1982. The ecology of the Nile crocodile, *Crocodylus niloticus*, in Zululand. Unpublished MSc thesis, University of Natal, South Africa
- Pooley, A. C. and Gans, C. 1976. The Nile crocodile. *Scientific American*. 234 (4): 114 - 124
- Pozio, E., Foggin, C. M., Marucci, G., La Rosa, G. Sacchi, L. Corona, S., Rossi, P., Mukaratirwa. 2002. *Trichinella zimbabwensis* n.sp. (Nematoda), a new non-encapsulated species from crocodiles (*Crocodylus niloticus*) in Zimbabwe also infecting mammals. *International Journal for Parasitology*. 32: 1787 - 1799
- Putterill, J. F. and Soley, J. T. 2003. General morphology of the oral cavity of the Nile crocodile, *Crocodylus niloticus* (Laurenti, 1768). I. Palate and ginigivae. *Onderstepoort Journal of Veterinary Research*. 70 (4): 281 - 297

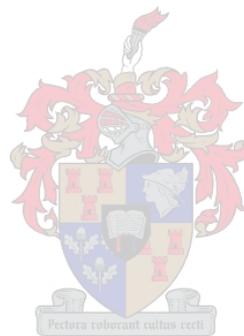
- Putterill, J. F. and Soley, J. T. 2006. Morphology of the gular valve of the Nile crocodile, *Crocodylus niloticus* (Laurenti, 1768). *Journal of Morphology*. 267 (8): 924 - 939
- Reed, C. C., Basson, L. and Van As, L. L. 2003. Myxozoans infecting the sharptooth catfish, *Clarias Gariepinus* in the Okavango River and Delta, Botswana, including descriptions of two new Species, *Henneguya samochimensis* sp. n. and *Myxobolus gariepinus* sp. n. 2003. *Folia Parasitologica*. 50: 183 - 189
- Rice, A.N. 2004. Diet and condition of American alligators (*Alligator mississippiensis*) in three central Florida Lakes. Unpublished MSc Thesis. University of Florida
- Riley, J., and Huchzermeyer, F. W. 2000. Diet and lung parasites of swamp forest Dwarf crocodiles (*Osteolaemus tetraspis osborni*) in the Northern Congo Republic. *Copeia*. (2): 582 - 586
- Rindorf, A. 2004. Estimation of evacuation rates in the field. *Journal of Fish Biology*. 65: 262 - 281
- Ruggerone, G. T., 1989. Gastric evacuation rates and daily ration of piscivorous coho salmon, *Onorhynchus Kisutch* Walbaum. *Journal of Fish Biology*. 34: 451 - 463
- Skoczylas, R. 1978. Physiology of the digestive tract. In *Biology of the Reptilia* (Edited by Gans, C.), Vol. 8, pp 231 - 286. Academic Press, New York
- Stafford, P.J. Diet and reproductive ecology of the Yucatán cricket-eating snake *Symphimus mayae* (Colubridae). 2005. *Journal of Zoology London*. 265: 301 - 310
- Sokol, O. M. 1971. Lithography and geophagy in reptiles. *Journal of Herpetology*. 5: 69 - 71
- Taylor, G. W. 1973. Nile crocodile in the Okavango Delta. A report on a wildlife population for Botswana Game Industries. pp 36 - 73.

- Taylor, J. A. 1979. The foods and feeding habits of subadult *Crocodylus porosus* Scheider in northern Australia. *Australian Wildlife Research*. 6: 347 - 359
- Taylor, J. A. Webb, G. J. W. and Magnusson, W. E. 1978. Methods of obtaining stomach contents from live crocodilians (Reptilia, crocodilidae). *Journal of Herpetology*. 12 (3): 413 - 415
- Taylor, M. A. 1993. Stomach stones for feeding or buoyancy? The occurrence and function of gastroliths in marine tetrapods. *Philosophical Transactions of the Royal Society of London*. B. 341: 163 - 175
- Taylor, M. A. 1994. Stone, bone or blubber? Buoyancy control strategies in aquatic tetrapods. *In: Mechanics and physiology of animal swimming*, 151. Maddock, L., Bone, Q., & Rayner, J. M. V. (Eds) Cambridge: Cambridge University Press
- Thorbjarnarson, J.B. 1988. The status and ecology of the American crocodile in Haiti. *Bulletin of the Florida State Museum*
- Thorbjarnarson, J. B. 1993. Diet of the Spectacled Caiman (*Caiman crocodilus*) in the Central Venezuelan Llanos. *Herpetologica*. 49 (1): 108 - 117
- Tucker, A. D., Limpus, C. J., McCallum, H. I. and McDonald, K. R. 1996. Ontogenetic dietary partitioning by *Crocodylus johnstoni* during the dry season. *Copeia*. 4: 978 - 988
- Valentine, J. M., Walther, J. R., McCartney, K. M. and Ivy, L. M. 1972. Alligator diets on the Sabine National Wildlife Refuge, Louisiana. *Journal of Wildlife Management*. 36 (3): 809 - 815
- Webb, G. J. W., Manolis, S. C. and Buckworth, R. 1982. *Crocodylus johnstoni* in the McKinlay River area, N. T. I. Variation in the diet and a new method of assessing the relative importance of prey. *Australian Journal of Zoology*. 30: 877 - 899

Webb, G. J. W., Hollis, G. J. and Manolis, S. C. 1991. Feeding, growth, and food conversion rates of wild juvenile Saltwater crocodiles (*Crocodylus porosus*). *Journal of Herpetology*. 25: 462 - 473

Whitfield, A. K., Blaber, S. J. M. 1979. Predation on Striped Mullet (*Mugil cephalus*) by *Crocodylus Niloticus* at St. Lucia, South Africa. *Copeia*. 2: 266 - 269

Wolfe, J. L., Bradshaw, D. K., Chabreck, R. H., 1987. Alligator feeding habits: New data and a review. *Northeast Gulf Science*. 9 (1): 1 - 8



CHAPTER 2

Study site and study animal

Hydrology and topography

The Okavango River originates in the central highlands of Angola. Two tributaries, the Cubango and Cuito Rivers flow south-easterly to form the Okavango River when the river enters North-western Botswana. At this point it is approximately 200m wide and 4 m deep (Ashton *et al.* 2003). The upper part of the Delta, the Panhandle, is a 15 km broad fault-bounded, flat-bottomed valley, with a well defined meandering channel (Figure 2.0) (Wolski and Murray-Hudson, 2005) with a gradient of 1: 5 000 (Medelsohn and Obeid, 2003) and a flow rate up to 0.9 m / sec. Sediment deposition on the convex banks gives rise to point bars and gently undulating topography surrounds the river (Ashton *et al.* 2003). The Okavango River branches out to form the Okavango Delta, a tectonically forced alluvial fan (22 000 km²) subject to annual flooding, composed of a mosaic of floodplains and islands with a gradient of 1: 3 470 (Andersson *et al.* 2003). The Okavango Delta is classified as a RAMSAR site and a flood-pulsed wetland (Wolski and Murray-Hudson, 2005).

Rainfall in the Okavango catchment occurs in summer, from December to February, the annual average rainfall is approximately 500 mm (Ellery and McCarthy, 1994). The annual flood (due to the Angolan rainfall) peaks in the north at Mohebo, between February and April reaching the town of Maun (in the south) between June and August (McCarthy, 1992; Giske, 1996). The extent of the flooding in the Delta varies seasonally from low in December (3 000 – 5 0000 km²) to high in August (6 000 – 12 000 km²) (Andersson *et al.* 2003). The river has a mean annual discharge of 11 000 million cubic meters (McCarthy *et al.* 2000).

The river channels are mainly oligotrophic, the swamps and flood plains vary between oligotrophic to mesotrophic, while isolated water bodies are mesotrophic to eutrophic. The main channel waters are poor in most solutes and trace elements, moderately richer in silica, dissolved organic carbon and inorganic nitrogen (Gronberg *et al.* 1995) and bicarbonates dominate the Panhandle region. Phytoplankton communities are low in the

Panhandle region

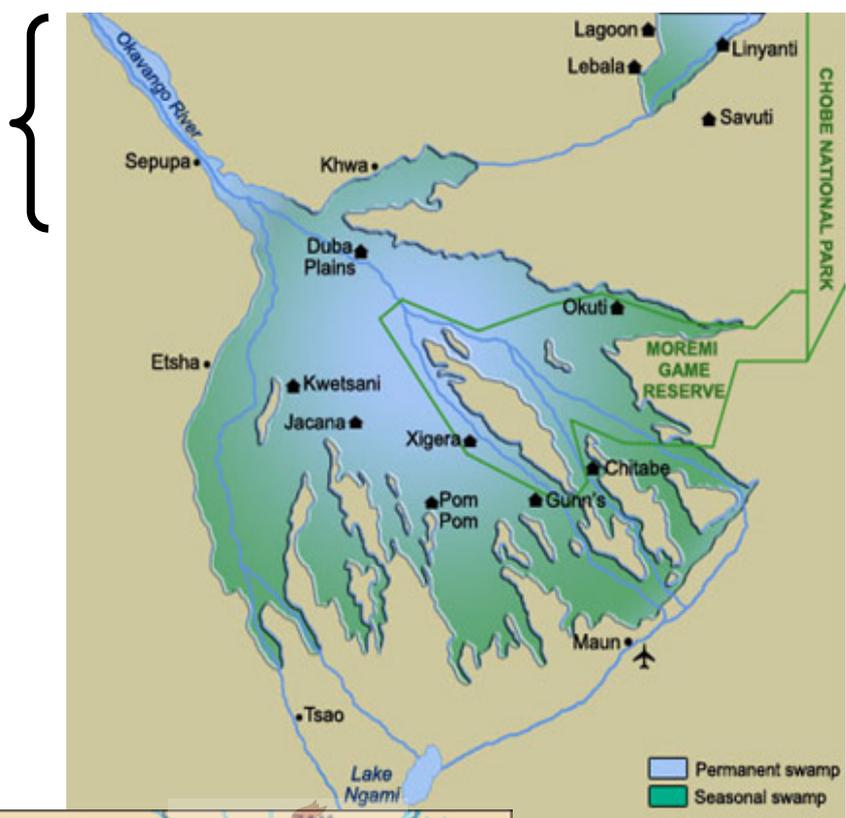


Figure 2.0. The Panhandle study area, Okavango Delta, Botswana.

main river channels with few algal groups present, but are well developed in the southern swamp areas and isolated water bodies (McCarthy, 1992).

The upper panhandle region has a high water quality, low concentrations of dissolved salts and 65 - 95 % dissolved oxygen, with low concentrations of nitrogen and phosphorus. Mixing and aeration is slower in lagoons and marginal pools, but does not adversely affect water quality. In the main river channel, from the upper reaches to the lower panhandle, the pH remains relatively constant (6.75 - 7.05 and 7.0 - 7.2 respectively), however in the lagoons, pH values can reach 5.5 (Ashton *et al.* 2003). In the larger lagoons further south, dissolved oxygen is below 20 % saturation, due to the water being filtered through the swamps or beneath the mats of floating vegetation. Considerable quantities of dissolved and particulate organic matter accumulate during times of low flow rate. During the dry season the water is relatively clear, but in the wet season the river is stained a yellowish-brown with humic compounds (Ashton *et al.* 2003). Seasonal fish kills occur in certain areas due to the flood waters flushing detritus laden water (with a high biological oxygen demand) from under the papyrus mats into open waters (Tweddle *et al.* 2003).

The fauna and flora of the region

Seventy-one species of fish have been identified in the Okavango Delta (Merron and Bruton, 1988; Merron, 1991), dominated by four or five species. The primary fish species of commercial interest are three-spot (*Oreochromis andersonii*) and red-breast tilapia (*Tilapia rendalli*). Other commercially important species are green-head tilapia (*Oreochromis macrochir*); thin-face large mouth (*Serranochromis angusticeps*); nembwe (*S. robustus*); sharp-tooth catfish (*Clarius gariepinus*) and tigerfish (*Hydrocynus vittatus*). Abundances of these species within the Okavango all have temporal and spatial variation related to the hydrological cycle. Tilapia species are the most frequently landed by fisherman (Mosepele, 2000). There are local religious and cultural taboos against eating catfish (pers. obs). Catfish are the most important predators of the other fish, due to their abundance and distribution (Patterson, 1976). Timing and duration of the annual flood is a primary factor in determining the recruitment, growth and survival rates of fish stocks (Skelton *et al.* 1985). Under the papyrus mats where light penetration is poor, respiration often exceeds photosynthesis and dissolved oxygen concentrations are low. Decomposing vegetation causes a substantial oxygen demand. Such areas are dominated by the air-breathing catfish (*Clarias sp.*) (Fox, 1976).

Invertebrate biodiversity is lowest in the main flowing channels, slightly higher in the vegetated side channels, and higher still in quiet vegetated backwaters and lagoons. The main channel marginal vegetation (mostly *Cyperus papyrus*) is dominated by Anisoptera (Dragonflies). Aquatic fauna of the side channels and lagoons are dominated by the shrimp *Caridina africana*. Bivalve molluscs, *Corbicula fluminalis* and *Coelatura kunensis*, are found within the sand banks. Lagoon fringes are dominated by terrestrial Heteropterans, Zygoptera (damselflies) and Gastropoda (snails) (Appleton *et al.* 2003).

The panhandle region is dominated by the grasses *Vossia cupidata* (hippo grass) and *Echinochloa* (Limpopo grass), the sedge *C. papyrus* (papyrus), rushes *Typha capensis* (bullrush) and reeds *Phragmites mauritianus* (phragmites). Floral diversity is higher along the channel fringe and terrestrial islands than the backwaters or slow flowing channels and hippo trails (Ellery and Tacheba, 2003). Date palm (*Phoenix reclinata*) and Gomoti (*Ficus verruculosa*) are the main types of trees (Patterson, 1976) and the main ferns present are *Polygonum pulchrum* and *Commelinaceae* species (Smith, 1976). Papyrus whilst enriching the waters with nutrients, deposits nutrients below the floating reed mat. This 'nutrient trap' could be one of the reasons for the oligotrophic nature of the Delta, especially the panhandle region (Thompson, 1976).

The only large wild animals in the panhandle area are the Nile Crocodile (*C. niloticus*), Hippopotamus (*Hippopotamus amphibious*), Elephant (*Loxodonta Africana*), Lechwe (*Kobus leche*), two types of large monitor lizard (*Varanus niloticus* and *V. albigularis*) the occasional leopard (*Panthera pardus*) (Patterson, 1976), as well as bushbuck (*Tragelaphus scriptus*) and sitatunga (*Tragelaphus spekei*) (pers. obs).

The Okavango Delta is a major tourist attraction and the main water source for north-central Botswana (McCarthy, 1992). The delta also supports small-scale commercial, subsistence and recreational fishing (Merron and Bruton, 1988).

Study Animal: The Nile Crocodile (*Crocodylus niloticus*)

Of the three African crocodile species, the Nile crocodile (*C. niloticus*) is the most widely distributed throughout Africa (excluding North Africa) and Madagascar (Pooley and Gans, 1976) and is one of the few crocodile species worldwide that have an estuarine population (Taplin and Loveridge, 1988; Leslie and Spotila, 2000). The Nile crocodile was heavily

exploited throughout Africa during the 1950's and 1960's, primarily for its hide (Cott, 1961; Parker and Watson, 1970).

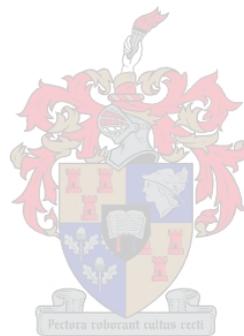
The diet of the Nile crocodile changes ontogenetically (Cott, 1954, 1961; Corbett, 1959a, b; Cott, 1961; Modha, 1967; Taylor, 1973; Blomberg, 1976; Pooley and Gans, 1976; Whitfield and Blaber, 1979; Hutton, 1984, 1987; Games, 1990). Insects dominate the diet of young crocodiles along with arachnids, crustaceans and amphibians. The diet then changes to a fish dominated diet as they mature (Corbett, 1959a; Cott, 1961; Graham, 1968; Blomberg, 1976, Hutton, 1984; Games, 1990) with the largest crocodiles having a higher intake of large mammals (Cott, 1961). The main dietary shift coincides with changes in allometric head dimensions (Hutton, 1984, 1987, Games 1990). Both scavenging (Pooley and Gans, 1976) and communal feeding (Pooley and Gans, 1976; Whitfield and Blaber, 1979) have been recorded.

The Nile crocodile can breed once a year (Cott, 1961; Modha, 1967; Pooley, 1969; Graham, 1976; Leslie, 1997) although there is no evidence that the same female breeds in successive years (pers. comm. Leslie, 2006). The month of oviposition varies with location, from September (Hutton, 1984) to November (Leslie, 1997) in an excavated depression in sandy areas. Clutch size varies from 16 - 80 eggs, depending on the size of the female (Blake and Loveridge, 1975; Pooley & Gans, 1976; Games 1991; Leslie 1997). The eggs rely on heat from insolation and metabolism for gestation (Webb *et al.* 1983). Nile crocodiles exhibit temperature-dependent sex determination (TSD) [Leslie, 1997]. The female guards the nest for the three months of the incubation period (Cott, 1961; Modha, 1967; Pooley, 1969; Hutton, 1984; Games, 1991; Leslie, 1997). She then moves the hatchlings to the water in her jaws (Pooley, 1976) and may continue to guard the hatchlings for up to 6 weeks (Modha, 1967).

Initial growth is rapid and decreases with age (Cott, 1961). Sexual maturity within the wild may vary between populations, but occurs between 2.7 - 3.3 m for males and 1.8 - 2.8 m for females (Cott, 1961; Graham, 1968). Thermoregulation is achieved by habitat selection and basking behaviour (Cott, 1961; Modha, 1968; Loveridge, 1984).

The aim of this study was to gain a better understanding as to the diet of the Nile crocodile in the Okavango Delta, Botswana, with particular reference to the ontogenetic shift in diet

and daily food intake and conversion rates. Additionally, an attempt was made to determine digestion, nutrient assimilation and satiation rates. These data will contribute towards the formulation of an energy budget for crocodiles in the Okavango region, thereby forming an essential component of the Management Plan for the crocodiles of the Okavango Region.



REFERENCES

- Andersson L., Gumbrecht T., Hughes D., Kniveton D., Ringrose S., Savenije H., Todd M., Wilk J. and Wolski P. 2003. Water flow dynamics in the Okavango River Basin and Delta – a prerequisite for the ecosystems of the Delta. *Physics and Chemistry of the Earth*.
- Appelton, C.C., Curtis, B.A., Alonso, L.E. and Kipping, J. 2003. Freshwater Invertebrates of the Okavango Delta, Botswana. Chapter 4. In: *A rapid biological assessment of aquatic ecosystems of the Okavango Delta, Botswana: High water Survey*. RAP Bulletin of Biological Assessment 27. Conservation International, Washington, DC
- Ashton, P.J., Masundire, H., Hart, R., Prince-Nengu, J., Botshelo, O., Lekhuru, M., Mehlomakulu, M. and Tylol, I. 2003. *In: Alonso, L.E. and Nordin L. (editors). 2003. A rapid biological assessment of the aquatic ecosystems of the Okavango Delta, Botswana: High water survey*. RAP Bulletin of Biological Assessment 27. Conservation International, Washington, D.C. pp. 38 - 53
- Blake, D. K. and Loveridge, J. P. 1975. The role of commercial crocodile farming in crocodile conservation. *Biological Conservation*. 8: 261 - 272.
- Blomberg, G. E. D. 1976. Feeding and nesting ecology and habitat preferences of Okavango crocodiles. *Proceedings of the Symposium: Okavango Delta and its future utilisation*, Botswana Society, Gaborone, Botswana
- Corbett. P. S. 1959a. The food of a sample of crocodiles (*Crocodylus niloticus* L.) from Lake Victoria. *Proceedings of the Zoological Society of London*. 133 (4): 561 - 572
- Corbett, P. S. 1959b. Notes on the insect food of the Nile crocodile in Uganda. *Proceedings of the Royal Entomological Society of London*. Series. A. Gen 34: 17 - 22
- Cott. H. B. 1954. The status of the Nile crocodile in Uganda. *Uganda Journal*. 18 (1): 1 - 12

- Cott, H. B. 1961. Scientific results of an enquiry 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 - 356.
- Ellery, W. N. and McCarthy, T. S. 1994. Principles for the sustainable utilization of the Okavango River ecosystem, Botswana. Biological Conservation. 70: 159 - 168
- Ellery, W.N. and Tacheba, B. 2003. Floristic diversity of the Okavango Delta, Botswana. *In: Alonso, L.E. and Nordin L. (editors). 2003. A rapid biological assessment of the aquatic ecosystems of the Okavango Delta, Botswana: High water survey. RAP Bulletin of Biological Assessment 27. Conservation International, Washington, D.C. pp. 69 - 96*
- Fox, P.J. 1976. Preliminary observations on fish communities of the Okavango Delta. P 125 - 129. *In: Proceedings of the symposium on the Okavango Delta and future utilization. National Museum, Gaborone, Botswana*
- Games, I. 1990. The feeding ecology of two Nile crocodile populations in the Zambezi valley. Unpublished PhD Thesis, University of Zimbabwe
- Giske, A. 1996. Modelling surface outflow from the Okavango. Botswana Notes and Records. 28: 165 - 192
- Graham, A. 1968. The Lake Rudolf crocodile (*Crocodylus niloticus* Laurenti) population. Mimeographed report to Kenya Game Department, Nairobi.
- Graham, A. 1976. A management plan for Okavango crocodiles. Proceedings of the Okavango Delta Symposium. Botswana Society, Gaborone, pp 223 - 34
- Gronberg, G. Giske, A. Martins, E. Prince-Nengu, J. and Stenstrom, I-M. 1995. Hydrobiological studies of the Okavango Delta and Kwando/Linyanti/Chobe River, Botswana. Surface water quality analysis: Botswana Notes and Records. 27: 151 - 226

- Hutton, J. M. 1984. Population ecology of the Nile crocodile *Crocodylus niloticus* Laurenti, 1768, at Ngezi, Zimbabwe. Unpublished PhD Thesis, University of Zimbabwe
- Hutton, J. M. 1987. Growth and feeding ecology of the Nile crocodile, *Crocodylus niloticus* at Ngezi, Zimbabwe. *Journal of Animal Ecology*. 56: 25 - 38
- Leslie A. J., 1997. The ecology and physiology of the Nile crocodile, *Crocodylus niloticus*, in Lake St Lucia, Kwazulu/Natal, South Africa. Unpublished PhD Thesis, Drexel University, USA
- Leslie, A. J. and Spotila, J. R. 2000. Osmoregulation of the Nile crocodile, *Crocodylus niloticus*, in Lake St. Lucia, Kwazulu/Natal, South Africa. *Comparative Biochemistry and Physiology Part A* 126: 351 - 365.
- Loveridge, J.P. 1984. Thermoregulation in the Nile crocodile, *Crocodylus niloticus*. *Symposium of the Zoological Society of London*. 52: 443 - 467.
- McCarthy, T. S. 1992. Physical and biological processes controlling the Okavango Delta – A review of recent research. *Botswana Notes and Records*. 24: 57 - 86
- McCarthy, T. S., Cooper, G. R. J., Tyson, P. D. and Ellery W. N. 2000. Seasonal flooding in the Okavango Delta, Botswana – recent history and future prospects. *South African Journal of Science*. 96: 25 - 33
- Mendelsohn J. and Obeid S. el. 2004. *In: Okavango River: The flow of a lifeline*. Mendelsohn, J. and el Obeid, S. Struik Publishers, South Africa
- Merron, G. S. 1991. The ecology and management of the fishes of the Okavango Delta, Botswana, with particular reference to the role of seasonal floods. Unpublished PhD thesis, Rhodes University, RSA

- Merron, G. S. and Bruton, 1988. The ecology and management of fishes of the Okavango Delta, Botswana, with particular reference to the role of seasonal floods. J.L.B. Smith Institute of Ichthyology Investigational Report No. 29
- Modha, M. L. 1967. The ecology of the Nile crocodile (*Crocodylus niloticus*) on Central Island, Lake Rudolf. East African Wildlife Journal. 5: 74 - 95
- Modha, M.L. 1968. Basking behaviour of the Nile crocodile on Central Island, Lake Rudolf. East African Wildlife Journal. 6: 81 - 88.
- Mosepele, K. 2000. Preliminary length based stock assessment of the main exploited stocks of The Okavango Delta fishery. MPhil Thesis. Department of Fisheries and Marine Biology, University of Bergen, Norway
- Parker, I.S.C. and Watson, R.M. 1970. Crocodile distribution and status in the major waters of western and central Uganda in 1969. East African Wildlife Journal 8: 85 - 103
- Patterson, L. 1976. An introduction to the ecology and zoogeology of the Okavango Delta. p. 55 - 60. *In*: Proceedings of the symposium on the Okavango Delta and future utilization. National Museum, Gaborone, Botswana
- Pooley, A. 1969. Preliminary studies on the breeding of the Nile crocodile in Zululand. Lammergeyer. 10: 22 - 44.
- Pooley, A. C. and Gans, C. 1976. The Nile crocodile. Scientific American. 234 (4): 114 - 124
- Skelton, P.H., Bryton, M.N, Merron, G.S. and van der Waal B.C.W. 1985. The fishes of the Okavango Drainage system in Angola, South West Africa and Botswana: Taxonomy and distribution. Ichthyological bulletin of the J.L.B. Smith Institute of Ichthyology, Grahamstown, Republic of South Africa

- Smith, P. 1976. An outline of the vegetation of the Okavango drainage system, p. 93 - 112.
In: Proceedings of the symposium on the Okavango Delta and future utilization.
 National Museum, Gaborone, Botswana
- Taplin, L.E. and Loveridge, J.P. 1988. Nile crocodiles, *Crocodylus niloticus*, and estuarine crocodiles, *Crocodylus porosus*, show similar osmoregulatory responses on exposure to seawater. *Comparative Biochemistry and Physiology*. 89A: 443 - 448.
- Taylor, G. W. 1973. Nile crocodile in the Okavango Delta. A report on a wildlife population for Botswana Game Industries. Pp. 36 - 73.
- Thompson, K. 1976. The primary productivity of African wetlands, with particular reference to the Okavango Delta, p. 67 - 79. *In: Proceedings of the symposium on the Okavango Delta and future utilization.* National Museum, Gaborone, Botswana
- Tweedle, D., Bills, R., van der Waal, B., Skelton, P., Kolding, J. and Nengu, S. 2003. Fish diversity and fisheries in the Okavango Delta, Botswana. *In: Alonso, L.E. and Nordin L. (editors). 2003. A rapid biological assessment of the aquatic ecosystems of the Okavango Delta, Botswana: High water survey. RAP Bulletin of Biological Assessment 27. Conservation International, Washington, D.C. pp. 97 - 110*
- Webb, G.J.W., Buckworth, R. and Manolis, S.C. 1983. *Crocodylus johnstoni* in the McKinlay River area, N.T. VI. Nesting biology. *Australian Wildlife Research*. 10: 607 - 637.
- Whitfield, A. K. and Blaber, S. J. M. 1979. Predation on Striped Mullet (*Mugil cepalus*) by *Crocodylus niloticus* at St. Lucia, South Africa. *Copeia*. 2: 266 - 269
- Wolski, P. and Murray-Hudson, M. 2005. Flooding dynamics in a large low-gradient alluvial fan, the Okavango Delta, Botswana, from analysis and interpretation of a 30-year hydrometric record. *Hydrology and Earth System Sciences Discussions*. 1865 - 1892

CHAPTER 3

Dietary habits of the Nile crocodile, *Crocodylus niloticus*, in the Okavango Delta, Botswana.

INTRODUCTION

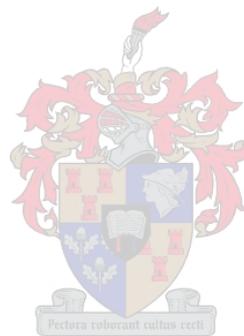
The dietary habits of the Nile crocodile have been shown to vary with age and geographical location (Cott, 1954, 1961; Corbett, 1959a; Cott, 1961; Modha, 1967; Taylor, 1973; Blomberg, 1976; Pooley *et al.* 1976; Whitfield and Blaber, 1979; Pooley, 1982; Hutton, 1984, 1987; Games, 1990; Leslie, 1997). Bias in crocodylian dietary studies due to differential digestion rates of prey items, in particular slow digestion of chitinous material, was first suggested by Neill (1971) and later by Jackson *et al.* (1974) and Garnett (1985). Corbett (1959b) noted that the condition of prey items found in the stomach could provide information on when predation took place, shedding light on feeding rates. However, only a few recent studies on crocodylians have taken gastric residence time into account, for example: *Alligator mississippiensis* (Delaney and Abercrombie, 1986; Barr, 1997), *Crocodylus niloticus* (Games, 1990) and *Crocodylus porosus* (Webb *et al.* 1991).

Most dietary studies make use of numerical traits (% occurrence) and prey mass (% composition), Corbet (1959a) first suggested use of a scoring system to take into account the volume of the food ingested. Some studies have used regression methods or measurements of prey items to extrapolate the original morphometric size and mass of whole prey from recovered fragments (Valentine *et al.* 1972; Taylor, 1979; Wolfe *et al.* 1987). However, these studies did not account for gastric residence time and so may have overestimated the importance of certain prey items that persist for a longer period of time in the stomach.

A few, more recent studies have 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, therefore eliminating bias as only freshly ingested prey was used in the primary analysis (Games, 1990; 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, behaviour and

reproduction (Lang, 1987). This study examined the diet of the Nile crocodile in the Okavango River 'Panhandle' area with reference to size class and season, taking into account differential digestion rates. Fresh prey items ingested within twenty-four hours were regressed to their original mass for the analysis.



METHODS

Crocodile capture and stomach content retrieval

From August 2003 to August 2005, 286 crocodiles were captured and stomach lavaged. The animals were allocated to one of three size classes based on snout-to-vent length (SVL): yearlings (17.0 - 38.9 cm SVL), juveniles (39.0 - 66.3 cm SVL) and sub-adults (66.4 - 115.8 cm SVL) [Leslie 1997]. Seven adult (>115.9 cm SVL) crocodiles were also processed but due to the small sample size and being at the lowest range of the adult size class, they were included within the sub-adult group.

Crocodiles were caught from a boat at night either by hand or noose using a spotlight. Three larger individuals were caught in box traps (Appendix 1). Animals were 'processed' immediately (Appendix 2) at the site of capture and subsequently released. Stomach samples were obtained using a modification of the technique originally devised by Ayarzagüena (1983) and modified and evaluated by Fitzgerald (1989), namely the hose-heimlich technique, utilising a water pump to flush out stomach contents (Appendix 3).

Stomach samples were initially sorted into prey items and non-prey items. Prey item samples were then further separated into two distinct groups: (i) fresh prey items (ingested <24 h of capture) (Appendix 4), and (ii) old prey items (ingested >24 h before capture). Non-prey items consisted of parasites, stones (gastroliths) and vegetation. Prey items were digitally photographed and a wet mass was recorded. Samples were frozen for identification purposes and transport to the Department of Conservation Ecology at the University of Stellenbosch, South Africa.

Prey identification

Prey items were identified making use of text books and internet resources. Additional advice was sought from University of Stellenbosch staff; The Agricultural Research Council, Pretoria; The South African Institute for Aquatic Biodiversity, Grahamstown and the Department of Veterinary Tropical Diseases, University of Pretoria. The original mass of the fresh prey items was estimated using museum collections and field data (Appendix 6).

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 non-normally distributed composition mass data. An ANOVA was used for the morphometric analysis. Arcsine transformation was used on data converted to percentages and analysed using a one-way ANOVA. Species richness and accumulation curves were calculated using EstimateS: Statistical estimation of species richness and shared species from samples, (Version 7.5, R.K. Colwell, <http://purl.oclc.org/estimates>). All statistical analyses were performed using Statsoft Inc (2005) Statistica version 7.1.

An overlapping group analysis was used to show 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 5 heaviest animals and excluded the 5 lightest animals, etc. (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).



RESULTS

The stomach contents of 286 crocodiles from the Panhandle area of the Okavango River were examined. The proportion of stomachs containing fresh prey decreased with an increase in crocodile size (Figure 3.0). Fresh prey remnants were found in 41.3 % of the combined sample: 55.6 % of the yearling stomachs contained fresh prey, 29.3 % of the juveniles stomachs and 18.9 % of the sub-adults stomachs contained fresh prey items. Fresh prey items were more frequently found within yearling stomachs than those of either juveniles or sub-adults ($p < 0.01$).

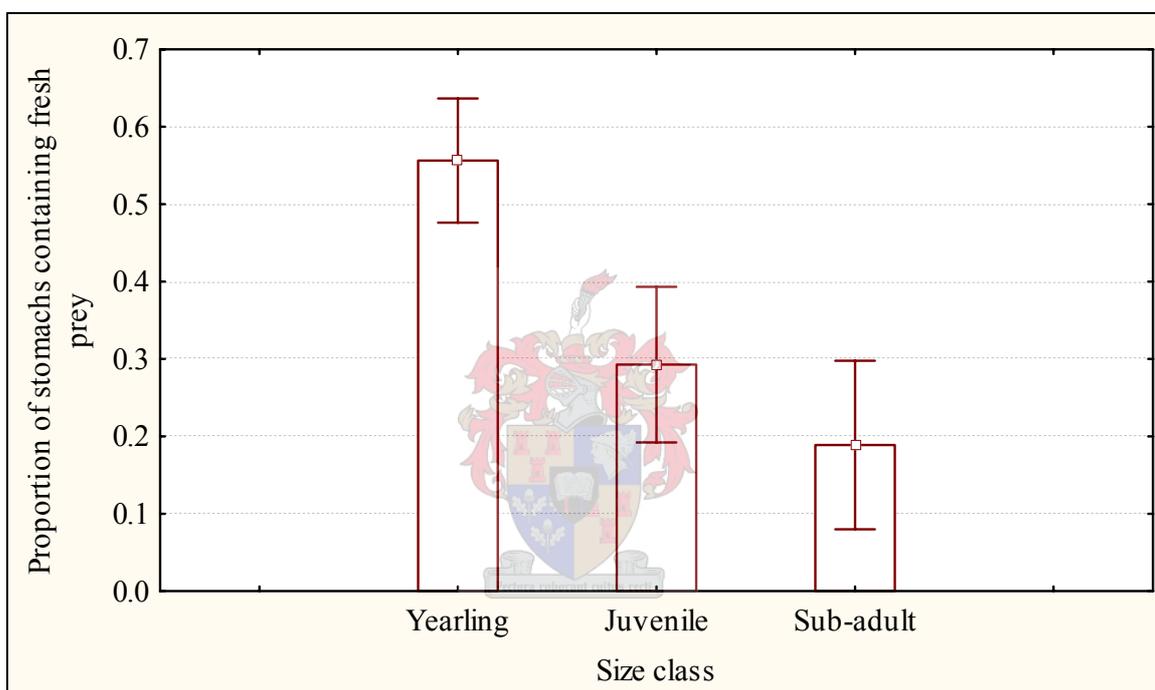


Figure 3.0 Proportion of stomachs containing fresh prey items (mean and \pm 95 % confidence limits)

Fresh stomach contents occurred more frequently in juvenile stomachs than those of sub-adults ($p < 0.05$). Figure 3.1 shows the mean percentage of stomachs containing fresh prey items relative to crocodile size. The gradual decrease in the occurrence of stomachs that contained fresh prey with an increase in crocodile size is clearly illustrated.

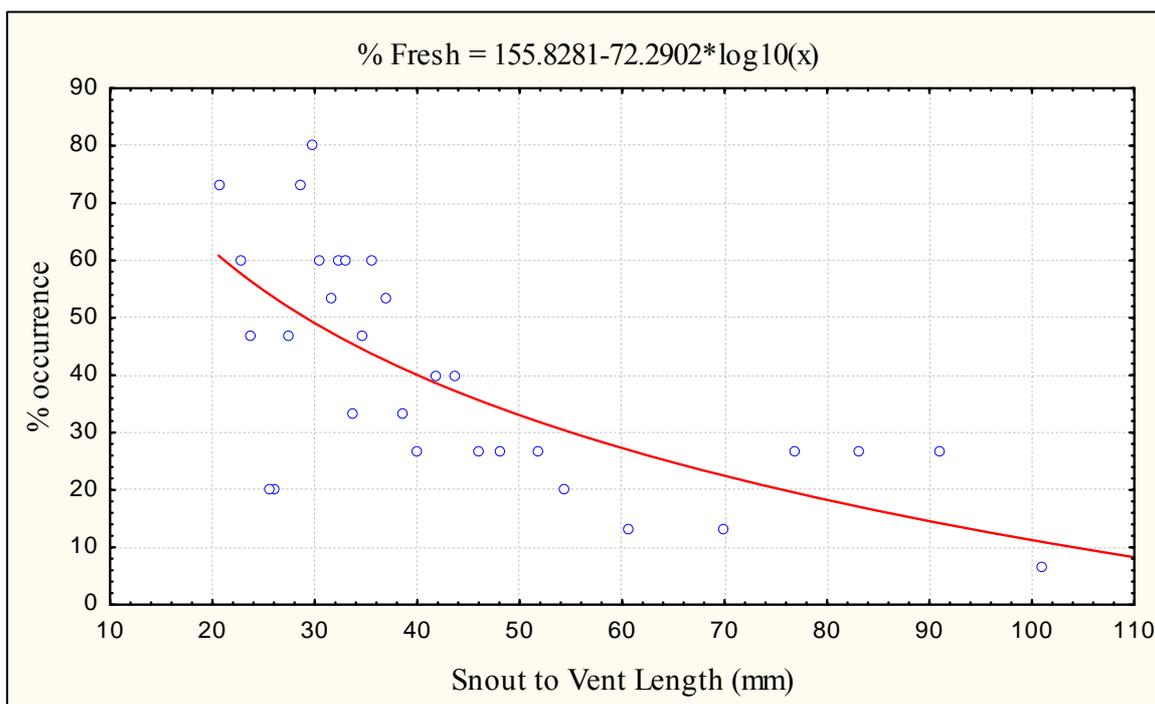


Figure 3.1 Overlapping analysis showing mean percentage of stomachs containing fresh prey relative to crocodile size (SVL)

The frequency of fresh stomach contents was slightly higher in males than in females, although not significantly ($p > 0.05$) (Figure 3.2). Fresh stomach contents were recovered from 57.9 % of male yearlings, 31.7 % of male juveniles and 19 % of male sub-adults and from 48.8 % of female yearlings, 21.0 % of female juveniles and from 18.8 % of female sub-adults.

The mean ingested fresh prey mass (fresh prey items regressed to original mass [Appendix 6]) increased with crocodile size (Figure 3.3). Yearling stomachs contained a mean of 1.9g (± 0.4 g S.E.), juveniles 5.6 g (± 1.7 g S.E.) and sub-adults 16.7 g (± 6.6 g S.E.). The mass of fresh prey relative to body mass decreased with an increase in crocodile size (Figure 3.4). Yearling stomachs contained a significantly higher mass of fresh prey relative to body mass (0.4 g ± 0.1 g S.E.) than sub-adults (0.1 g ± 0.03 S.E.) ($p < 0.05$). Juveniles (0.3 g ± 0.1 g S.E.) did not differ significantly to either the yearlings or sub-adults ($p > 0.05$).

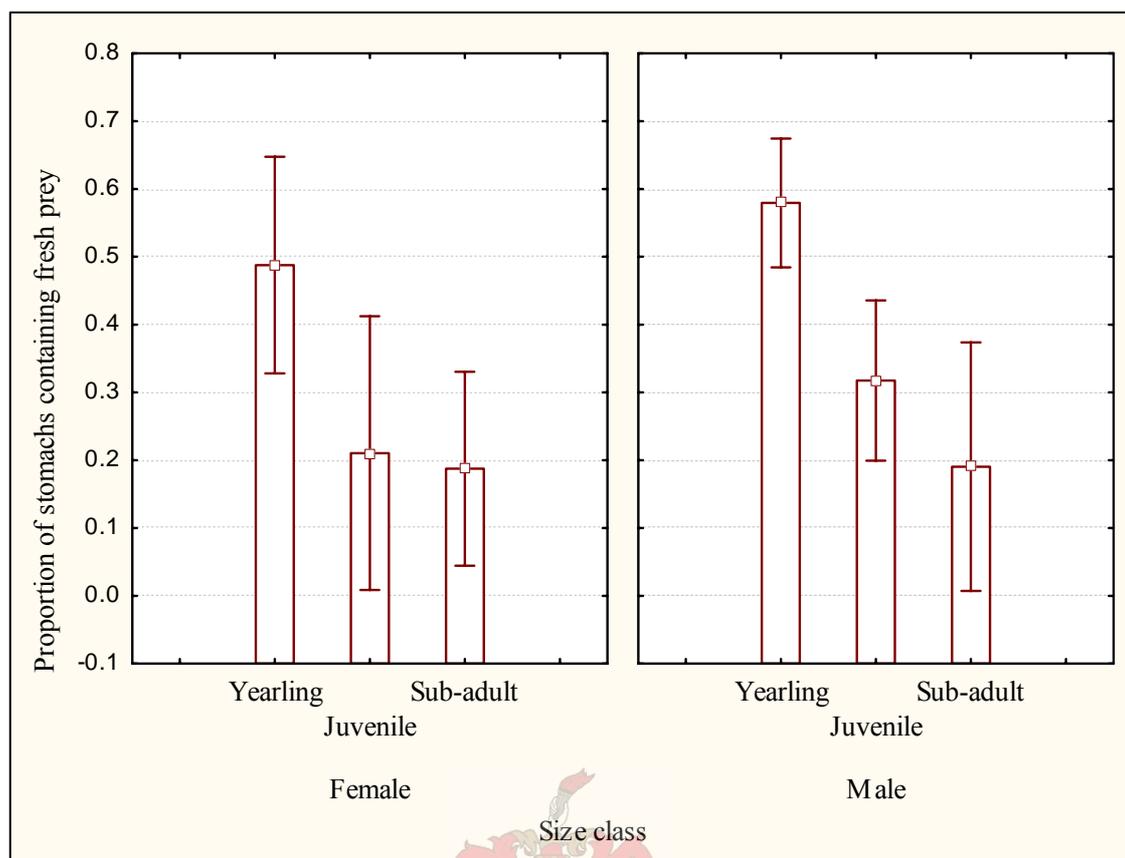


Figure 3.2 Variation in the proportion of stomachs containing fresh prey items between the sexes (mean and \pm 95 % confidence limits)

The stomach contents of all crocodiles are summarized in Table 3.0. To avoid bias in the analysis, the fresh stomach contents and regressed original prey mass (Appendix 6) were used to recalculate prey occurrence and diet composition (Table 3.1).

A significantly higher proportion of invertebrates were consumed by yearlings and juveniles when compared to sub-adults ($p < 0.01$). Yearlings and juveniles also consumed a significantly higher proportion of arachnids than sub-adults ($p < 0.01$). Sub-adults had a significantly higher proportion of fish items present when compared to both juveniles and yearlings ($p < 0.01$).

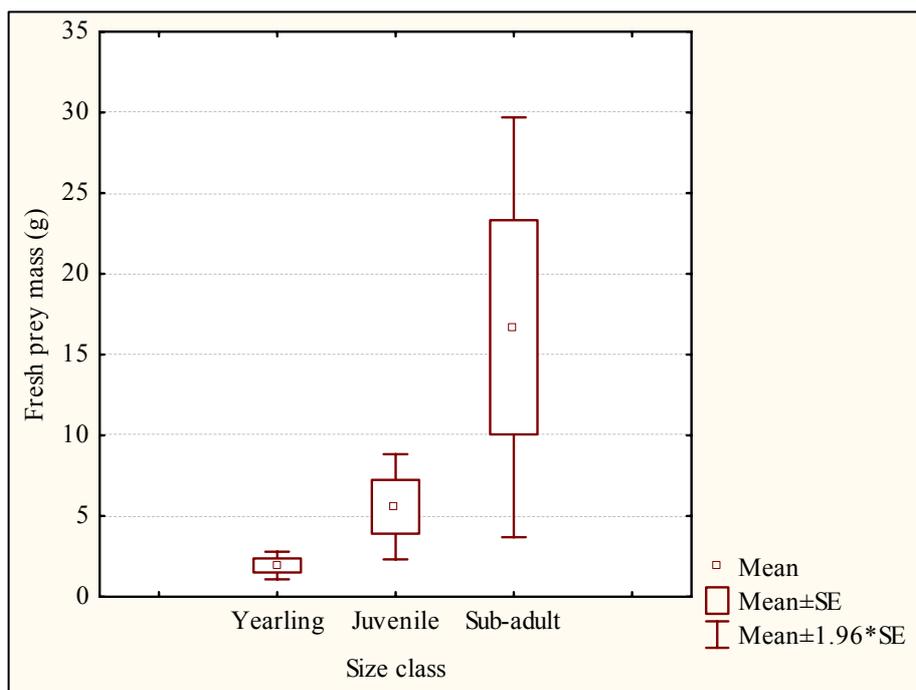


Figure 3.3 Mean mass of fresh prey (regressed to original mass [Appendix 6]) found in stomachs of the three size classes of crocodiles (mean, standard error and 95 % confidence limits)

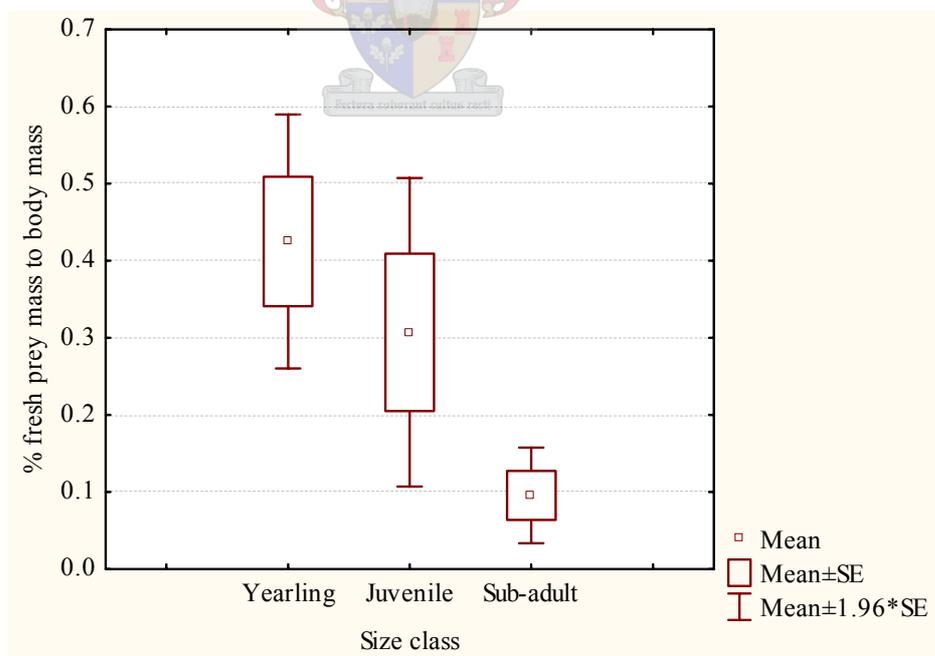


Figure 3.4. Mean percentage of fresh prey (regressed to original mass [Appendix 6]) found in stomachs relative to crocodile mean body mass (mean, standard error and 95 % confidence limits)

The total yearling stomachs contained a mean mass of 1.7 g (\pm 0.3 S.E.) fresh prey items, a significantly higher amount ($p < 0.05$) than juveniles 0.5 g (\pm 0.1 S.E.) and sub-adults 0.4 g (\pm 0.2 S.E.). Yearling stomachs contained a greater number ($p < 0.05$) of fresh prey items (Figure 3.5) than either juvenile (Figure 3.6) or sub-adult stomachs (Figure 3.7). The largest number of fresh prey items was found in one yearling stomach containing thirty-six freshly ingested *Aplocheilichtys johnstoni* (Johnstons topminnow), one *Cybister* sp. (water beetle) and an unidentified arachnid. One sub-adult stomach contained eight *Pollimyrus castelnaui* (Dwarf stonebasher fish) and one unidentified teleostei. Within all the size classes there was no significant difference ($p > 0.05$) between the occurrence of a single prey item in a stomach and stomachs that contained two or more recently ingested prey items, indicating that the feeding interval was not always longer than the digestion time.

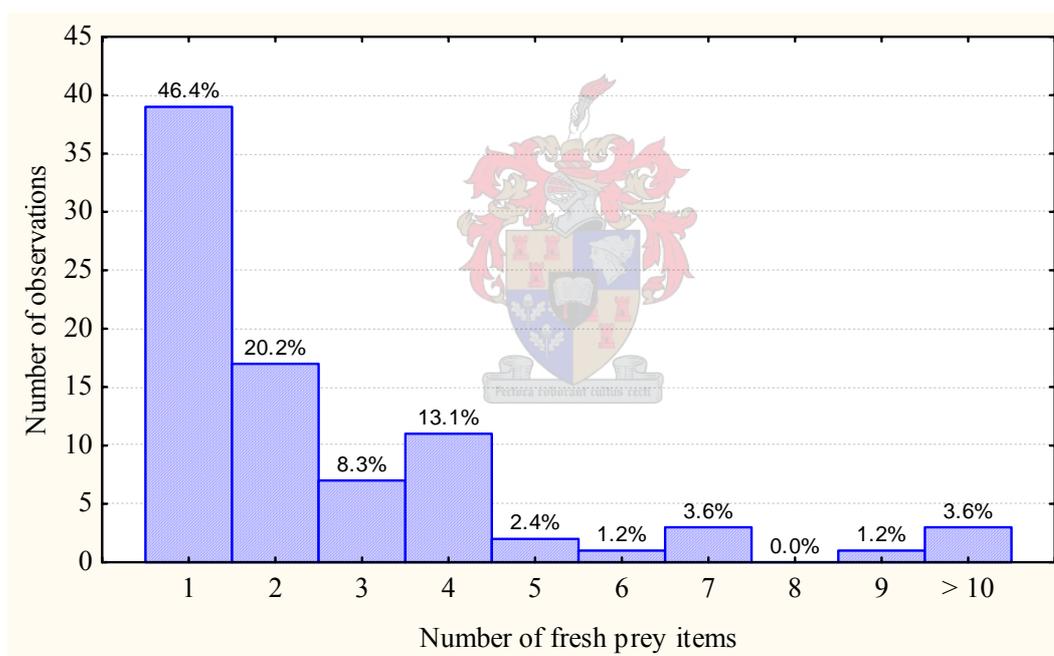


Figure 3.5 Number and percentage of fresh prey items found in the sample of yearlings that had predated prey < 24 hours previously

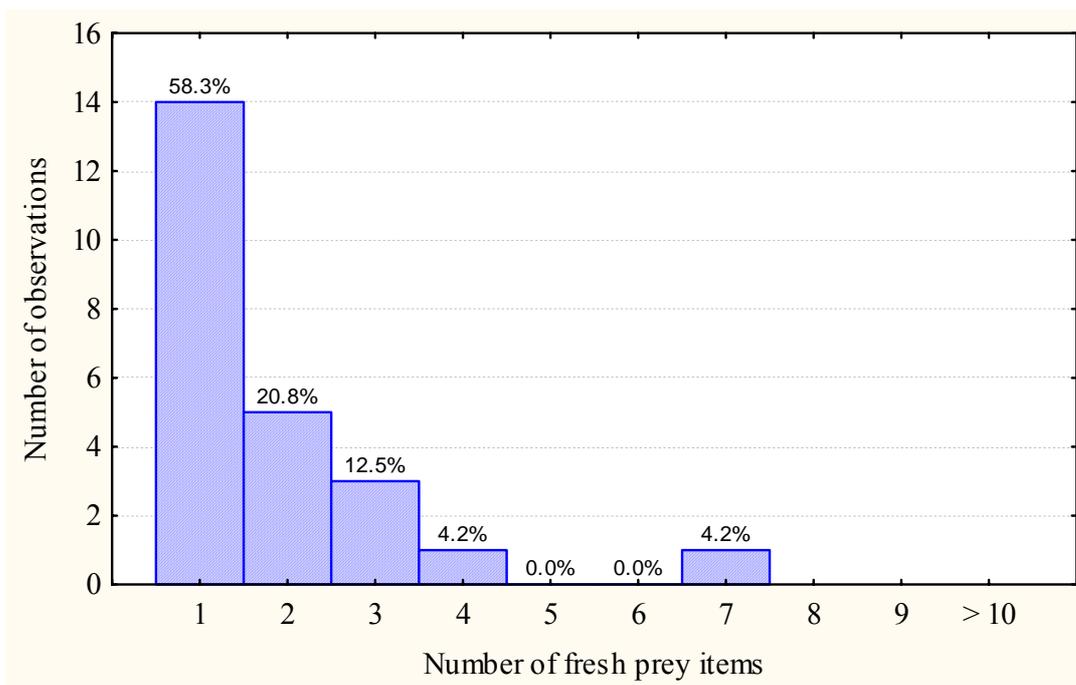


Figure 3.6 Number and percentage of fresh prey items found in the sample of juveniles that had predated prey < 24 hours previously.

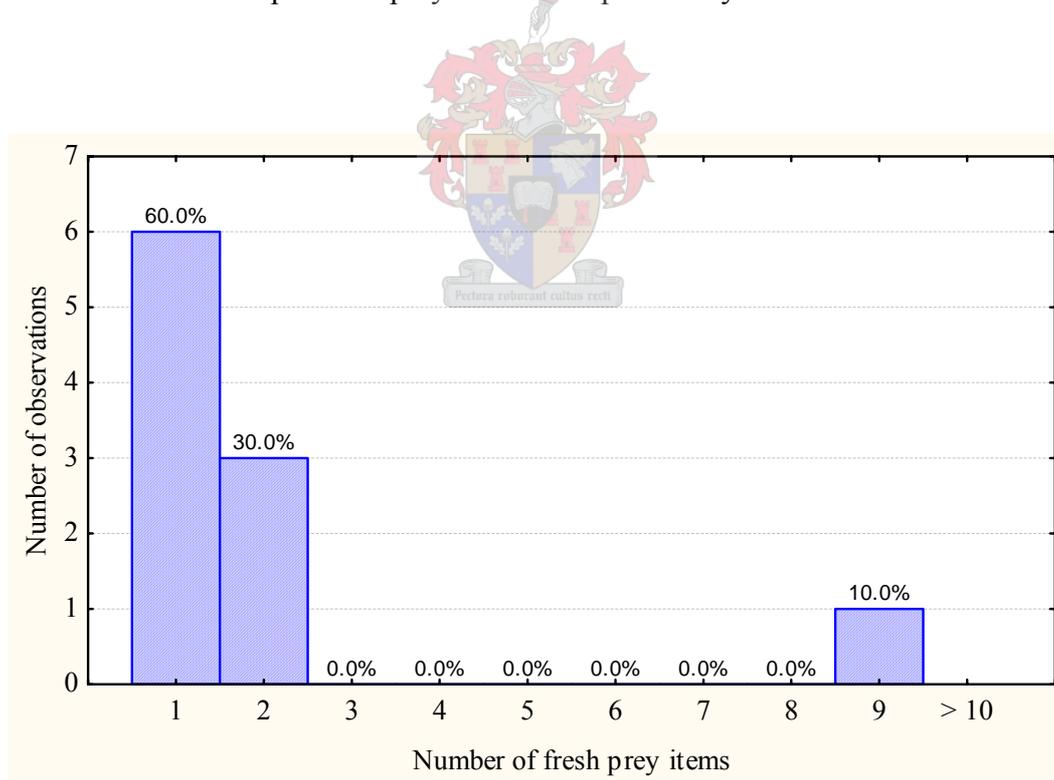


Figure 3.7 Number and percentage of fresh prey items found in the sample of sub-adults that had predated prey < 24 hours previously.

Table 3.0. Type and mass of all prey remnants found in stomachs.

% Composition (% of the total prey mass that belongs to that taxon)

% Occurrence (% of the sample that contained the particular taxon)

Prey group	% Composition			% Occurrence		
	Yearling	Juvenile	Sub-adult	Yearling	Juvenile	Sub-adult
UNIDENTIFIED	12.7	8.2	11.5	16.6	11.0	11.3
INVERTEBRATA	38.4	49.1	6.3	96.0	89.1	47.2
Crustacea	2.9	6.7	0.8	16.6	30.5	7.5
Decapoda	2.9	6.7	0.8	16.0	30.0	7.5
Bivalvia		0.2	0.6		3.7	17.0
Arachnida	2.6	0.3	0.0	35.5	15.9	1.9
Insecta	13.9	14.3	2.5	88.7	85.4	32.1
Dermaptera	0.0			1.3		
Orthoptera	1.7	1.9	0.5	13.8	3.7	1.2
Tettigonidae	0.3	0.0		4.0	1.2	
Gryllotalpidae	0.1	0.1		0.6	2.4	
Hymenoptera	0.0			2.0		
Coleoptera	9.7	11.5	1.8	39.1	52.4	17.0
Terrestrial						
Coleoptera	0.4	0.0		5.3	9.8	
Hydrophilid		0.1			2.7	
Dytiscidae	9.3	11.3	1.8	37.4	51.1	17.0
Gyrinidae		0.0			2.4	
Caribidae						
Lepidoptera	0.3			4.6		
Unidentified						
Lepidoptera	0.3			4.6		
Noctuidae	0.1			1.3		
Diptera	0.0	0.0		1.3	1.2	
Odonata	0.1	0.2	0.0	5.3	2.4	1.9
Libellulidae	0.0			1.3		
Unidentified odonata	0.1	0.0	0.0	4.0	2.4	1.9

Table 3.0 continued Type and mass of all prey remnants found in stomachs.

% Composition (% of the total prey mass that belongs to that taxon)

% Occurrence (% of the sample that contained the particular taxon)

Prey group	% Composition			% Occurrence		
	Yearling	Juvenile	Sub-adult	Yearling	Juvenile	Sub-adult
Hemiptera	1.9	0.7	0.2	37.1	23.2	3.8
Nepidae	0.1	0.0		2.0	1.2	
Belostomatidae	1.6	0.7	0.2	26.6	32.9	3.8
Gerridae	0.2			13.9		
Unidentified insecta	13.8	27.6	2.5	42.0	52.8	22.6
VERTEBRATA	44.6	34.4	46.7	36.4	31.7	66.0
Teleosti	2.3	7.0	24.3	7.9	17.1	62.3
Hepsetidae		3.3	5.1		1.2	1.9
Catfish		0.8			6.1	11.3
Cichlidae	0.1	1.1	1.6	0.7	1.2	1.9
Mochokiae		1.1	1.6		1.2	1.9
Momyridae			6.1			3.8
Poecillidae		0.2	0.3		1.2	1.9
Characin	1.3			4.0		
Cyprinidae	0.3			1.3		
Unidentified teleosti	0.0			0.7		
Rodentia	0.6	1.5	11.2	2.0	7.3	43.4
Muroidea	40.4	27.1	22.3	27.2	15.9	1.9
Soricidae	4.7	1.0	0.7	2.6	1.2	1.9
Unidentified mammal	1.0		0.7	0.7		1.9
Amphibia	35.7	26.1	21.6	28.0	18.5	1.9
Hyperolidae	1.2	0.1		3.8	1.2	
Unidentified amphibia	0.3	0.1		1.8	1.2	

Table 3.0 continued Type and mass of all prey remnants found in stomachs.

% Composition (% of the total prey mass that belongs to that taxon)

% Occurrence (% of the sample that contained the particular taxon)

Prey group	% Composition			% Occurrence		
	Yearling	Juvenile	Sub-adult	Yearling	Juvenile	Sub-adult
Reptilia	0.9			2.0		
Unidentified snake		0.2			1.2	
Unidentified turtle		0.2			1.2	
Aves		0.0			1.2	
Other	0.7	0.0	0.1	1.3	1.2	1.9
Stones	1.5	8.1	35.5	47.7	1.2	60.4
Parasites	0.6	7.2	31.3	4.0	65.9	26.4
Vegetation	0.3	0.1	0.9	38.4	21.6	39.6

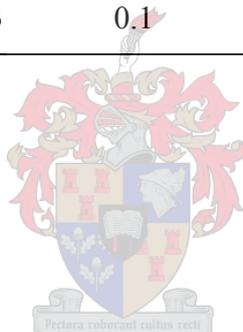


Table 3.1. Type and mass [Appendix 6] of recently ingested prey found in stomachs.
 % Composition (% of the total prey mass that belongs to that taxon)
 % Occurrence (% of the sample that contained the particular taxon)

Prey group	% Composition			% Occurrence		
	Yearling	Juvenile	Sub- adult	Yearling	Juvenile	Sub- adult
INVERTEBRATA	45.6	44.1	1.2	86.9	83.3	30.0
Crustacea		17.2			8.3	
Decapoda		17.2			8.3	
Arachnida	7.6	1.6	0.1	57.1	41.7	10.0
Pisauridae	3.5	1.0		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	20.0	8.3	10.0
Insecta	38.0	25.3	1.1	57.1	45.8	20.0
Dermaptera	0.2			2.4		
Orthoptera	5.6	3.1		7.1	4.2	
Unk Orthoptera						
Tettigonidae	4.3			6.0		
Gryllotalpidae	1.3	3.1		1.2	4.2	
Hymenoptera	0.1	0.0		2.4		
Coleoptera	18.2	18.0	0.8	11.9	20.8	10.0
Terrestrial						
Coleoptera	0.3	0.1		2.4	4.2	
Hydrophilid	6.0	9.3	0.8	4.8	12.5	10.0
Dytiscidae	11.9	8.2		9.5	12.5	
Gyrinidae		0.3			4.2	
Caribidae						
Lepidoptera	1.5	0.7		7.1	4.2	
Unidentified Lepidoptera	0.2	0.7		2.4	4.2	

Table 3.1 continued Type and mass [Appendix 6] of recently ingested prey found in stomachs.

% Composition (% of the total prey mass that belongs to that taxon)

% Occurrence (% of the sample that contained the particular taxon)

Prey group	% Composition			% Occurrence		
	Yearling	Juvenile	Sub-adult	Yearling	Juvenile	Sub-adult
Noctuidae	1.3			3.6		
Diptera	0.2	0.1		2.4	4.2	
Odonata	3.8		0.2	2.4		10.0
Libellulidae	3.8			2.4		
Unidentified odonata			0.2			10.0
Hemiptera	9.9	4.0		29.8	8.3	
Nepidae	0.1			2.4		
Belostomatidae	8.4	4.0		23.8	8.3	
Gerridae	1.4			13.1		
VERTEBRATA	51.0	51.6	77.0	25.0	25.0	90.0
Teleosti	11.6	35.0	68.0	10.7	12.5	80.0
Hepsetidae		26.2	27.0		4.2	10.0
Catfish			12.6			20.0
Cichlidae	3.1	7.3	6.9	1.2	4.2	10.0
Mochokiae			7.2			10.0
Momyridae		1.5	4.2		4.2	10.0
Poecillidae	3.8			7.1		
Characin	2.0			2.4		
Cyprinidae	0.9			1.2		
Unidentified teleosti	1.8		10.2	3.5		20.0
Rodentia	30.8	11.2	9.0	3.6	4.2	10.0
Muroidea		11.2	9.0		4.2	10.0
Soricidae	12.3			2.4		
Unidentified mammal	18.5	11.2	9.0	1.2	4.2	10.0

Table 3.1 continued Type and mass [Appendix 6] of recently ingested prey found in stomachs.

% Composition (% of the total prey mass that belongs to that taxon)

% Occurrence (% of the sample that contained the particular taxon)

Prey group	% Composition			% Occurrence		
	Yearling	Juvenile	Sub-adult	Yearling	Juvenile	Sub-adult
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 snake		4.5			4.2	
Other	3.4	4.3	21.8	50.0	66.7	80.0
Stones	0.4	0.3	20.8	3.6	20.8	50.0
Parasites	0.6	0.7	0.7	40.5	45.8	30.0
Vegetation	2.5	3.4	0.3	22.6	29.2	25.0

The primary fresh invertebrate and vertebrate prey taxa that were found in the stomach samples are shown for yearlings, juveniles and sub-adults in Figure 3.8A - C. The dietary composition of the primary fresh prey taxa (prey regressed to the original mass) is shown for the same three size classes in Figure 3.9A - C.

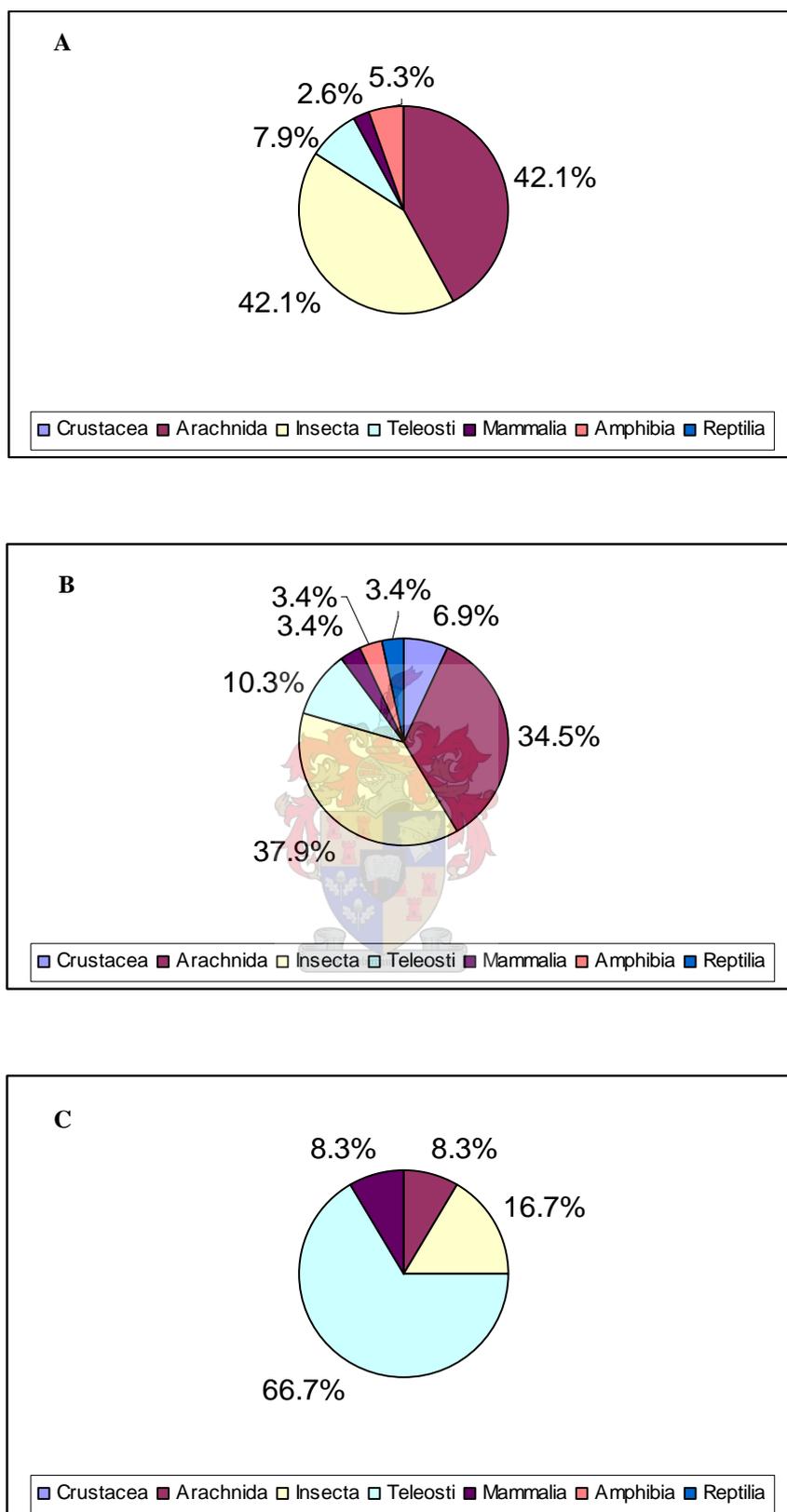


Figure 3.8 (A-C) Percent occurrence of the main prey groups recently ingested by yearlings (A), juveniles (B) and sub-adults (C).

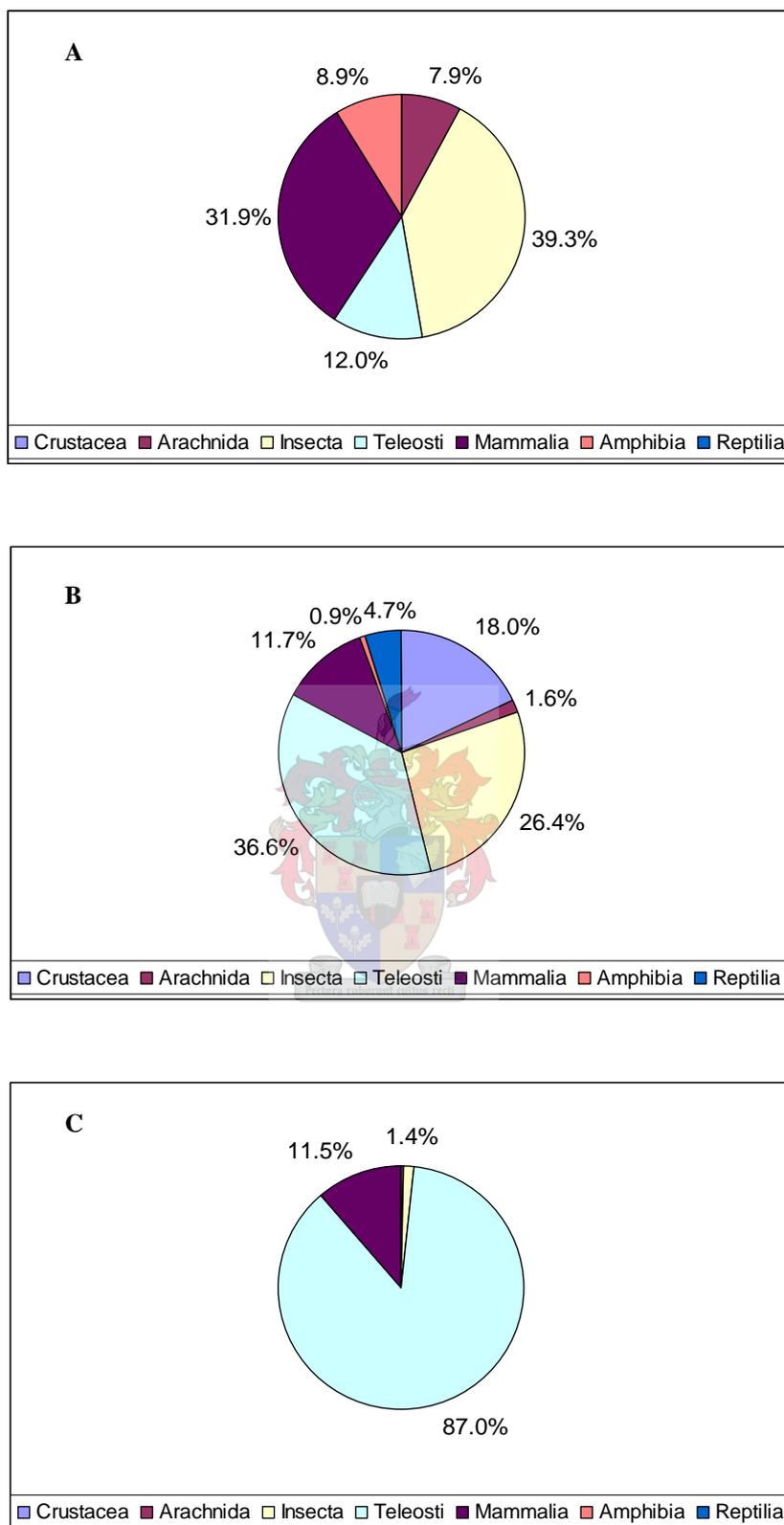
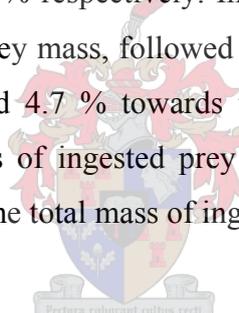


Figure 3.9 (A-C) Percentage composition [Appendix 6] of the main prey groups recently ingested by yearlings (**A**), juveniles (**B**) and sub-adults (**C**).

When comparing recently ingested prey, the percent occurrence per taxon (% of the sample that contained a particular taxon): in yearlings, both arachnids and insects accounted for 84.2 % of the diet, followed by fish (7.9 %), amphibians (5.3 %) and small mammals (2.6 %). In juveniles, both insects and arachnids again dominated the diet, at 37.9 and 34.5 % respectively. Fish were better represented at 10.3 %, crustaceans made up 6.9 %, followed by amphibians, reptiles and mammals each representing a minor 3.4 % of the juveniles diet. The diet of the sub-adults consisted primarily of fish (66.7 %), followed by insects (16.7%) and both mammals and arachnids representing 8.3 % each of the diet.

When comparing the percent composition (regressed to the original prey mass [Appendix 6]) of the main prey taxa (% of total prey mass per taxon)): in yearlings, insects accounted for 39.3 % of total mass of ingested prey, followed by mammals making up 31.9 % of total mass of ingested prey. Fish accounted for 12.0 % of total mass and arachnids and amphibians made up 7.9 and 8.9 % respectively. In juveniles, fish and insects accounted for 36.6 % and 26.4 % of total prey mass, followed by crustaceans, mammals and reptiles contributing 18.0 %, 11.7 % and 4.7 % towards the total mass of ingested prey. The teleosti dominated the total mass of ingested prey in the sub-adult age class (87.0 %). Mammals contributed 11.5 % to the total mass of ingested prey and insects a mere 1.4 %.



INVERTEBRATES

Insecta

Aquatic hemipterans were the most common insect prey of yearlings (26.2 %). Adult *Appasus grassei* constituted 40% of this order with other *Appasus* sp. (adult and nymph), *Limnogeton fiebberi* (adult) and *Hydrometra* sp. (adult) making up the rest. Other common insects included those from the family Gerridae, *Limnogonus capensis* (adult) and the occasional Hydrometridae, *Hydrometra* sp. (adult) and Nepidae, *Ranatra* sp. (adult).

Aquatic coleoptera formed the bulk of invertebrate prey mass within both the yearling and juvenile size classes, 38.6 % and 39.4 %, respectively. Hydrophilids (adult), *Hydrophilus aceleatus*, *Hydrochara* sp. (adult and nymph), *Hydrophilus* sp. and Dysticidae, *Cybister* sp. (adult) dominated the diet of the smaller size classes. Terrestrial insects that were occasionally found included adult Colepterans of the Carbidae, Cleridae and Curculionidae families, and adult Orthopterans. Tettigonidae and *Gryllotalpa africana* were only found

within the juvenile size class. Both yearlings and juveniles had occasional lepidoptera and tabanidae larvae present. Noctuidae moths accounted for 86.6 % of the Lepidoptera predated by yearlings.

Arachnida

The Pisauridae family was the dominant arachnid occurring in the stomachs of 56.5 % of yearlings and 44 % of juveniles. Within these smaller size classes, *Dolomedes gracilis* and *Thalassius marginatus* constituted 80% of this family. The remaining 20 % were members of the Araneidae family. Both *Neoscona subfusca* and *Pararaneus cyrtoscapus* were occasionally found within the two smaller size classes. Yearlings preyed on *Tetragnatha angolaensis* and *T. boydi* representing 83.3 % and 16.7 % of the Tetragnathidae family, respectively. Two recently predated Lycosidae were found in yearling stomachs.

Crustacea

Old Decapoda remnants were found only within the juvenile size class and constituted a major part of the diet (37.6 % of the total invertebrate mass).

Bivalvia

Old remnants of fresh water mussels were recovered from 3.6 % of juvenile and 17 % of sub-adult stomachs.



VERTEBRATES

Teleosti

Both the occurrence of recently ingested fish and its percentage mass of total diet increased with crocodile size, but that of mammals and amphibians decreased. Fish comprised a minor dietary component for both yearlings and juveniles. Yearlings predated on *Aplocheilichthys johnstoni* (31.6 % of dietary mass), along with the occasional Cichlidae. Members of the Characin family included *Rhabdalestes maunensis* and *Barbus mulitneatus*. The largest fish predated by the juvenile size class was *Hepsetus odoe* (50.7 % of teleosti dietary composition). Other fish species found were *Tilapia sparrmanii* and *Pollimyrus castelnaui*. The sub-adult class showed the highest diversity of fish, with *Synodontis sp.* occurring most frequently (22.2 %), although *H. odoe* formed the bulk of the dietary mass (56 %). Catfish sp., *H. odoe*, *Tilapia rendalli* and *P. castelnaui* accounted

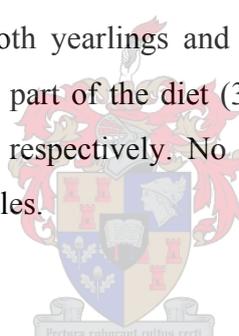
for 88.8 % of total vertebrates recently predated upon and 88.3 % of the total fresh vertebrate prey mass.

Mammalia

Small mammals occurred most frequently within the yearling size class and composed the bulk of the diet (30.8 % of the total prey mass). Two yearling stomachs contained recently ingested adult *Crocidura mariquensis* representing 50 % of small mammals predated. The remaining 50% consisted of unidentified recently ingested small mammals. A single unidentified small mammal (ingested <24 h) was found in both the juvenile and sub-adult size classes. Old remnants of mammal hair (often forming hairballs) were recovered from 28.3 % of yearling stomachs, 18.1 % of the juvenile stomachs and from 1.9 % of the sub-adults stomachs.

Amphibia

Amphibians were predated by both yearlings and juveniles. The reed frog, *Hyperolius marmoratus* formed an important part of the diet (31.6 % and 28.6 % of vertebrate prey mass) in yearlings and juveniles respectively. No amphibians were recovered from the stomachs of any sub-adult crocodiles.



Reptilia

A single recently ingested unidentified snake was recovered from a juveniles' stomach as well as an old unidentified turtle remnant.

Aves

Unidentified remnants of birds (feathers and claws) were found in both the yearling and sub-adult size classes.

PREY DIVERSITY

The species accumulation curves for the separate size classes and for the three size classes combined, did not asymptote (Figure 3.10). However, using the Incidence-based Coverage Estimator (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 were predicted. An estimated total of 53 different species were predicted within the yearling size class. ICE was not

calculated for the juvenile or sub-adult size classes as the sample size was not adequate for reliable estimates.

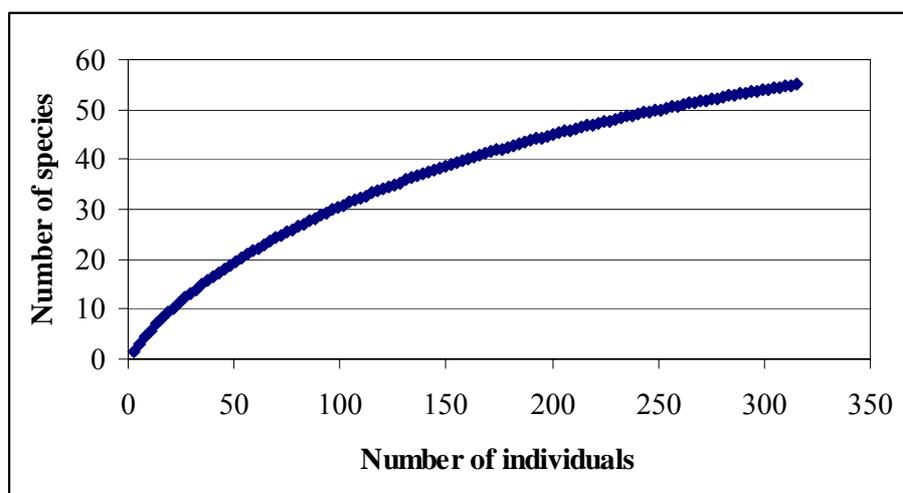


Figure 3.10 Species accumulation curve for fresh prey species recovered from all crocodile stomachs combined.

Table 3.2 shows the Shannon-Wiener Diversity Index, Species Richness and Total abundance of species predated. The two smaller size classes predated a similar diversity of prey, both significantly higher than that of the sub-adults ($p < 0.05$).

Table 3.2 Shannon-Wiener diversity index indicating species richness of the diet between the three size classes.

Species richness = Total number of species predated

Total abundance = Total number of individuals predated

	Yearling	Juvenile	Sub-adult
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

Diet and skull morphometrics

The transition to different prey types occurs at the upper end of the juvenile size class. Figures 3.11 and 3.12 show the importance of different prey groups in relation to crocodile

size. The occurrence of both insects and arachnids declined with increasing crocodile size (Figure 3.11). There was a marked change in the diet as fish became more dominant and mammals declined in importance when crocodiles exceeded a SVL of 40cm (Figure 3.12).

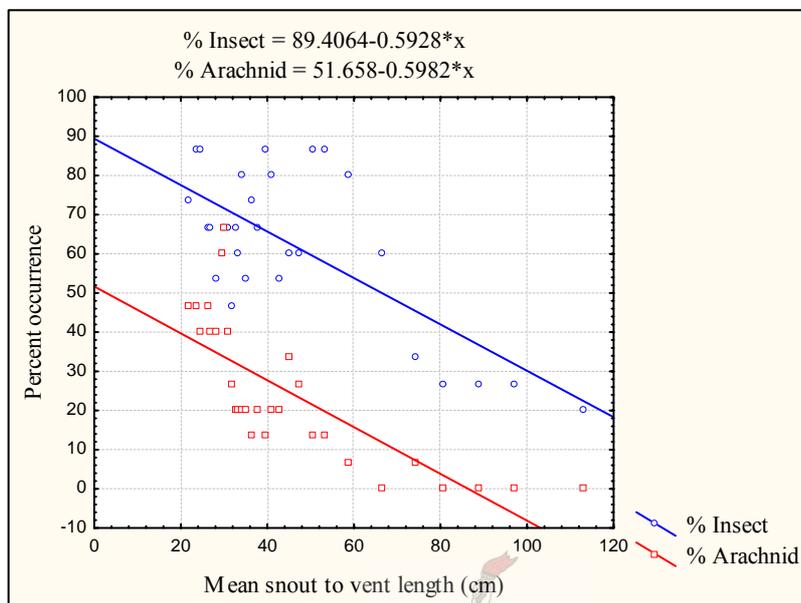


Figure 3.11 Percent occurrence of stomachs containing all remnants of the main invertebrate prey groups using an 'overlapping group analysis'.

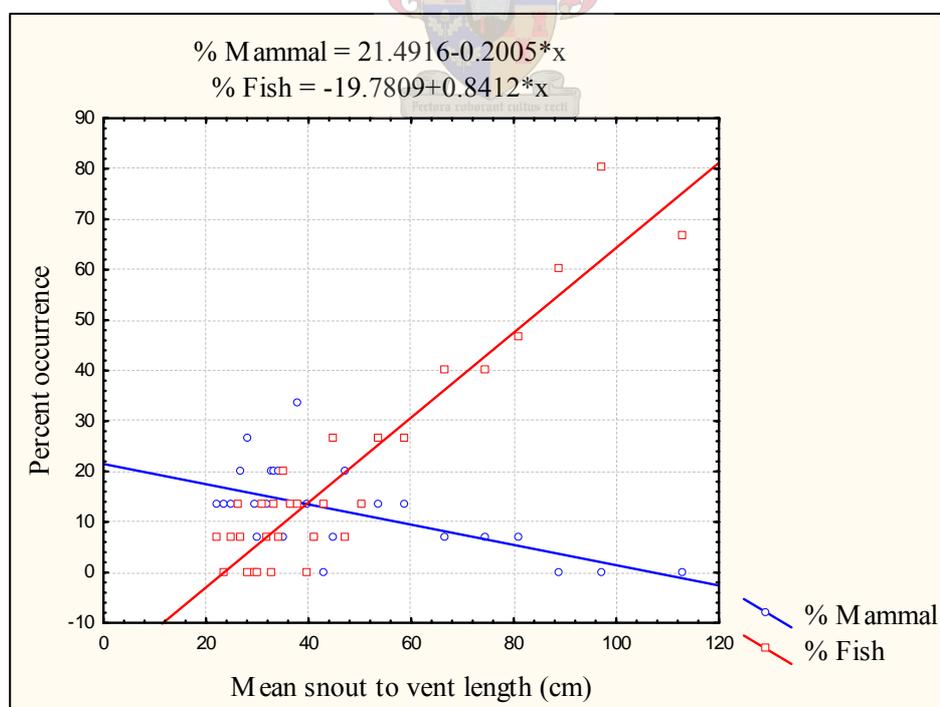


Figure 3.12 Percent occurrence of stomachs containing all remnants of the main vertebrate prey groups using an 'overlapping group analysis'.

Figure 3.13 and 3.14 illustrate the ratios between head width (HW), head depth (HD) and head length (HL) of the crocodiles. Initially, both the ratios increased as the snout elongated relative to width and depth up to a length of 32 cm SVL ($p > 0.001$). The ratios eventually decreased as the snout became broader and deeper relative to length. This coincided with the change in diet shown in Figure 3.12.

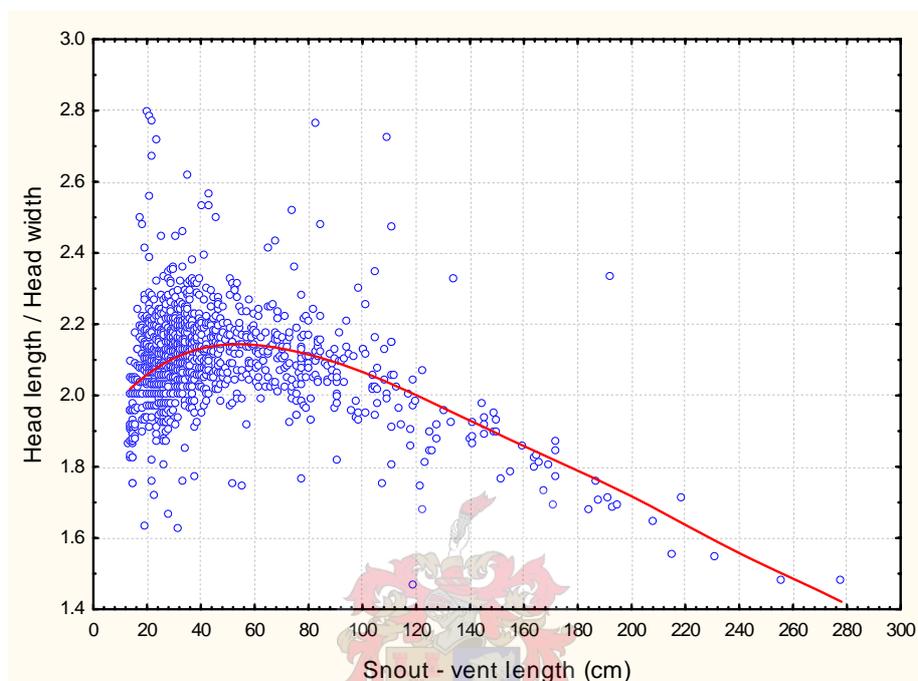


Figure 3.13 Ratio of head length / head width relative to snout-to-vent length (SVL).

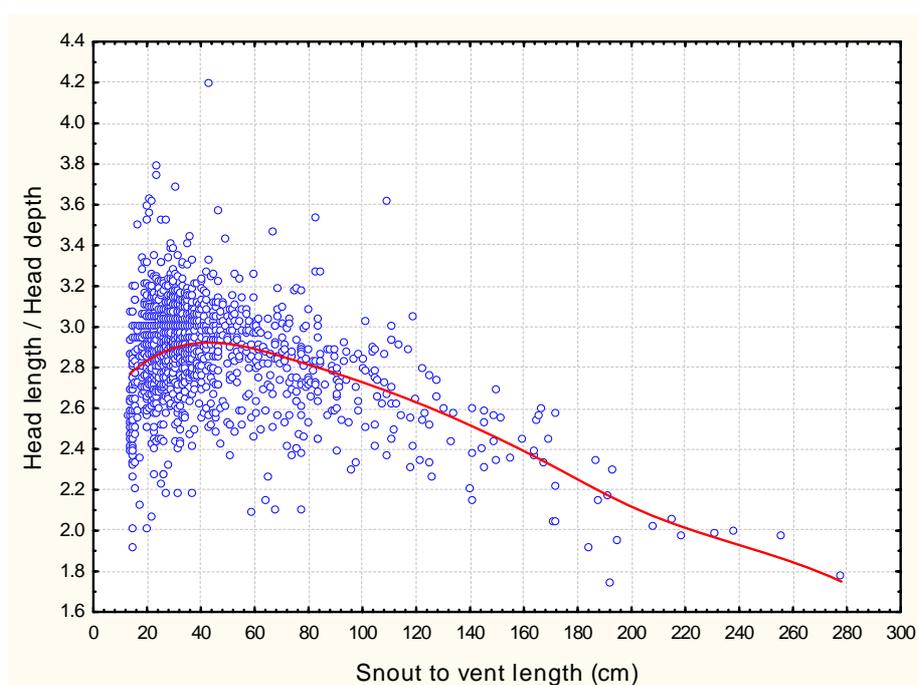


Figure 3.14 Ratio of head length / head depth relative to snout-to-vent length

Seasonal differences

The seasons of winter (June to August) and summer (September through May) were based on mean monthly temperatures recorded whenever a crocodile was captured (Table 3.3).

Table 3.3 Mean monthly crocodile body, air and water temperatures ($^{\circ}\text{C}$) recorded during nightshifts between August 2003 and August 2005. The project was not operational during April in either year.

	BODY	AIR	WATER
J	26.5	23.1	27.4
F	26.8	23.6	26.7
M	26.4	26	22.8
A	n/a	n/a	n/a
M	22.8	19.5	22.4
J	19.8	14.1	18.8
J	16	12	16
A	18.2	13.5	17.5
S	25.9	16.2	21.1
O	24	20.6	24.6
N	25.1	21.3	26.4
D	26.3	21.5	27.2

No significant difference ($p > 0.05$) was found between the proportion of fresh stomach contents collected during the summer months (44.6 %) when compared to samples collected during the winter months (36.4 %) for all the size classes combined (Figure 3.15). The proportion of yearlings with fresh prey items present did not differ significantly between summer (59.5 %) and winter (51.4 %) ($p > 0.05$). However, the proportion of juveniles with fresh stomach contents present was significantly higher in summer (37.3 %) than in winter (16.1 %) ($p < 0.05$). None of the 15 sub-adult crocodiles caught during the winter months had any fresh prey items present when compared with 23.7 % of stomachs with fresh prey items during the summer months ($p < 0.01$). There was no significant difference between prey mass consumed, for either yearlings or juveniles between seasons ($p > 0.01$).

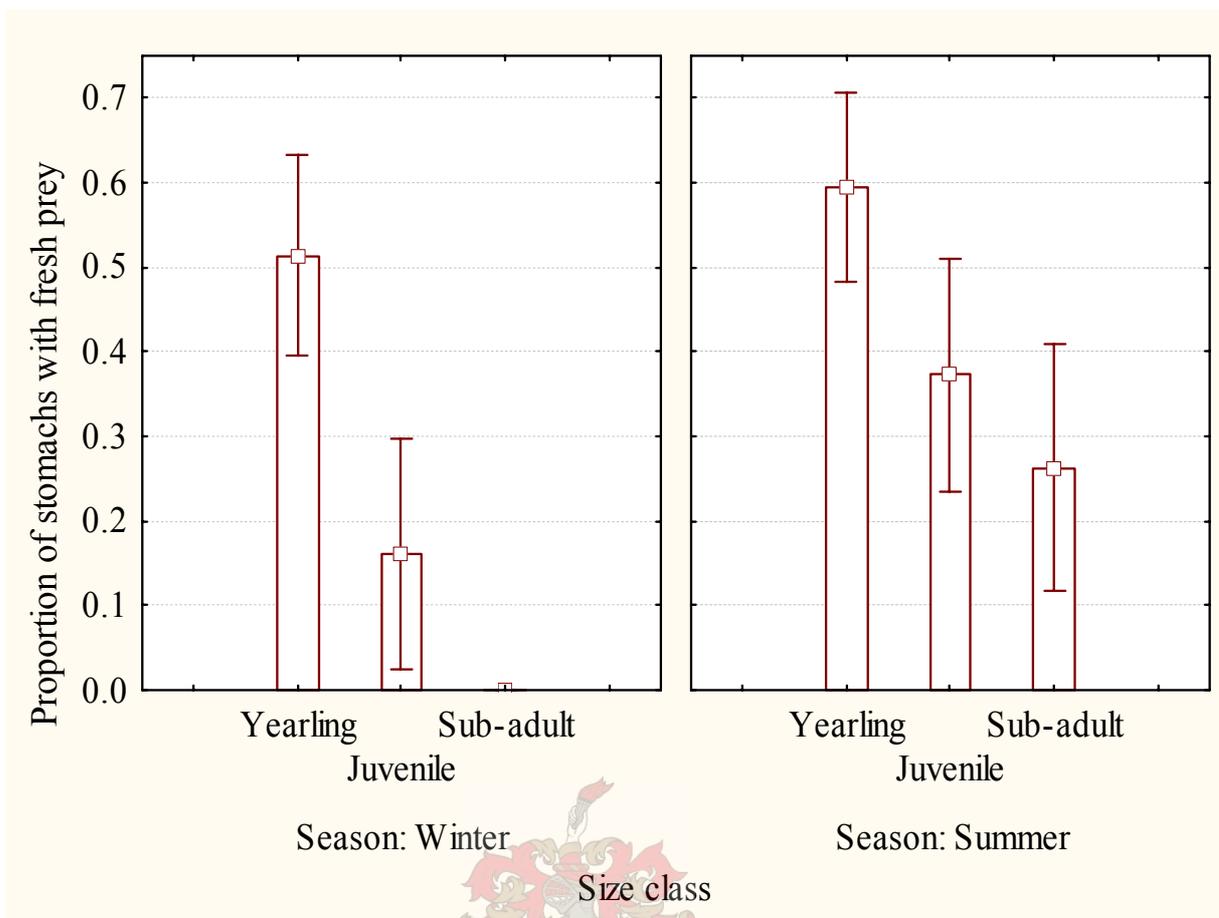


Figure 3.15 Seasonal differences in the proportion of stomachs with fresh prey items present (mean and \pm 95 % Confidence interval)

DISCUSSION

Allometric changes in head dimensions have been associated with ontogenetic shifts in diet. In a study on Nile crocodiles in Zimbabwe, Hutton (1987) found that Lake Ngezi crocodiles shifted from a diet of insects to fish and birds at approximately 60 cm SVL. This also coincided with a dispersal of crocodiles from the Ngezi River into the lake itself. Tucker *et al.* (1996) found an ontogenetic diet shift in *C. johnstoni* as body size exceeded 60 cm TL. This shift occurred as the cranium broadened. Games (1990) found a similar shift closer to 70 cm SVL in Lake Kariba Nile crocodiles. Blomberg's (1976) study in the Okavango region showed a shift in diet towards fish around 75 - 100 cm TL (approx. 35 - 50 cm SVL). This study from the Okavango showed a similar shift in diet away from mammals to fish after 40 cm SVL, with fish dominating the diet after 60 cm SVL. 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 range of insects predated was indicative of the smaller crocodiles hunting style and habitat. They relied primarily on surface and sub-surface feeding at the littoral vegetated fringe of the river. With an increase in body length there was a shift away from insect prey towards fish. Okavango crocodiles showed a preference for *H. odoe*, catfish sp. and *Synodontis* sp. which are all predacious fish, as well as for some other 'non-commercial' fish species such as top minnows, characins and momyrids. Blomberg (1976) found squeakers (*Synodontis* sp.) to be the primary fish predated upon up to a TL of 150cm (larger crocodiles took less of this species), along with *Clarius* and *Tilapia* sp. Freshwater crabs were also recorded as an important food item, although it is not known how 'fresh' the remnants were.

Due to the high insect and fish diversity of the Okavango region and the opportunistic feeding habits of crocodiles, it was unlikely that the prey accumulation curves would reach an asymptote. An increased sampling effort could have yielded a greater number of species within the diet. A total of 58 different species were found in the combined size class sample of the predicted 75 species.

The proportion of empty stomachs was not significantly different between seasons for the yearlings, possibly due to higher metabolic demands (Coulson *et al.*, 1973) that require continuous feeding. Seasonal differences between 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 still consumed a similar total prey mass when compared to the summer months. The summer months (September to May) represent receding to low water levels with decreased foraging habitat available as the surrounding plains dry out while the winter months encompass the highest water levels increasing the aquatic foraging area, but cooler temperatures also reduce the crocodiles metabolism (Diefenbach, 1975a, b; Coulson *et al.* 1990).

The diet of the Okavango crocodiles was almost entirely predated from within the river itself. Pisuridae spiders (the main arachnid prey) spend most of their time on or very close to the waters surface. The family, Lycosidae, are able to traverse the waters surface and often live close-to water (Corbet, 1959). The invertebrate portion of the diet consists 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 invertebrate prey was found in sub-adult stomachs, this could be attributed to secondary digestion, accidental digestion or opportunism. A future study may attempt to quantify the effect of secondary digestion on diet analysis. 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. Games (1990) found that the majority of the juvenile's diet consisted of terrestrial invertebrates in both Lake Kariba and in the Zambezi River. The principle food of crocodiles less than 2.0 m TL in Uganda was Belastomatidae, Naucoridae and Anisoptera (Cott, 1954).

Overall, the proportion of empty stomachs found was similar to results from the Zambezi River, but lower than results obtained from Lake Kariba's Nile crocodiles (Games, 1990). The Okavango crocodiles were highly dependent on aquatic prey species and although many species of 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.

REFERENCES

- Ayarzagüena, S. J. 1983. Ecología del caiman de anteojos en los llanos de Apure Venezuela. Donana Acta Vertebrata numero especial. 10: 1 - 136
- Barr, B. 1997. Food habits of the American alligator, *Alligator mississippiensis*, in the Southern Everglades. Unpublished PhD Thesis, University of Miami
- Blomberg, G. E. D. 1976. Feeding and nesting ecology and habitat preferences of Okavango crocodiles. Proceedings of the Symposium: Okavango Delta and its future utilisation, Botswana Society, Gaborone, Botswana
- Corbett, P. S. 1959a. The food of a sample of crocodiles (*Crocodylus niloticus* L.) from Lake Victoria. Proceedings of the Zoological Society of London. 133 (4): 561 - 572
- Corbett, P. S. 1959b. Notes on the insect food of the Nile crocodile in Uganda Proceedings of the Royal Entomological Society of London. Series. A. Gen 34: 17 - 22
- Cott, H. B. 1954. The status of the Nile crocodile in Uganda. Uganda Journal. 18 (1): 1 - 12
- Cott, H. B. 1961. Scientific results of an enquiry 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 - 356
- Coulson, T. D., Coulson, R. A. and Hernandez, T. 1973. Some observations on the growth of captive alligators. Zoologica. 58: 47 - 52
- Coulson, R. A., Coulson, T. D. and Herbert, J. D. 1990. How do digestion and assimilation rates in alligators vary with temperature? Comparative Biochemistry and Physiology. 96A: 441 - 449
- Delaney, M. F. and Abercrombie, C. L. 1986. American alligator food habits in North Central Florida. Journal of Wildlife Management. 50 (2): 348 - 353

- Diefenbach, C. O Da C. 1975a. Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia) - I. Rate of gastric digestion and gastric motility as a function of temperature. *Comparative Biochemistry and Physiology*. 51A: 259 - 265
- Diefenbach, C. O Da C. 1975b. Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia) - II. Effects of temperature on pH and proteolysis. *Comparative Biochemistry and Physiology*. 51A: 267 - 274
- Fitzgerald, L. A. 1989. An evaluation of stomach flushing techniques for crocodilians. *Journal of Herpetology*. 23 (2): 170 - 172
- Games, I. 1990. The feeding ecology of two Nile crocodile populations in the Zambezi valley. Unpublished PhD Thesis, University of Zimbabwe
- Garnett, S. T. 1985. The consequences of slow chitin digestion on crocodilian diet analyses. *Journal of Hepetology*. 19: 303 - 304
- Hirai, T. and Matsui, M. 2001. Attempts to estimate the original size of partly digested prey recovered from stomachs of Japanese anurans. *Herpetological Review*. 32 (1): 14 - 16
- Hutton, J. M. 1984. Population ecology of the Nile crocodile, *Crocodylus niloticus* Laurenti, 1768, at Ngezi, Zimbabwe. Unpublished PhD Thesis, University of Zimbabwe
- Hutton, J. M. 1987. Growth and feeding ecology of the Nile crocodile, *Crocodylus niloticus* at Ngezi, Zimbabwe. *Journal of Animal Ecology*. 56: 25 - 38
- Jackson, J. F., Campbell, H. W. & Campbell, K. E. 1974. The feeding habits of crocodilians: validity of the evidence from stomach contents. *Journal of Herpetology*. 8: 378 - 381

- Lang, J. 1987. Crocodylian thermal selection, pp. 301-317. In: G.J.W. Webb, S.C. Manolis and P.J. Whitehead (eds), *Wildlife Management: Crocodiles and Alligators*. Surrey Beatty, Chipping, Norton, NSW, Australia
- Leslie A. J., 1997. The ecology and physiology of the Nile crocodile, *Crocodylus niloticus*, in Lake St Lucia, Kwazulu/Natal, South Africa. Unpublished PhD Thesis, Drexel University, USA
- Magnusson, W. E., Da Silva, E. V. and Lima A. P. 1986. Diets of Amazonian Crocodylians. *Journal of Herpetology*. 21 (2): 85 - 95
- Modha, M. L., 1967 The ecology of the Nile crocodile (*Crocodylus niloticus*) on Central Island, Lake Rudolf. *East African Wildlife Journal*. 5: 74 - 95
- Neill, W. T. 1971. The last of the ruling reptiles: alligators, crocodiles and their kin. Columbia Univ. Press, Ithaca. pp 486
- Pooley, A. C. 1982. The ecology of the Nile crocodile, *Crocodylus niloticus*, in Zululand Unpublished MSc Thesis, University of Natal, South Africa
- Pooley, A. C. and Gans, C. 1976. The Nile crocodile. *Scientific American*. 234 (4): 114 - 124
- Rosenburg, K. V. and Cooper, R. J. 1990. Approaches to avian diet analysis. *Studies in Avian Biology* 13: 80 - 90
- Taylor, G. W. 1973. Nile crocodile in the Okavango Delta. A report on a wildlife population for Botswana Game Industries. pp 36 - 73
- Taylor, J. A. 1979. The foods and feeding habits of sub-adult *Crocodylus porosus* Schneider in northern Australia. *Australian Wildlife Research*. 6: 347 - 359

- Tucker, A. D., Limpus, C. J., McCallum, H. I. and McDonald, K. R. 1996. Ontogenetic dietary partitioning by *Crocodylus johnstoni* during the dry season. *Copeia*. 4: 978 - 988
- Valentine, J. M., Walther, J. R., McCartney, K. M. and Ivy, L. M. 1972. Alligator diets on the Sabine National Wildlife Refuge, Louisiana *Journal of Wildlife Management*. 36 (3): 809 - 815
- Webb, G. J. W. and Messel, H., Crawford, J. and Yerbury, M. J. 1978. Growth rate of *Crocodylus porosus* (Reptilia: Crocodylia) from Arnhem Land, Northern Australia. *Australian Wildlife Research*. 5: 385 - 399
- Webb, G. J. W., Hollis, G. J. and Manolis, S. C. 1991. Feeding, growth, and food conversion rates of wild juvenile Saltwater crocodiles (*Crocodylus porosus*). *Journal of Herpetology*. 25: 462 - 473
- Whitfield, A. K., Blaber, S. J. M. 1979. Predation on Striped Mullet (*Mugil cepalus*) by *Crocodylus niloticus* at St. Lucia, South Africa. *Copeia*. 2: 266 - 269
- Wolfe, J. L., Bradshaw, D. K., Chabreck, R. H., 1987. Alligator feeding habits: New data and a review. *Northeast Gulf Science*. 9 (1): 1 - 8

CHAPTER 4

Non-food items found in stomachs of the Nile crocodile, *Crocodylus niloticus*, in the Okavango Delta, Botswana.

INTRODUCTION

Stones, pebbles and gravel found residing in the alimentary track are collectively termed 'gastroliths' (Skoczylas, 1978). They are found in a wide range of both terrestrial and aquatic tetrapods (Taylor, 1993) as well as in diving birds such as the Emperor penguin (Spletstoeser and Todd, 1999). Terrestrial animals use gastroliths as a digestive aid (Skoczylas, 1978), however, the reason as to why crocodilians accumulate gastroliths is still under speculation. The possible functions of gastroliths are currently being debated. One possibility is that gastroliths may have a hydrostatic function, such as ballast, in order to achieve negative buoyancy to assist diving (Cott, 1961). Gastroliths in the stomach lie directly below the lungs, the area of most positive buoyancy, therefore they could help control longitudinal posture and rolling (Taylor, 1993). Henderson (2003) produced a model showing that relatively small quantities of gastroliths (< 2.0 % body mass) found in aquatic tetrapods, are considered inconsequential for buoyancy and stability, the lungs being the principle agent for hydrostatic buoyancy control.



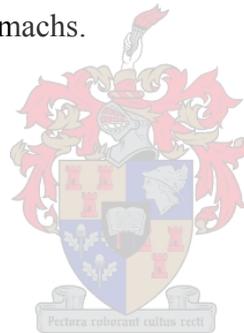
A second possible function is as an aid to digestion (Sokol, 1971; Diefenbach, 1975; Davenport *et al.* 1990). Gastroliths however, do not appear to be essential for digestion. Alligators raised with no access to gastroliths have grown seven times faster than wild alligators of the same age (Coulson *et al.* 1973) and gastroliths have been observed in the stomach of *C. niloticus* with fragile prey items present (Cott, 1961).

The parasite genus *Dujardinascaris* contains eleven species, all of which parasitize crocodilians (Sprent, 1977). The life cycle is as yet undetermined, although in Zimbabwe, the lake sardine is thought to be the intermediate host (Foggin, 1987). Both mature and immature parasites have been found in crocodiles (Ladds and Sims, 1990) which may represent auto-infection. Three species have been reported from African crocodiles, *D. dujardini* (Cott, 1961), *D. gedoelsti* (Sprent, 1977) and *D. puylaerti* (Sprent, 1977).

Other parasites found within *C. niloticus* stomachs include *Multicaecum agile* and *Contracaecum* sp. (Cott, 1961). Taylor (1973) recorded that 20 % of all *C. niloticus* stomachs contained a tightly spiraled nematode and massive infestations of ascarids that usually formed an ulcer in the stomach. *Trichinella zimbabwensis* larvae have been found in the skeletal muscle and the small intestine of Zimbabwean Nile crocodiles only (Pozio, 2002). Parasites specific to certain common prey species such as catfish may be passed on to crocodiles (Reed, 2003).

Studies have shown that the frequency of plant remains in stomachs increase with crocodile size (Taylor, 1973; Blomberg 1976). Taylor (1973) suggested that plant material may have a nutritional value, however, crocodilians are unable to digest either vegetable proteins or polysaccharides (Coulson and Hernandez, 1983).

This chapter examines the possible relationship between non-food items and actual prey items retrieved from crocodile stomachs.



METHODS

Crocodile capture and stomach content retrieval

From August 2003 to August 2005, 286 crocodiles were captured and stomach lavaged. The animals were allocated to one of three size classes based on snout-to-vent length (SVL): yearlings (17.0 - 38.9 cm SVL), juveniles (39.0 - 66.3 cm SVL) and sub-adults (66.4 - 115.8 cm SVL) [Leslie 1997]. Seven adult (< 115.9 cm SVL) crocodiles were also processed but due to the small sample size they were included within the sub-adult group.

Crocodiles were caught from a boat at night either by hand or noose using a spotlight. Three larger individuals were caught in box traps (Appendix 1). Animals were 'processed' immediately (Appendix 2) at the site of capture and subsequently released. Stomach samples were obtained using a modification of the technique originally devised by Ayarzagüena (1983) and modified and evaluated by Fitzgerald (1989), namely the hose-heimlich technique, which utilizes a water pump to flush out stomach contents (Appendix 3). The method was evaluated at being 83 % effective for removing stones (100 % effective for prey items). According to Fitzgerald (1989) large stones and parasites embedded within the gastrointestinal tract are not always removed.

Non-prey items, such as parasites, stones (gastroliths) and vegetation were identified, digitally photographed and wet mass recorded. Parasites were stored in 80 % alcohol for transport to the Department of Conservation Ecology at the University of Stellenbosch in South Africa for identification purposes.

Stomach Stones (Gastroliths)

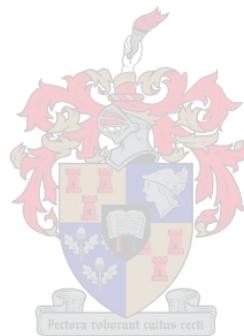
Using a Leo® 1430VP Scanning Electron Microscope, stomach stones were identified using backscattered electron (BSE) and/or Secondary electron images. Phase compositions were quantified by EDS analysis using an Oxford Instruments® 133KeV detector and Oxford INCA software (Appendix 5), Geology Department, University of Stellenbosch.

Parasites

Parasites were sent to the Department of Veterinary Tropical Diseases, University of Pretoria for identification.

Statistical analysis

A Maximum likelihood chi squared test was used for ranked occurrence data and a Kruskal-Wallis analysis of variance by ranks, for non-normally distributed composition mass data. Arcsine transformation was used on data converted to percentages and analysed using one-way ANOVA. All statistical analyses were performed using Statsoft Inc (2005) Statistica version 7.1.



RESULTS

Stomach stones (Gastroliths)

The majority of stomachs did not contain gastroliths ($p < 0.01$). Larger crocodiles did not contain larger gastroliths, only the cumulative mass of the gastroliths increased with crocodile size. Gastroliths occurred with increasing frequency with an increase in crocodile size ($p < 0.01$) [Figure 4.0]. Four percent of yearling, 20.8 % of juvenile and 26.4 % of sub-adult stomachs contained gastroliths. Total gastrolith mass relative to crocodile body mass increased with crocodile size, but not significantly ($p > 0.05$). Yearling stomachs contained gastroliths that constituted 0.13 % (± 0.05 S.E.) of total crocodile body mass, juveniles stomach contained gastroliths that constituted 0.18 % (± 0.1 S.E.) and the stomachs of sub-adults contained gastroliths that constituted 0.26 % (± 0.11 S.E.) [Figure 4.1].

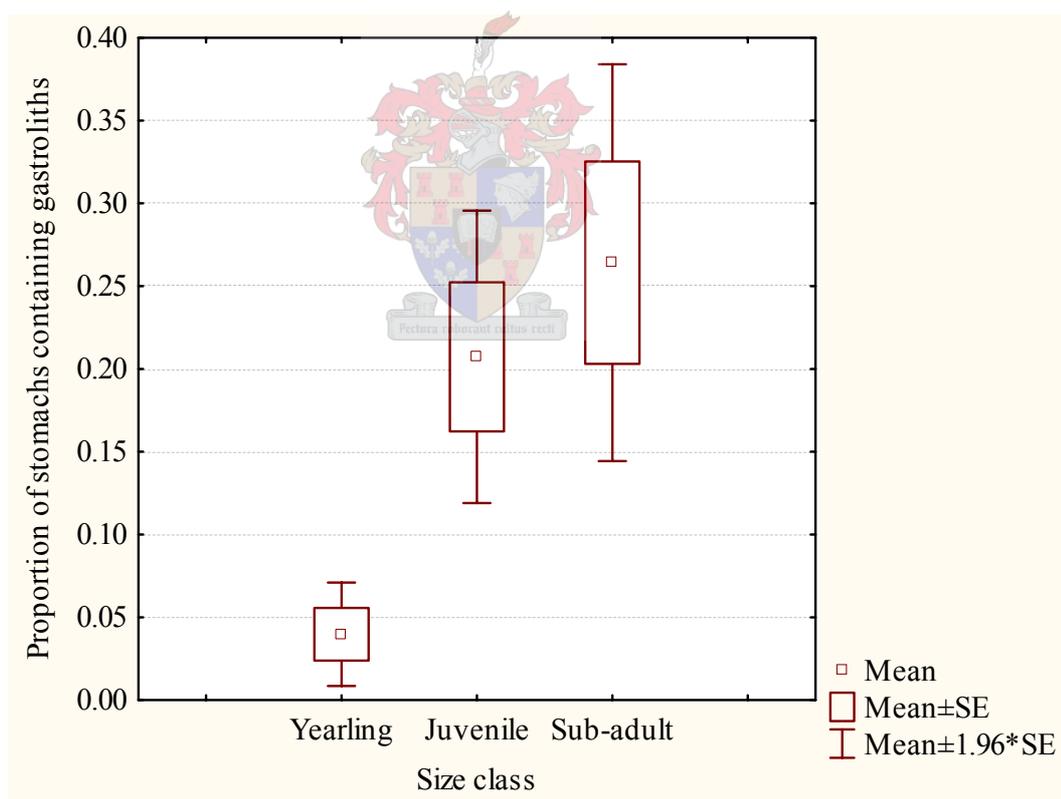


Figure 4.0 The proportion of all crocodile stomachs lavaged that contained gastroliths

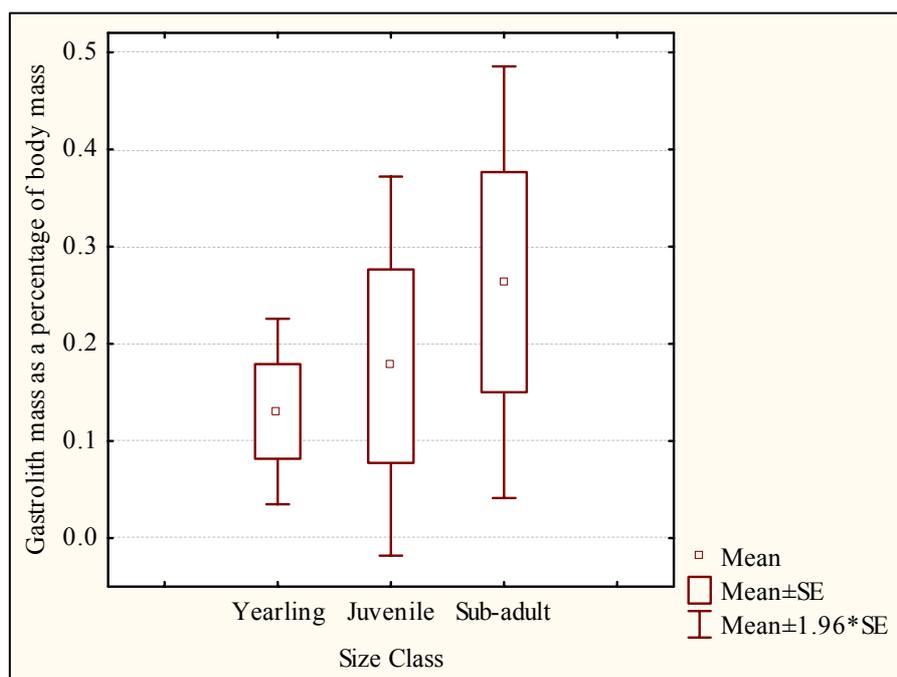


Figure 4.1 Gastrolith mass as a percentage of mean crocodile body mass for three size classes of crocodiles, namely: yearlings, juveniles and sub-adults.

Parasites

Although fresh stomach contents had slightly higher occurrence of parasites, no significant differences were found intra - or inter size class ($p > 0.05$) [Table 4.0]. Thirty-eight point four percent of yearling, 42.7 % of juvenile and 39.6 % of sub-adult stomachs that were lavaged yielded parasites. No parasites were recovered from stomachs that were devoid of any prey remnants.

Table 4.0 Occurrence of parasites in stomachs

Size class	% Occurrence		
	All stomachs	Fresh prey stomachs	Empty stomachs
Yearling	39.6	40.5	35.8
Juvenile	42.7	45.8	41.4
Sub-adult	38.4	50	37.2

A total of 466 parasites were identified (Table 4.1). *Dujardinascaris madagascariensis* was the most common species. The highest infestation in a juvenile crocodile consisted of 148 *D. madagascariensis* individuals.

Table 4.1 The species, total number and % occurrence of parasites found in stomach samples from three size classes of crocodiles (yearlings, juveniles and sub-adults).

Species	n	% occurrence
<i>Dujardinascaris madagascariensis</i>	437	93.8
Male	73	15.7
Female	364	78.1
<i>Dujardinascaris dujardini</i>	2	0.4
Male	1	0.2
Female	1	0.2
<i>Dujardinascaris sp.</i>	13	2.8
Female	13	2.8
<i>Gedoelestascaris vandenbrandeni</i>	1	0.2
Female	1	0.2
<i>Multicaecum agile</i>	3	0.6
Male	3	0.6
<i>Ascaridoidea</i>	8	1.7
<i>Eustrongylides sp.</i>	2	1.7
Male	1	0.9
Female	1	0.9

Vegetation

The occurrence of vegetable matter (primarily papyrus with grasses and seeds) in stomachs increased with crocodile size ($p < 0.01$). Seventeen point nine percent of yearling, 25.6 % of juvenile and 39.6 % of sub-adult stomachs contained vegetation (Figure 4.2). Vegetation constituted 0.08 % (± 0.02 S.E.) of yearling, 0.05 % (± 0.02 S.E.) of juvenile and 0.07 % (± 0.04 S.E.) of sub-adult body mass.

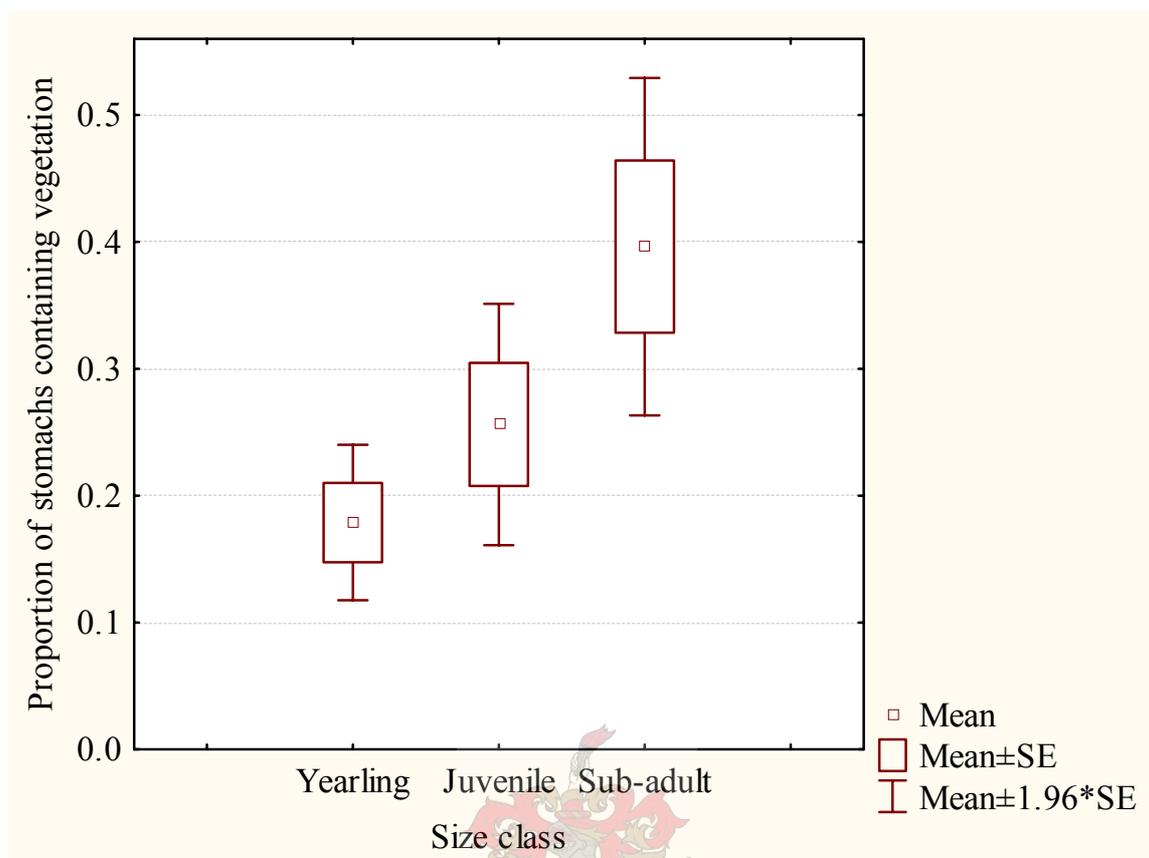
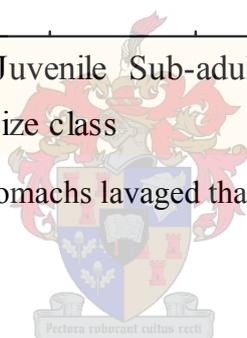


Figure 4.2 Proportion of all stomachs lavaged that contained vegetation



DISCUSSION

Gastroliths

All gastroliths recovered from stomachs were quartz, although one crocodile contained a single feldspar stone amongst other quartz stones. The porous nature of some of the quartz stones indicate that they may have formed within the stomach due to calcium precipitation from the bones of prey (pers. comm. Spicer, E. 2006).

Total 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 in other areas that have been found to contain stones that account for up to 1.0 % of the body mass (Brazaitis, 1969). Gastroliths occurred at a higher frequency within juvenile and sub-adults stomachs than yearlings. Data from this study indicates a relatively low occurrence of stomach gastroliths possibly due to the geology of the area. Stones in general are infrequently encountered in the Panhandle area (pers. obs.). 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 post-mortem analysis would have been a more effective technique for stone retrieval than the method used in this study. The fact that the relative mass of gastroliths remains constant throughout the size classes of crocodilians (no accumulation of gastroliths is seen in the larger crocodiles), discounts the opinion that gastroliths are as a result of accidental ingestion only.

Parasites

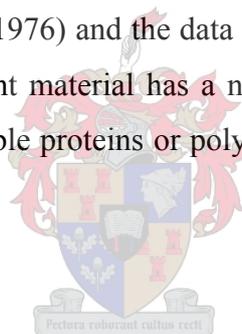
The parasitic load was evenly distributed throughout the samples with no significant correlation found between stomachs with fresh or old prey present, or between prey groups found in the stomachs ($p > 0.05$). However, parasites did occur slightly more frequently in stomachs containing fresh prey. The stomach lavage technique may not give an accurate estimate of parasitic load as embedded stomach and oesophageal parasites are not removed (Fitzgerald, 1989).

All parasites recovered from the crocodiles have previously been documented parasitizing crocodilians (Yamaguti, 1961). However, the identification of *D. dujardini*, *D.*

madagascariensis, *G. vandenbrandeni* and *Multicaecum agile* from the Okavango represents new geographical records (Junker *et al.* 2006). *Eustrongylides sp.* utilize oligochaetes then fish as intermediate hosts for an avian final host. As the specimens recovered were adults they were assumed to come from a bird (Measures, 1987). There have been occasional reports of *Eustrongylides sp.* from crocodilian hosts (Ladds and Sims, 1990). The crocodile stomach sample that contained the *Eustrongylides sp.* contained no bird remnants. The occurrence of parasites and the lack of any correlation to various prey items found in the stomachs indicated that the parasites may reside within the stomach for a considerable time period after the original host has been digested. Tucker *et al.* (1996) suggested that nematode burdens corresponded to the proportion of fish in the diet.

Vegetation

Plant remains increasing in frequency with crocodile size have been reported from several studies (Taylor, 1973; Blomberg 1976) and the data from this study shows the same trend. Taylor (1973) suggested that plant material has a nutritional value although crocodilians are unable to digest either vegetable proteins or polysaccharides (Coulson and Hernandez, 1983).



REFERENCES

- Andrews, P.L.R., Axelsson, M., Franklin C. and Holmgren, S. 2000. The emetic response in a reptile. *Journal of Experimental Biology*. 203: 1625 - 1632
- Ayarzaguena, S. J. 1983. Ecología del caiman de anteojos en los llanos de Apure Venezuela. *Donana Acta Vertebrata numero especial*. 10: 1 - 136
- Blomberg, G. E. D. 1976. Feeding and nesting ecology and habitat preferences of Okavango crocodiles. *Proceedings of the Symposium: Okavango Delta and its future utilisation*, Botswana Society, Gaborone, Botswana
- Brazaitis, P. 1969. The occurrence and ingestion of gastroliths in two captive crocodylians. *Herpetologica*. 25(1): 63 - 64
- Cott, H. B. 1961. Scientific results of an enquiry 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 - 356.
- Coulson, R.A. and T. Hernandez. 1983. Alligator metabolism, studies on chemical reactions in vivo. *Comparative Biochemistry and Physiology*. 74B: 1 - 182.
- Coulson, T. D., Coulson, R. A. and Hernandez, T. 1973. Some observations on the growth of captive alligators. *Zoologica*. 58: 47 - 52
- Davenport, J., Grove, D. J., Cannon, J., Ellis, T. R. and Stables, R. 1990. Food capture, appetite, digestion rate and efficiency in hatchling and juvenile *Crocodylus porosus*. *Journal of Zoology London*. 220: 569 - 592
- Diefenbach, C. O. Da C. 1975. Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia) - I. Rate of gastric digestion and gastric motility as a function of temperature. *Comparative Biochemistry and Physiology*. 51A: 259 - 265

- Fitzgerald, L. A. 1989. An evaluation of stomach flushing techniques for crocodylians. *Journal of Herpetology*. 23 (2): 170 - 172
- Foggin, C. M. 1987. Diseases and disease control on crocodile farms in Zimbabwe. pp. 351-362. In: Webb, G., C. Manolis, and P. Whitehead (Eds.). *Wildlife Management: Crocodiles and Alligators*. Surrey Beatty & Sons, Chipping Norton, NSW, Australia.
- Henderson, D.M. 2003. Effects of stomach stones on the buoyancy and equilibrium of a floating crocodylian: a computational analysis. *Canadian Journal of Zoology*. 81: 1346 - 1357
- Junker, K., Wallace, K., Leslie, A.J. and Boomker, J. 2006. Gastric nematodes of Nile crocodiles, *Crocodylus niloticus* Laurenti, 1768, from the Okavango River, Botswana. *Onderstepoort Journal of Veterinary Research*. 73: 111 - 114
- Ladds, P.W. and Sims, L.D. 1990. Diseases of young captive crocodiles in Papua New Guinea. *Australian Veterinary Journal*. 67: 323 - 330
- Leslie A. J., 1997. The ecology and physiology of the Nile crocodile, *Crocodylus niloticus*, in Lake St Lucia, Kwazulu/Natal, South Africa. Unpublished PhD Thesis, Drexel University, USA
- Measures, L.N. 1988. Epizootiology, pathology and description of *Eustrongyides tuifex* (Nematoda: Dicotophymatoidea) in fish. *Canadian Journal of Zoology*. 66: 2212 - 2222
- Pozio, E., Foggin, C. M., Marucci, G., La Rosa, G. Sacchi, L. Corona, S., Rossi, P., Mukaratirwa., 2002. *Trichinella zimbabwensis* n.sp. (Nematoda), a new non-encapsulated species from crocodiles (*Crocodylus niloticus*) in Zimbabwe also infecting mammals. *International Journal for Parasitology*. 32: 1787 - 1799

- Reed, C. C., Basson, L. and Van As, L. L. 2003. Myxozoans infecting the sharptooth catfish, *Clarias gariepinus* in the Okavango River and Delta, Botswana, including descriptions of two new Species, *Henneguya samochimensis* sp. n. and *Myxobolus gariepinus* sp. n. 2003. *Folia Parasitologica*. 50: 183 - 189
- Skoczylas, R. 1978. Physiology of the digestive tract. *In: Biology of the Reptilia* (Edited by Gans, C.), Vol. 8, pp 231 - 286. Academic Press, New York
- Sokol, O. M. 1971. Lithography and geophagy in reptiles. *Journal of Herpetology*. 5: 69 - 71
- Spicer, E. 2006. Department of Geology, University of Stellenbosch. Pers. Comm..
- Spletstoesser, J. and Todd, F. S. 1999. Stomach stones from emperor penguin *Aptenodytes forsteri* colonies in the Weddell Sea. *Marine Ornithology*. 27: 97 - 100.
- Sprent, J.F.A. 1977. Ascaridoid nematodes of amphibians and reptiles: *Dujardinascaris*. *Journal of Helminthology*. 51: 251 - 285
- Taylor, G. W. 1973. Nile crocodile in the Okavango Delta. A report on a wildlife population for Botswana Game Industries. pp 36 - 73.
- Taylor, M. A. 1993. Stomach stones for feeding or buoyancy? The occurrence and function of Gastroliths in marine tetrapods. *Philosophical Transactions of the Royal Society of London*. B. 341: 163 - 175
- Tucker, A. D., Limpus, C. J., McCallum, H. I. and McDonald, K. R. 1996. Ontogenetic dietary partitioning by *Crocodylus johnstoni* during the dry season. *Copeia*. 4: 978 - 988
- Yamaguti, S. 1961. The nematodes of vertebrates. Vol. 3, Part I and II. *In: Systema Helminthum*. New York, Interscience Publishers

CHAPTER 5

Digestion, nutrient assimilation and satiation level of the Nile crocodile, *Crocodylus niloticus*, in the Okavango Delta, Botswana.

INTRODUCTION

In crocodylians the rate of digestion is proportional to the metabolic rate (Coulson *et al.* 1990). Animals absorb the osmotically active particles at the rate at which they are released and this is primarily due to blood flow through the villi. The correlation of digestion to blood flow may explain why small animals (with a large relative mucosal area and high flow g^{-1}) digest food at a faster rate than larger animals (Coulson *et al.* 1990). In reptiles specifically, gastro-intestinal passage time (therefore also metabolic rate) increases with increasing temperature (Coulson *et al.* 1990; Kanui *et al.*, 1991).

Previous studies have used a number of gut transit measurements to estimate digestive efficiency in crocodylians. Gastro-intestinal residence time (GIRT) is the time taken for the first faeces to appear after a meal (Kanui, 1991). Gastric emptying time (GET) is the time recorded between the appearance of the first and last faeces (Davenport *et al.* 1992; Bromley, 1994). Total gut clearance time (TGCT) is the time recorded between the meal and the last faeces (Davenport, *et al.* 1992; Bromley, 1994). Gastric residence times are difficult to realise, as the bulk of a liquid meal, for example, may have left the stomach long before the last remnants do (Davenport, 1971) and prey species often have different gastric residence times (Jackson and Ryan, 1986; Games 1990; Barr 1997; Andersen, 2001). Also in their natural habitat, reptiles may not be able to maintain an optimum thermal temperature, therefore in the wild they may take longer to digest similar quantities of food.

Crocodyles in their natural environment may have more efficient digestive systems than crocodyles in captivity. This could be attributed to the fact that wild animals feed less frequently, therefore their physiological digestive and assimilation mechanisms may be more efficient than captive crocodyles that routinely have full stomachs (Webb *et al.* 1990). Webb *et al.* (1991) demonstrated that hatchling, *Crocodylus porosus*, fed daily, have lower conversion rates (28 %) when compared to those fed every two days (40 %).

The rate of assimilation of various nutritional elements from food is important, as this relates to the energy available for maintenance and production. This can be used to formulate an energy and nutritional budget for the crocodile (Garnett, 1988). *Crocodylus porosus* has a higher assimilation rate for long-chain polyunsaturated fatty acids (PUFAs) than saturated fatty acids, ranging from 100 % - 28 % respectively. *Caiman crocodilus* also has a requirement for 'marine' PUFAs which are probably provided by the crustacean component of the diet (Davenport, *et al.* 1992). This also suggests that ecological factors are most likely the result of differences in lipid metabolism amongst crocodylians rather than taxonomic patterns (Davenport, 1992). Up to 92 % of dietary protein is digested by *C. porosus*, but is adversely affected by high levels of dietary fat. Approximately 56.8 % of the ingested energy is stored and the remainder is utilised in digestion, assimilation and tissue maintenance (Garnett, 1988). Rates of assimilation for protein (97.4 %), energy (85.2 %) and dry mass (77.5 %) in *C. porosus* (Davenport *et al.* 1990) are higher than those found in the *C. crocodilus* (protein, 91.8 %, energy 68.2 % and dry mass 62.0 %). Assimilation of nutrients in *C. porosus* occurs not only in the small intestine, but also in the large intestine, and possibly also in the rectum (Davenport *et al.*, 1992). Digestibility of protein (87.3 - 89.2 %) and energy (84.6 - 86.8 %) by *Alligator mississippiensis*, decreased with an increase in calorific density of the diet and glucose supplementation of high-protein diets increased the rate of body mass gain (Staton *et al.* 1990).



Wild crocodylian nutritional studies are important due to the increasing importance of commercial crocodile and alligator farming. A nutritionally efficient feeding regime will help to maximize crocodile growth and has economic implications (Staton *et al.* 1990). The evacuation rates of prey are important to relate to feeding rate and consumption models, in order to gain an accurate understanding of the feeding ecology of crocodiles in their natural environment. This study examined the digestive and nutrient assimilation rates for wild caught crocodiles (under captive conditions) to compare to other studies that made use of only captive bred crocodiles.

METHODS

A shaded (90 % shade cloth) experimental area containing a cement pond was constructed with individual movable holding cages that allowed access to both water and a basking area. The holding cages incorporated a mesh floor that allowed faeces to fall through onto collection trays (Appendix 8). Nineteen crocodiles were caught from the Panhandle region of the Okavango Delta (Appendix 1), including eight yearlings (17.0 - 38.9 cm SVL), eight juveniles (39.0 - 66.3 cm SVL) and three sub-adults (66.4 - 115.8 cm SVL) [Leslie 1997]. Crocodiles were acclimated for two weeks prior to commencement of the study. The animals were fed chicken whilst acclimatizing and donkey meat during the experimental period. Minimum and maximum ambient temperatures were recorded daily throughout the study.

The experiment was divided into two phases:

Phase I: SATIATION LEVEL

The cages were angled so that crocodiles had access to both a dry basking area and enough water to completely submerge. Satiation level was determined by depriving the crocodiles of food for a period of three days, which is the minimum time estimated for most prey species to be digested and voided (Games, 1990; Barr, 1997). Pre-weighed food, at 5 % of total body mass, was initially offered to the crocodiles. Additional smaller portions were then offered on a feeding platform in the cage and the quantity of meat consumed was calculated and expressed as a percentage of crocodile body mass.

Phase II: GUT PASSAGE TIME (gastric passage and assimilation study).

Half the cage remained submerged until the crocodile had completed feeding. After twenty-four hours the cage was placed on a stand above the faecal collection tray. This allowed for a visual record and timing of first appearance of labelled and unlabelled faeces. The trays also allowed for collection of faeces for the nutrient assimilation rate analysis. Crocodiles were fed their satiation level (determined in Phase 1) in chromic-oxide (CR_2O_3) labelled food (2 % wet mass) from a feeding platform. Twenty-four hours post-feeding the minimum amount of time before the first faeces would be voided [Kanui, 1991], the cages were removed from the water for reasons explained above. The trays were checked and

cleaned every three hours. During this time, the crocodiles drank water from a hose to prevent dehydration.

Three gut passage measurements were recorded: (i) gastro-intestinal residence time (GIRT), ie: time after the meal to the first appearance of labelled faeces (Kanui, 1991); (ii) gastric evacuation time (GET), ie: time between appearance of first and last labelled faeces (Davenport *et al.* 1992); (iii) total gut clearance time (TGCT), ie: time between meal and last appearance of labelled faeces (Davenport *et al.* 1992).

This study was planned to ascertain the rates of gastric passage of the main natural prey items (determined in Chapter 3) and assimilation rates of dry mass, energy content (calories) and protein by the different size classes utilizing the ratio of chromic oxide in labelled food and faeces (Equation 1). However, due to unforeseen circumstances (mentioned below) the experiment was not completed.

Equation 1. Equation to ascertain percentage of nutrient uptake (Davenport *et al.* 1992)

$$\% \text{ Efficiency} = \frac{(\text{CR}_2\text{O}_3 : \text{nutrient in food})}{(\text{CR}_2\text{O}_3 : \text{nutrient in faeces})} \times 100$$

STATISTICAL ANALYSIS

Arcsine transformation was used on data converted to percentages and analysed using a one-way ANOVA. All statistical analyses were performed using Statsoft Inc (2005) Statistica version 7.1.

RESULTS

Satiation level decreased with an increase in crocodile size, from a mean of 11.3 % (± 1.6 S.E.) for yearlings, to 9.2 % (± 1.5 S.E.) for juveniles and 6.5 % (± 1.3 S.E.) for sub-adults. However, this decrease in satiation level was not significant ($p > 0.05$) (Figure 5.0). All crocodiles combined, averaged a mean satiation rate of 9.6 % (± 1.0 S.E.) of mean crocodile body mass.

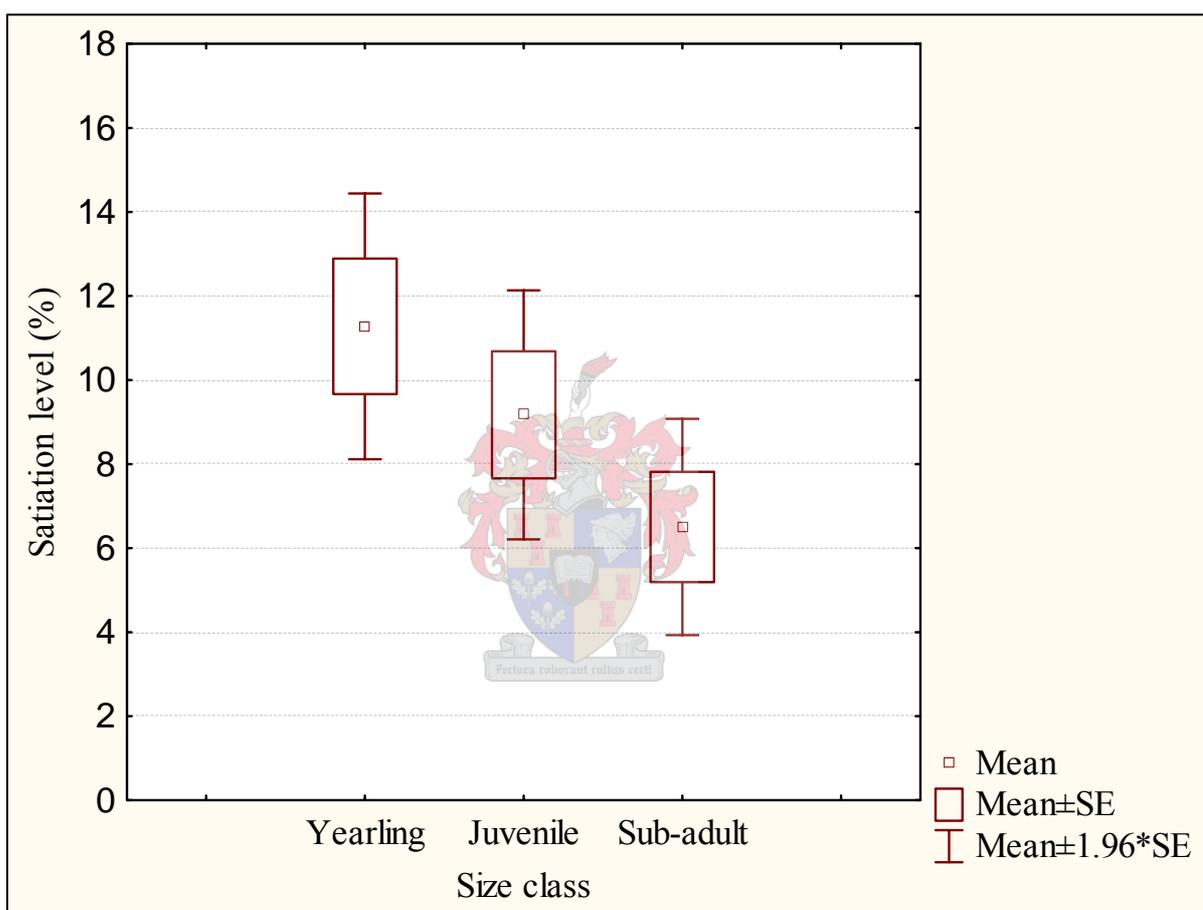


Figure 5.0 Mass of food consumed by crocodiles of various size classes (yearlings, juveniles and sub-adults) in a given time period, expressed as a percentage of total body mass (satiation level)

The GIRT did not differ significantly between the three size classes ($p > 0.05$). A mean GET of 62.8 hours (2.6 days) and mean TGCT of 103.5 hours (4.3 days) [Table 5] was ascertained for six of the eight juveniles. It should be noted that three of the six juveniles had also regurgitated food, possibly increasing gastric passage rate due to there being less food in the stomach (Ruggerone, 1989).

The experiment was unfortunately not completed. The first crocodile regurgitated food on day twenty-four of the study (including the fourteen day acclimation period). A total of seven crocodiles (three yearlings, two juveniles and two sub-adults) regurgitated food and loss of condition became visibly apparent. The experiment was therefore abandoned and the crocodiles released back into the wild at the original site of capture. The majority of faeces at the time of release were still chromic-oxide labelled, therefore GET and TGCT could not be ascertained for either the yearling or sub-adult size class (Table 5.0). Gastric passage time and rates of nutrient assimilation could also not be ascertained for the different prey types. At the time of release, six juveniles had defecated unlabelled faeces allowing calculation of the GET and TGCT.

Table 5.0 Digestive and satiation rates for the three size classes of crocodiles (\pm S.E.) Gastro-intestinal residence time (GIRT), gastric evacuation time (GET), total gut clearance time (TGCT) and satiation level. GIRT, GET and TGCT were calculated for the juveniles, but not for the yearlings and sub-adults due to too small a sample size.

Size class	n	Mean SVL (cm)	Mean mass (g)	GIRT (h)	GET (h)	TGCT (h)	Satiation (%)
Yearling	8	32 \pm 2.5	674.4 \pm 153	43.7 \pm 7.2	> 99	> 140	11.3 \pm 1.6
Juvenile	8*	47.6 \pm 3.6	2884.4 \pm 807.8	45.6 \pm 6.1	62.8 \pm 27.4	103.5 \pm 6.1	9.2 \pm 1.5
Sub-adult	3	96.3 \pm 3.9	20500 \pm 3329.2	39.6 \pm 4.6	> 99	> 140	6.5 \pm 2.3

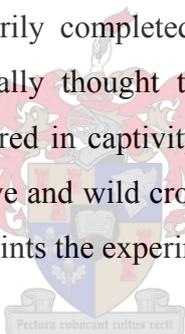
* n = 8 for satiation; n = 6 for GIRT, GET and TGCT

DISCUSSION

Satiation level for *C. niloticus* was higher than for *C. crocodilus* (Davenport *et al.* 1992) and similar to that of *C. porosus* (Davenport, 1990) for animals of a similar size. Satiation level decreased with an increase in crocodile size. Within crocodylians, metabolism decreases with an increase in size and a smaller percentage of body mass to prey is therefore required for tissue maintenance and growth (Coulson *et al.* 1973; Coulson and Hernandez, 1983).

The GIRT determined in this experiment was similar to that of captive bred *C. niloticus* (Kanui, 1991) and *C. porosus* (Garnett 1988). The GET and TGCT of the six juvenile Nile crocodiles exceeded that of *C. porosus* but was less than those of *C. niloticus* (Table 5.1.).

The experiment was not satisfactorily completed due to loss of animal condition and regurgitation of food. It was initially thought that the benefits of using wild caught crocodiles (as opposed to those reared in captivity) would provide more accurate gastric data, due to the differences in captive and wild crocodile digestive systems (Coulson *et al.* 1973). However, due to time constraints the experiment could not be repeated.



Initially the crocodiles showed signs of captive stress. They hissed or returned to the water and submerged when approached. The sub-adults also probed the cage walls and roof with the tip of the jaw, possibly searching for weaknesses in the wire frame. However, this behaviour ceased within two days. After an acclimation period of two weeks, all crocodiles appeared relaxed and could be approached by two staff members (only) with no adverse visible reaction from the animals. During the study, all crocodiles ate the food offered to them, basked in the sun and ignored the approach of the designated persons responsible for feeding. Excessive rainfall during the first five days of the study (152 mm) caused the crocodiles to either eat less or not to feed at all and the cooler temperatures presumably affected the digestive process (Coulson *et al.* 1973; Diefenbach, 1975a, b; Kanui *et al.* 1991). Water stress may also have been a contributing factor during phase two of the experiment when the cages were removed from the water and suspended above the faecal collection trays. However, crocodiles did not experience heat stress due to the shade cloth and rainfall and they eagerly drank from a hose during this time.

Table 5.1 Comparative digestive studies for *C. niloticus*, *C. porosus* and *Caiman crocodilus*.

Source	Species	TL (cm)	Mass (g)	Temp. (°C)	GIRT (h)	GET (h)	TGCT (h)	Satiation (% BWT)
This study Yearlings	<i>C. niloticus</i>	-	674.4	29	43.7	-	-	11.3
This study Juveniles	<i>C. niloticus</i>	-	2884.4	29	45.6	62.8	103.5	9.2
This study Sub-adults	<i>C. niloticus</i>	-	20500	29	39.6	-	-	6.5
Davenport <i>et. al.</i> (1992)	<i>C. crocodilus</i>	-	240 - 600	30	-	97	136	8
Kanui <i>et. al.</i> (1991)	<i>C. niloticus</i>	-	97.7 - 100.6	25 - 30	35 - 44	-	-	-
Davenport <i>et. al.</i> (1990)	<i>C. porosus</i>	-	79 - 233	30 ± 1	68	29	97	9 - 10
Garnett (1988)	<i>C. porosus</i>	-	257 - 522	30	34 - 50	24 - 36	84 - 96	-
Diefenbach (1975a)	<i>C. crocodilus</i>	30.5 - 96	-	15 - 30	-	-	85 - 290	-

The emetic response can be a mechanism for voiding indigestible food residues as well as ingested toxins, indicating that periodic vomiting may have a role in crocodilian feeding habits (Andrews, 2000). However, the vomiting witnessed during the study and subsequent loss of body condition was thought to have been brought on by captive stress (Lance and Elsey, 1999). The use of donkey meat may also have been a poor choice of food, as the digestive system of the crocodiles may not be accustomed to red meat in such large quantities as their natural diet indicates (Chapter 3). A number of stressors have been identified (Huchzermeyer, 2003). In particular, handling and captivity can be a major cause of stress (Lance and Elsey 1999).

As natural prey was not initially fed to the crocodiles, nutritional supplements could perhaps have been added to the food (Huchzermeyer, 2003). A sufficient supply of natural prey items proved difficult to accumulate. Chicken and donkey meat was available and this was fed to the animals whilst an attempt was made at acquiring natural prey items. However, this attempt failed.

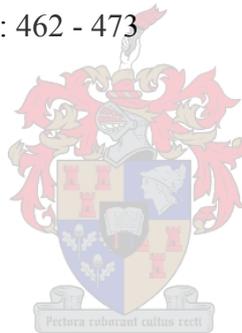
It is recommended that future studies that attempt a similar experiment should either use captive crocodilians, as they will be less prone to stress, or a longer acclimation period with natural prey as food and nutritional supplements. The results for the GIRT for the six juveniles (although possibly biased due to the aforementioned factors) do show a similar trend to that of captive *C. niloticus* (Kanui, *et al.* 1991) and *C. porosus* (Garnett, 1988). However, the time period is less than for *C. porosus* in the study by Davenport *et al.* (1990) and so it was therefore difficult to draw any definite conclusions.

REFERENCES

- Andersen, N.G. 2001. A gastric evacuation model for three predatory gadoids and implications of using pooled field data of stomach contents to estimate food rations. *Journal of Fish Biology*. 59: 1198 - 1217
- Andrews, P.L.R., Axelsson, M., Franklin C. and Holmgren, S. 2000. The emetic response in a reptile. *Journal of Experimental Biology*. 203: 1625 - 1632
- Barr, B. 1997. Food habits of the American alligator, *Alligator mississippiensis*, in the Southern Everglades. Unpublished PhD Thesis, University of Miami, Florida
- Bromley, P.J. 1994. The role of gastric evacuation experiments in quantifying the feeding Rates of predatory fish. *Reviews in Fish Biology and Fisheries*. 4: 36 - 66
- Coulson, R.A. and Hernandez T. 1983. Alligator metabolism, studies on chemical reactions in vivo. 74B: 1 - 182
- Coulson, T. D., Coulson, R. A. and Hernandez, T. 1973. Some observations on the growth of captive alligators. *Zoologica*. 58: 47 - 52
- Coulson, R. A., Coulson, T. D. and Herbert, J. D. 1990. How do digestion and assimilation rates in alligators vary with temperature? *Comparative Biochemistry and Physiology*. 96A: 4: 441 - 449
- Davenport, H. W. 1971. *Physiology of the digestive tract*, 3rd Ed. Year book Medical Publishers, Chicago
- Davenport, J., Andrews T. J. and Hudson G. (1992). Assimilation of energy, protein and fatty acids by the Spectacled Caiman, *Caiman crocodilus crocodilus* L. *Herpetological Journal*. 2: 72 - 76

- Davenport, J., Grove, D. J., Cannon, J., Ellis, T. R. and Stables, R. 1990. Food capture, appetite, digestion rate and efficiency in hatchling and juvenile *Crocodylus porosus*. *Journal of Zoology London*. 220: 569 - 592
- Diefenbach, C. O Da C. 1975a. Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia) - I. Rate of gastric digestion and gastric motility as a function of temperature. *Comparative Biochemistry and Physiology*. 51A: 259 - 265
- Diefenbach, C. O Da C. 1975b. Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia) - II. Effects of temperature on pH and proteolysis. *Comparative Biochemistry and Physiology*. 51A: 267 - 274
- Games, I. 1990. The feeding ecology of two Nile crocodile populations in the Zambezi valley. Published PhD Thesis, University of Zimbabwe
- Garnett, S.T. 1988. Digestion, assimilation and metabolism of captive estuarine crocodiles, *Crocodylus porosus*. *Comparative Biochemistry and Physiology*. 90A: 23 - 29
- Huchzermeyer, F.W. 2003 *In: Crocodiles, biology, husbandry and diseases*. CABI Publishing. CAB International, Wallingford, U.K.
- Jackson, S. and Ryan P.G. 1986. Differential digestion rates of prey by White-chinned Petrels (*Procellaria aequinoctialis*). *Auk*. 103: 617 - 619
- Kanui, T., Mwendia. C., Aulie, A. and Wanyoike, M. 1991. Effects of temperature on growth, food uptake and retention time of juvenile Nile crocodiles (*Crocodylus niloticus*). *Comparative Biochemistry and Physiology*. 99A: 3: 453 - 456
- Lance, V.A. and Elsey, R.M. 1999. Plasma catecholamines and plasma corticosterone following restraint stress in juvenile alligators. *Journal of experimental Zoology*. 283: 559 - 565
- Leslie A. J., 1997. The ecology and physiology of the Nile crocodile, *Crocodylus niloticus*, in Lake St Lucia, Kwazulu/Natal, South Africa. Unpublished PhD Thesis, Drexel University, USA

- Ruggerone, G. T., 1989. Gastric evacuation rates and daily ration of piscivorous coho salmon, *Oncorhynchus Kisutch* Walbaum. *Journal of Fish Biology*. 34: 451 - 463
- Staton, M.A., H.M. Edwards, I.L. Brisbin, L. McNease, and T. Joanen. 1990. Dietary energy-sources for the American alligator, *Alligator mississippiensis* (Daudin). *Aquaculture*. 89(3-4): 245 - 261
- Webb, G. J. W. and Cooper-Preston, H. 1990. Crocodile management and research in the Northern Territory: 1988-90. Proc. 10th Working Meeting IUCN-SSC Crocodile Specialist Group, Gainesville, Florida, April 1990, pp. 253 - 273. IUCN Publ., Gland, Switzerland
- Webb, G. J. W., Hollis, G. J. and Manolis, S. C. 1991. Feeding, growth, and food conversion rates of wild juvenile Saltwater crocodiles (*Crocodylus porosus*). *Journal of Herpetology*. 25: 462 - 473



CHAPTER 6

Daily food intake and conversion rates of wild Nile crocodiles, *Crocodylus niloticus*, in the Okavango Delta, Botswana

INTRODUCTION

A fundamental concept of understanding the ecology of an animal is knowledge of their dietary habits (Rosenburg and Cooper, 1990), which within crocodilians affects growth, behaviour and reproduction (Lang, 1987). However to fully utilize such data, it is important to relate this to the rate of predation. In particular, if this can be used in the context of predator population and prey abundance and more so if the prey has commercial value, such as Tilapia fish in the Okavango Delta. Understanding the rate of food conversion is important as crocodiles may have evolved a lifestyle allowing extended periods of digestive quiescence and tissue maintenance is an important component of the daily energy expenditure (Secor, 2001).

Food consumption represents the energy source for growth and metabolism (Hofer *et al.* 1982). Knowledge of food consumption is important in determining the extent of predation and competition among species, proving valuable data for conservation plans (Daan, 1973). Models to predict this require the type and amounts of food consumed by the predator.

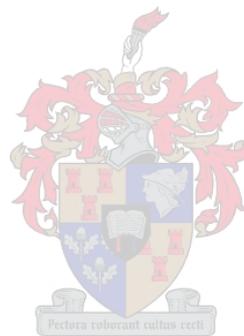
Stomach content data must be carefully interpreted due to different rates of prey evacuation and diurnal feeding habits of the predator (Jackson and Ryan, 1986; Games, 1990; Barr, 1997; Andersen, 2001). It is more complex to derive evacuation rate data for aquatic species, unlike terrestrial species, where continuous observation is not possible. Captive experiments using crocodilians (Games, 1990; Barr, 1997) do shed some light on evacuation rates but are inherently biased due to either captive stress on wild animals or the difference between captive bred versus wild animal digestion rates (Games, 1990; Webb *et al.* 1991). Fishery management studies have devised models that can be utilized to derive field evacuation rates of prey using stomach content analysis (Anderson, 2001; Rindorf, 2004; Richter *et al.* 2004). Once accurate field evacuation rates are obtained,

these can be combined in models with the stomach content data to derive a daily feed intake (DFI) of specific prey for a predator.

Stomach content modelling can be categorized into: (i) evacuation models, used to determine evacuation rates under controlled conditions and (ii) consumption models, which apply these evacuation rates to field data to estimate food consumption (Richter *et al.* 2004). Although there are a number of models available, combinations between stomach evacuation and food consumption models are mathematically problematic (Richter *et al.* 2004). A model to predict daily feeding that includes empty stomachs (when the length of time since the last feeding took place is unknown) will be biased due to prey having different gastric evacuation relationships (Bromley, 1994). However, the empty stomachs should not be omitted, as this may lead to a bias that omitted animals simply have the fastest evacuation rates (Bromley, 1994), either due to factors concerning the predator or the prey gastric residence time and should be considered as part of the feeding population (Diana, 1979). Recent fishery related studies have presented complex models to estimate field gastric evacuation rates and feeding frequencies, utilizing only stomachs with fresh prey items present (Anderson, 2001; Rindorf, 2004; Richter *et al.* 2004).

An important factor in the analysis of feeding rates is the quantification of differential prey evacuation rates (Bromley, 1994). Games (1990) performed a study using both wild caught and captive bred *C. niloticus* and Barr (1997) utilised wild caught *Alligator mississippiensis* in a laboratory controlled simulated natural environment to analyse stomach clearance rates of different prey items. Games (1990) estimated feeding rates using the model from Diana's (1979) study on fish, based on the proportion of empty stomachs within the sample, gastric residence time and a correction factor for small mammals. Webb *et al.* (1991) estimated daily feeding rates of juvenile *Crocodylus porosus* from stomach contents and incorporated a correction factor based on the probability of finding fresh small mammals, as infrequently eaten small mammals (a large prey item when the predator body mass is taken into consideration) can have a significant influence on the amount of prey eaten on a daily basis. Under controlled conditions, infrequently fed crocodiles had a higher conversion rate than those fed daily (Webb *et al.* 1991). This indicates that wild crocodilians that forage for prey should have higher conversion rates than those animals that are fed regularly on crocodile farms.

This study examined the relationship between crocodile size and daily food intake (DFI), using a model that examined gastric evacuation time and the proportion of fresh and old prey remnants recovered from stomachs. The estimated conversion rates indicated only the amount of wet prey mass utilized as wet mass gain by the crocodile, as different nutritional components have different rates of uptake within the body (Lance *et al.* 1983). Crocodile farms are an important source of economic wealth (Thorbjarnarson, 1999) and maximizing growth with an optimal feeding regime is vitally important. The amount of wet mass of prey converted to body tissue was estimated using the DFI and daily mass gain of the crocodile.



METHODS

Crocodile capture and stomach content retrieval

From August 2003 to August 2005, 286 crocodiles were captured and stomach lavaged. The animals were allocated to one of three size classes based on snout-to-vent length (SVL): yearlings (17.0 - 38.9 cm SVL), juveniles (39.0 - 66.3 cm SVL) and sub-adults (66.4 - 115.8 cm SVL) [Leslie 1997]. Seven adult (> 115.9 cm SVL) crocodiles were also processed but due to the small sample size they were included within the sub-adult group. Crocodiles were caught from a boat at night either by hand or noose using a spotlight. Three larger individuals were caught in box traps (Appendix 1). Animals were 'processed' immediately (Appendix 2) at the site of capture and subsequently released. Stomach samples were obtained using a modification of the technique originally devised by Ayarzagüena (1983) and modified and evaluated by Fitzgerald (1989), namely the hose-heimlich technique, which utilizes a water pump to flush out stomach contents (Appendix 3).

Stomach content analysis

Fresh prey items (ingested < 24 h of capture) (Appendix 4), were separated into six broad categories (insecta, crustacea, amphibia, rodentia, teleosti and squamata) based on differential gastric evacuation time (Games, 1990; Barr, 1997). The original mass of the prey items were estimated using museum collections and field data (Appendix 6).

Feeding frequency was calculated for each prey category for the yearling, juvenile and sub-adult size classes using an equation utilizing the proportion of empty stomachs (Equation 6.1, Diana 1979) and gastric evacuation time estimated from data from Games (1990) and Barr (1997). The model was slightly altered so that only stomachs that contained fresh prey (55.6 % of the sample for yearlings; 29.3 % of juveniles and 18.9 % of sub-adults) were included in an attempt to eliminate bias from stomachs that had been empty for at least a day (Bromley, 1994). Results were corrected using a formula to estimate the probability of finding a specific prey category within the entire sample (Equation 6.2, Games 1990). The larger the proportion of empty stomachs in the sample, the larger the potential error. Daily food intake (DFI) was estimated using Equation 6.3 (Diana, 1979).

Equation 6.1 Feeding frequency model equation (adapted from Diana, 1979)

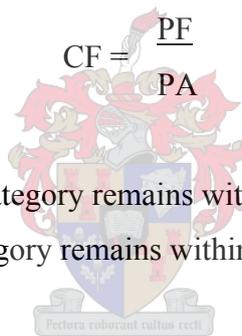
$$F = \frac{B}{(S / N)}$$

- F = Feeding frequency (days)
 B = Gastric evacuation time (days)
 S = # of crocodiles with fresh prey from a prey category (i.e. insecta, etc.)
 N = # of crocodile stomachs that contained any fresh prey remnants

Equation 6.2 Correction factor for probability of finding a fresh prey category item within the whole sample (adapted from Games, 1990)

$$CF = \frac{PF}{PA}$$

- PF = Proportion of fresh prey category remains within all stomachs containing fresh prey
 PA = Proportion of all prey category remains within the entire sample of stomachs (fresh and old)



Equation 6.3 Daily food intake (DFI) based on Diana's equation (1979)

$$DFI (g) = \frac{\text{Mean meal size (g)}}{\text{Feeding frequency (days)}}$$

Mark-recapture technique to estimate daily mass gain

Crocodiles were marked using a scute removal system developed by Leslie (1997). This allowed the identification of crocodiles that were recaptured at a later date. Measurements from recaptured crocodiles were used to estimate the daily mass gain (Equation 6.4). Daily mass gain was combined with DFI to estimate the amount of food converted to crocodile

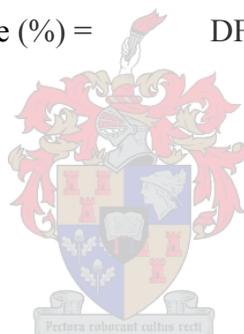
mass (Equation 6.5). Conversion rates were calculated for the yearling and juvenile size classes only, as there was insufficient recapture data for sub-adults to predict daily mass gain.

Equation 6.4 Mass gain equation (Haenel and John-Alder, 2002)

$$\text{Mass gain (g d}^{-1}\text{)} = \frac{\text{Mass (g) (later census)} - \text{Mass (g) (earlier census)}}{\text{Time elapsed (days)}}$$

Equation 6.5 Conversion rate equation (Games, 1990; Webb *et al.* 1991)

$$\text{Conversion rate (\%)} = \frac{\text{Mass gain (g d}^{-1}\text{)}}{\text{DFI (g)}}$$



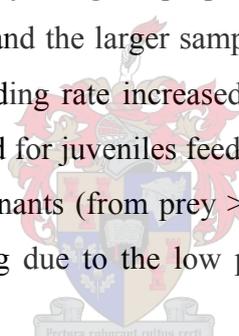
STATISTICAL ANALYSIS

A Maximum likelihood chi squared test was used for the ranked occurrence data and a Kruskal-Wallis analysis of variance by ranks, for non-normally distributed composition mass data. Arcsine transformation was used on data converted to percentages and analysed using a one-way ANOVA. All statistical analyses were performed using Statsoft Inc (2005) Statistica version 7.1.

RESULTS

Within all size classes there was no significant difference ($p > 0.05$) between the occurrence of a single prey item in a stomach and stomachs that contained 2 or more recently ingested prey items. Prey items were also found in various stages of digestion indicating that the feeding interval was not always longer than the digestion time but that feeding was asynchronous.

The DFI varies both between size classes and prey type. Table 6.0 shows the importance of the different prey groups between size classes utilizing a model based on the proportion of stomachs containing fresh prey items and the gastric evacuation time of prey categories. The DFI (Table 6.0) indicates the daily food intake by those animals that had fed within the previous twenty-four hours. This was then adjusted to estimate the corrected daily feeding rate of the entire sample, by using the proportion of fresh remains in stomachs that contained fresh prey items only, and the larger sample that contained old remnants of that prey category. The corrected feeding rate increased the rate of predation for insects and arachnids for both size classes and for juveniles feeding on fish and crustaceans, due to the high proportion of prey item remnants (from prey > 24 hours). The other prey categories showed a reduced rate of feeding due to the low proportion of the older prey category remnants recovered.



Yearlings

Small mammals were eaten every 10.8 days providing the highest DFI (1.55 g d^{-1}) and 0.3 % of mean crocodile mass (Table 6). Insects and arachnids were the most commonly predated prey item, consumed every 2.2 and 2.6 days respectively. Combined, these prey items provided 0.67 g d^{-1} . Fish and amphibians were consumed every 25.2 days contributing 0.8 and 0.9 g d^{-1} respectively. Insects, arachnids, amphibians and small mammals were predated more often by yearlings than juveniles and the dietary mass per day was greater with the exception of the arachnid prey mass. Seventy five point one percent ($\pm 4.4 \text{ S.E.}$) of the dietary mass consisted of invertebrates that contained chitinous structures.

Juveniles

Juveniles consumed fish every 11.7 days which provided the highest DFI at 1.33 g d^{-1} . This constituted 0.06 % of the crocodile body mass (Table 6). Amphibians and snakes were infrequently predated upon and contributed the lowest daily prey mass intake of 0.08 g d^{-1} per day. Insects and arachnids were predated every 2.3 - 2.5 days respectively, together providing 0.29 g d^{-1} . Crustaceans were predated every 6.6 days and provided 0.48 g d^{-1} . Fish were predated upon at a higher rate by juveniles than yearlings, and juveniles were the only class that predated on crustaceans (fresh water crab) and squamata (an unidentified snake). Sixty point one percent ($\pm 9.3 \text{ S.E.}$) of the dietary mass consisted of invertebrates that contain chitinous structures.

Sub-adults

The estimated DFI for the sub-adult class was lower than that for the juvenile size class, at 4.8 g per day. Fish were the primary source of food providing 92 % of the daily dietary intake. Unfortunately there was insufficient recapture data to estimate the rate of food conversion.

Conversion rates

The corrected DFI for the various prey categories for each size class was combined and compared to daily crocodile mass gain to estimate the conversion rate of prey mass to crocodile body mass (Table 6.1). Yearlings gained 0.8 g per day and juveniles 2.1 g per day over the course of an entire year (recapture intervals spanned a mean of 290 and 485 days respectively). The conversion rate was higher for juveniles (39.9 %) than yearlings (32.0 %) and the percentage of crocodile body mass consumed to prey mass decreased with an increase in crocodile mass.

Table 6.0 Prey mass and daily food intake (DFI) for two size classes of crocodile based on differing rates of gastric evacuation.

Yearlings: n fresh = 84, mean SVL 30 ± 0.5 cm, mean mass 495.7 ± 29 g

Juveniles: n fresh = 24, mean SVL 47.3 ± 5 cm, mean mass 2307.9 ± 294.2 g

Sub-adults: n fresh = 10, mean SVL 84.17 ± 3.3 cm, mean mass 16800 ± 1819.9 g

Prey	Size class	Gastric evac. (days)	Feed. freq. (days)	Mean prey mass (g)	DFI (g / d ⁻¹)	CF	Corr.	Corr.
							feed. freq. (days)	DFI (g / d ⁻¹)
INSECTA	Yearling	2	3.5	1.3	0.4	0.7	2.2	0.6
	Juvenile	2	4.4	3.1	0.70	0.5	2.3	1.3
	Sub-adult	2	10	0.9	0.09	0.3	3.0	0.30
ARACHNIDA	Yearling	1	1.8	0.3	0.15	1.5	2.6	0.10
	Juvenile	1	2.4	0.2	0.09	2.4	5.9	0.04
	Sub-adult	1	10	0.2	0.02	0.3	3.1	0.06
CRUSTACEA	Yearling	2	0	0.0	0.00	0	0	0
	Juvenile	2	24	11.5	0.48	0.3	6.56	1.75
	Sub-adult	2	0	0	0	0	0	0
MAMMALIA	Yearling	3	84	16.7	0.2	0.1	10.8	1.54
	Juvenile	3	72	15.0	0.21	0.3	18.9	0.79
	Sub-adult	3	30	15	0.5	5.3	159	0.09
TELEOSTI	Yearling	2	18.7	2.1	0.11	1.3	25.2	0.08
	Juvenile	2	16	15.6	0.98	0.7	11.7	1.3
	Sub-adult	2	2.5	14.2	5.7	1.3	3.2	4.4
AMPHIBIA	Yearling	1	14	2.3	0.17	1.8	25.2	0.09
	Juvenile	1	24	1.2	0.05	3.4	82	0.01
	Sub-adult	1	0	0	0	0	0	0
SQUAMATA	Yearling	2	0	0.0	0.00	0	0	0
	Juvenile	2	48	6.0	0.13	3.4	164	0.04
	Sub-adult	2	0	0	0	0	0	0

Gastric evac.	Time taken for prey to be digested to 10 % of the original mass
Feed. freq.	Uncorrected feeding frequency (Equation 6.1)
Mean prey mass.	Mean wet mass of prey consumed
DFI.	Uncorrected daily food intake (Equation 6.3)
CF.	Correction factor (Equation 6.2)
Corr. feed. freq.	Feeding frequency multiplied by the correction factor (Equation 6.1)
Corr. DFI	DFI (Equation 6.3) based on corrected feeding frequency

Table 6.1 Mean (\pm S.E.) conversion rates for yearlings and juveniles based on recapture data and DFI

Size class	n	Mean crocodile mass (g)	Mean recapture interval (days)	Mean mass increase (g / d ⁻¹)	DFI (g / d ⁻¹)	Mean conversion (%)	% of body mass consumed
Yearling	103	415 \pm 28.1	290 \pm 268.4	0.8 \pm 0.1	2.39	32	0.48
Juvenile	8	2237 \pm 284.8	485 \pm 282.7	2.1 \pm 1	5.3	39.9	0.23
Sub-adult*	10	16800 \pm 1819.9	-	-	4.8	-	0.03

* Insufficient recapture data to estimate daily growth rates and mean conversion percentage

Mean conversion	DFI converted to crocodile wet mass (Equation 6.5)
% of body mass consumed	DFI expressed as a percentage of crocodile mass

DISCUSSION

Carnivorous reptiles can digest between 80 and 90 % of the prey items they consume (Bennett and Dawson, 1976; Skoczylas, 1978; Harwood, 1979). The low conversion rate for yearling (32 %) and juvenile (39.9 %) crocodiles may be due to the diet containing a high percentage of invertebrate prey that contains an indigestible portion (75.1 % and 60.1 % respectively). Crustaceans and insects have chitin based structures such as an exoskeleton and crocodilians are unable to digest chitin (Neill, 1971; Jackson *et al.*, 1974; Garnett, 1985). It has been suggested that the emetic response can be a mechanism for disposing of indigestible food residues as well as a protective reflex to eject toxins accidentally ingested with food. Therefore, periodic vomiting may have a role in crocodilian feeding habits (Andrews *et al.* 2000). Due to the indigestible portion of some prey items, a smaller fraction of the total wet mass is available for digestion and conversion to body tissue. If this were taken into account by analyzing only the digestible portion of the prey, the conversion rates may be higher due to the digestible portion of the prey being smaller than the mass of the entire prey animal.

Two studies have estimated conversion rates utilizing wet mass of food intake to wet crocodile mass gain. Games (1990) estimated wild conversion rates of between 62.2 - 64.1 % for juvenile *C. niloticus* and Webb *et al.* (1991) calculated a conversion rate of 82.4 % for juvenile *C. porosus*. Both the natural diets in these studies contained prey with an indigestible portion (insects, crustacean and small mammals). This therefore insinuates that the conversion rates (taking into account that the digestible mass of the diet is lower) may exceed those estimates.

Relatively infrequently eaten larger prey items such as small mammals can significantly influence the DFI estimate. One crocodile (1050 g body mass) when caught had a rat (120 g) in its jaws which would have accounted for 11.4 % of the crocodiles body mass had it been consumed. Webb *et al.* (1991) derived a formula to predict the mean rat mass intake corresponding to crocodile mass and Games (1990) utilized a correction factor based on the probability of finding a fresh small mammal. In the stomach, prey with a rapid gastric digestion rate, such as amphibians and fish, may have been underestimated as there was a higher probability that evidence of the prey would be absent from the stomach. The use of a correction factor is therefore important when analyzing stomach content data

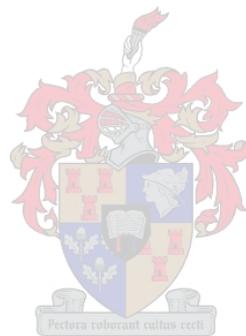
to estimate the DFI, especially when empty stomachs (animals that have not eaten for at least twenty-four hours) are included within the model (Richter, *et al.* 2004). Another aspect is that a fundamental variable, gastric residence time, not only varies between broad prey categories but also between species (Barr, 1997) and in turn is affected by numerous other variables such as size of the predator relative to the prey (Coulson and Hernandez, 1983), seasonal and diurnal temperature fluctuations (Diefenbach, 1975a; Andersen, 2001; Rindorf, 2004), prey surface area (Diefenbach, 1975b) and the quantity of additional prey eaten (Ruggerone, 1989).

Seasonal factors were not taken into consideration due to no significant difference in diet for yearlings ($p > 0.05$), although juvenile diet did differ with season ($p < 0.05$), but the sample size for winter prevented an accurate comparison. The results presented here represent an estimate of the DFI for two of the smaller size classes of wild crocodiles in the Okavango Delta. The analysis may have been affected by the aforementioned factors and the estimates should thus be viewed as the minimum rates of predation and food conversion.

The low daily food intake for the sub-adults was an unusual finding and could be due to the low number of individuals found with fresh prey items, and so the DFI estimate may not be a true representation. As the rate of digestion for fish is rapid (Games, 1990; Barr, 1997) a large sample size is needed for an accurate estimation of the DFI. For future studies it would be interesting to compare the sub-adult conversion rate to those of the smaller size classes, as these animals would have a minimum amount of prey that contains chitin, therefore they may show a much higher rate of food conversion.

The two main assumptions of the model (Diana, 1979) were that feeding was asynchronous and that the time between meals was longer than the digestion time. Prey items were found in various stages of digestion supporting the first assumption of the model. However, errors may have occurred with the second assumption, as there was no significant difference found between stomachs containing a single freshly ingested prey item and those that contained two or more prey items. This may have caused a certain bias with regards to the predicted feeding rates. Errors may also have arisen with the identification of prey items that were ingested within twenty-four hours, as the rate of digestion varies with species (Barr, 1997) and the reference series used was from different species than that

found in this study. The magnitude of error was difficult to evaluate but should be considered in future studies. A study by Medved *et al.* (1988) estimated the food ration of sharks using two different approaches, namely Diana's (1979) model and Winberg's (1956) bioenergetics approach, and found them both to give similar estimates.



REFERENCES

- Andersen, N.G. 2001. A gastric evacuation model for three predatory gadoids and implications of using pooled field data of stomach contents to estimate food rations. *Journal of Fish Biology*. 59: 1198 - 1217
- Andrews, P.L.R., Axelsson, M., Franklin C. and Holmgren, S. 2000. The emetic response in a reptile. *Journal of Experimental Biology*. 203: 1625 - 1632
- Ayarzaguena, S. J. 1983. Ecología del caiman de anteojos en los llanos de Apure Venezuela. *Donana Acta Vertebrata numero especial*. 10: 1 - 136
- Barr, B. 1997. Food habits of the American alligator, *Alligator mississippiensis*, in the Southern Everglades. Unpublished PhD Thesis. University of Miami
- Bennett, A. F. and W. R. Dawson. 1976. Metabolism. Pp.127-233. In C. Gans and W. R. Dawson (Eds.), *Biology of the Reptilia*, Vol. 5. Academic Press, New York, New York.
- Bromley, P.J. 1994. The role of gastric evacuation experiments in quantifying the Feeding rates of predatory fish. *Reviews in Fish Biology and Fisheries*, 4: 36 - 66
- Coulson, R.A. and Hernandez T. 1983. Alligator metabolism, studies on chemical reactions in vivo. *Comparative Biochemistry and Physiology*. 74B: 1 - 182.
- Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. *Netherland Journal of Research*. 6: 479 - 517
- Diana, J. S. 1979. The feeding pattern and daily ration of a top carnivore, the northern pike (*Esox lucius*). *Canadian Journal of Zoology*. 57: 212 1- 2127
- Diefenbach, C. O Da C. 1975a. Gastric function in *Caiman crocodilus* (Crocodylia:Reptilia) - I. Rate of gastric digestion and gastric motility as a function of temperature. *Comparative Biochemistry and Physiology*. 51A: 259 - 265.

- Diefenbach, C. O. Da C. 1975b. Gastric function in *Caiman crocodilus* (Crocodylia:Reptilia) - II. Effects of temperature on pH and proteolysis. *Comparative Biochemistry and Physiology*. 51A: 267 - 274.
- Fitzgerald, L. A. 1989. An evaluation of stomach flushing techniques for crocodylians. *Journal of Herpetology*. 23 (2): 170 - 172
- Games, I. 1990. The feeding ecology of two Nile crocodile populations in the Zambezi valley. Unpublished PhD Thesis, University of Zimbabwe
- Garnett, S. T. 1985. The consequences of slow chitin digestion on crocodylian diet analyses. *Journal of Herpetology*. 19: 303 - 304
- Haenel, G. J. and John-Alder, H. B. 2002. Experimental and demographic analyses of growth rate and sexual size dimorphism in a lizard, *Sceloporus undulatus*. *OIKOS* 96: 70 - 81
- Harwood, R. H. 1979. The effect of temperature on digestive efficiency of three species of lizards, *Cnemidophorus tigris*, *Gerrhonotus multicaratus* and *Sceloporus occidentalis*. *Comparative Biochemistry and Physiology*. 63A: 417 - 433
- Hofer, R., Forstner, H. and Rettenwander, R. 1982. Duration of gut passage and its dependence on temperature and food consumption in roach, *Rutilus rutilus* L.: Laboratory and field experiments. *Journal of Fish Biology*. 20: 289 - 299
- Jackson, J. F., Campbell, H. W. & Campbell, K. E. 1974. The feeding habits of crocodylians: validity of the evidence from stomach contents. *Journal of Herpetology*. 8: 378 - 381
- Jackson, S. and Ryan P.G. 1986. Differential digestion rates of prey by White-chinned Petrels (*Procellaria aequinoctialis*). *Auk*. 103: 617 - 619

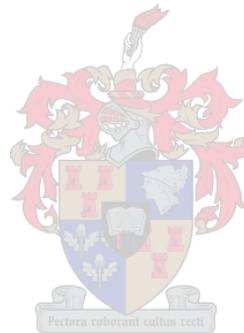
- Lance, V A., Joanen, T. and McNease, L. 1983. Selenium, vitamin E, and trace elements in the plasma of wild and farm-reared alligators during the reproductive cycle. *Canadian Journal of Zoology*. 61: 1744 - 1751.
- Lang, J. 1987. Crocodylian thermal selection, pp. 301-317. In: G.J.W. Webb, S.C. Manolis and P.J. Whitehead (eds), *Wildlife Management: Crocodiles and Alligators*. Surrey Beatty, Chipping, Norton, NSW, Australia
- Leslie A. J., 1997. The ecology and physiology of the Nile crocodile, *Crocodylus niloticus*, in Lake St Lucia, Kwazulu/Natal, South Africa. Unpublished PhD Thesis, Drexel University, USA
- Medved, R.J., Stillwell, C.E. and Casey J.G. 1988. The rate of food consumption of young sandbar sharks (*Carcharhinus plumbeus*) in Chincoteague Bay, Virginia. *Copeia*. 4: 956 - 963
- Neill, W. T. 1971. The last of the ruling reptiles: alligators, crocodiles and their kin. Columbia Univ. Press, Ithaca. p 486
- Richter, H. Lückstädt, C. Focken, U. and Becker, K. 2004. Some mathematical considerations in estimating daily food consumption models. *Ecological modeling*. 171: 381 - 393
- Rindorf, A. 2004. Estimation of evacuation rates in the field. *Journal of Fish Biology*. 65: 262 - 281
- Rosenburg, K. V. and Cooper, R. J. 1990. Approaches to avian diet analysis. *Studies in Avian Biology* 13: 80 - 90
- Ruggerone, G. T. 1989. Gastric evacuation rates and daily ration of piscivorous coho salmon, *Onorhynchus Kisutch* Walbaum. *Journal of Fish Biology*. 34: 451 - 463
- Secor, S. M. 2001. Regulation of digestive performance: a proposed adaptive response. *Comparative Biochemistry and Physiology*. Vol. 128 A: 565 - 577

Skoczylas, R. 1978. Physiology of the digestive tract. *In: Biology of the Reptilia* (Edited by Gans, C.), Vol. 8, pp 231 - 286. Academic Press, New York

Thorbjarnarson, J. 1999. Crocodile tears and skins: International trade, Economic constraints, and limits to the sustainable use of crocodilians. *Conservation Biology*. 13: 3: 465 - 470

Webb, G. J. W., Hollis, G. J. and Manolis, S. C. 1991. Feeding, growth, and food conversion rates of wild juvenile Saltwater crocodiles (*Crocodylus porosus*). *Journal of Herpetology*. 25: 462 - 473

Winberg, G.C. 1956. Rate of metabolism and food requirements of fishes. Belorussian University, Minsk, U.S.S.R. Fisheries Research Board of Canada, Translation Series No. 164, 1960.



CHAPTER 7

Summary

The prey found in the stomachs of the Nile crocodile was similar to that which Blomberg (1976) documented, although separating prey items into either fresh or old categories should give a more reliable estimate of the frequently eaten foods. The use of a feeding model (Diana, 1979) gave a more reliable estimate of the rate of predation of certain prey groups, although the model used may have had certain errors (Bromley, 1994). Future studies should look at a way of correcting this. The type of prey predated was similar to other crocodylian studies (Chapter 1). It was found that the Okavango crocodiles were more dependent on aquatic based prey as terrestrial prey was only infrequently predated. Stomach stones accounted for a smaller mass in proportion to total crocodile mass than other studies have shown (Brazaitis, 1969). Four parasites were described, which were new to the Okavango Delta region (Junker *et al.*, 2006). The digestion study concurred with the mass of prey found in the stomachs of crocodiles and the proportion of ingested prey relative to the total crocodile body mass decreased with an increase in crocodile size.

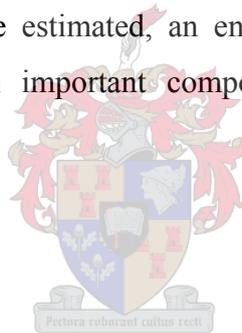
The Okavango fishery is an open access regime and could cause friction between various users of the common resources (Mosepele and Kolding, 2002). There are numerous threats to the Okavango system, in particular if the flood regime is altered. Other factors include pollution, erosion, fishing pressure and disruption of natural food webs by removals of crocodiles and other predators (Skelton *et al.* 1985). Recreational fishing has allegedly caused fish stock declines (Bills, 1996) together with the 1980 drought (Merron, 1993), tsetse fly (*Glossina morsitans*) spraying and the burning of riverine vegetation (Merron and Bruton, 1988). However, Mosepele and Kolding's (2002) fish stock assessment study suggested that the Okavango delta is in the initial stages of exploitation and there is a possibility for continued expansion.

Crocodiles play a beneficial role in fishery systems. Young crocodiles consume a number of invertebrate predators of fish fry, such as fish eating spiders, water bugs, water beetles and crabs. Larger crocodiles predate on aquatic piscivorous fish such as catfish and African pike (Chapter 3), as well as avian predators such as storks, darters and pelicans

(Santiapillai and de Silva, 2001). However, there is local conflict between crocodiles and fishermen (pers. obs.) as they compete for the same resources. Crocodiles become entangled in synthetic fiber gill nets and eventually drown and the predators also prey on livestock and people (Thomas, 2006).

In order to reach an optimal balance to maintain this pristine system, a thorough knowledge of the entire ecosystem is necessary to maintain biotic diversity and productivity. The Okavango Delta is a primary resource for people, livestock and wildlife and it is important that those who depend upon it should also make an effort to protect the ecosystem. Projects such as the AquaRAP 2000 project, aims to create an awareness of the importance of the aquatic resources of the Okavango Delta (Nordin and Mosepele, 2003).

In conjunction with a thorough crocodile population survey, the daily feeding rate of specific prey could be extrapolated to the entire ecosystem. An annual feeding rate of certain prey items could then be estimated, an energy budget for crocodiles could be determined and included as an important component of the management plan for crocodiles of the Okavango Delta.



REFERENCES

- Bills, R. 1996. Fish Stock Assessment of the Okavango River. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa. Investigational Report No. 56.
- Blomberg, G. E. D. 1976. Feeding and nesting ecology and habitat preferences of Okavango crocodiles. Proceedings of the Symposium: Okavango Delta and its future utilisation, Botswana Society, Gaborone, Botswana
- Brazaitis, P. 1969. The occurrence and ingestion of gastroliths in two captive crocodilians. *Herpetologica*. 25(1): 63 - 64
- Bromley, P.J. 1994. The role of gastric evacuation experiments in quantifying the Feeding rates of predatory fish. *Reviews in Fish Biology and Fisheries*, 4: 36 - 66
- Diana, J. S. 1979. The feeding pattern and daily ration of a top carnivore, the northern Pike (*Esox lucius*). *Canadian Journal of Zoology*. 57: 2121 - 2127
- Junker, K., Wallace, K., Leslie, A.J. and Boomker, J. 2006. Gastric nematodes of Nile crocodiles, *Crocodylus niloticus* Laurenti, 1768, from the Okavango River, Botswana. *Onderstepoort Journal of Veterinary Research*. 73: 111 - 114
- Merron, G. S. 1993. Pack-hunting in two species of catfish, *Clarias gariepinus* and *C. ngamensis*, in the Okavango Delta, Botswana. *Journal of Fish Biology*. 43: 575 - 584.
- Merron, G. S. and Bruton, 1988. The ecology and management of fishes of the Okavango Delta, Botswana, with particular reference to the role of seasonal floods. J.L.B. Smith Institute of Ichthyology Investigational Report No. 29
- Mosepele, K and Kolding, J. 2002. Fish stock assessment in the Okavango Delta, Botswana – preliminary results from a length based analysis. Paper presented at the “Environmental Monitoring of Tropical and Subtropical Wetlands”

international conference held at Maun Lodge, 4 - 6 December 2002, Maun, Botswana. 25 pp

Nordin, L.A. and Mosepele, B.Q. 2003. Suggestions for an aquatic monitoring programme for the Okavango Delta. *In: Alonso, L.E. and Nordin L. (editors). 2003. A rapid biological assessment of the aquatic ecosystems of the Okavango Delta, Botswana: High water survey. RAP Bulletin of Biological Assessment 27. Conservation International, Washington, D.C. pp. 111 - 119*

Santiapillai, C. and de Silva M. 2001. Status, distribution and conservation of crocodiles in Sri Lanka. *Biological Conservation. 97: 305 - 318*

Skelton, P.H., Bryton, M.N, Merron, G.S. and van der Waal B.C.W. 1985. The fishes of the Okavango Drainage system in Angola, South West Africa and Botswana: Taxonomy and Distribution. *Ichthyological bulletin of the J.L.B. Smith Institute of Ichthyology, Grahamstown, Republic of South Africa*

Thomas, G. 2006. Human-crocodile conflict in the Okavango Delta, Botswana. Unpublished MSc Thesis, University of Stellenbosch, South Africa



APPENDIX 1

Crocodile capture techniques

Night- shifts

Crocodiles were caught between dusk and dawn from a boat (4.8 m aluminium flat-bottomed swamp cruiser). A 500 000 candle power spot-light was used to search for crocodiles, their eyes reflecting from the spotlight beam due to the tapetum lucidum. The crocodile was then approached and captured. Depending on the size of the crocodile one of two methods were utilised. Crocodiles up to 1.2 m were caught by hand and crocodiles >1.2 m were caught using a rigid aluminium noose. In both cases the crocodile was immediately brought onto the boat and 'processed' (Appendix 2) and then released at the site of capture.

Box traps

Box traps used varied in length from 1.5 to 2 m. Bait was hung at the rear end of the trap and attached by line to a guillotine style trap door at the front of the cage. Once the bait was pulled the door shut, trapping the crocodile.

Traps were set at dusk, baited with offal and checked at dawn. Crocodiles caught in baited traps may cause a bias in sampling technique towards hungry animals. In the case of the trapped crocodiles, nothing was found in their stomachs (other than the bait).

APPENDIX 2

Processing

A number of morphometric measurements were recorded using a flexible tape measure and a pair of callipers.

TL	Total length	Tip of snout to tip of tail
SVL	Snout-to-vent length	Tip of snout to posterior edge of cloaca
NC	Neck circumference	Around the nuchal rosette of the neck
BTC	Base of tail circumference	Around the tail just behind the hind legs
HL	Head length	Tip of snout to posterior edge of supra-occipital bone
HW	Head width	Laterally between extremities of quadratojugals
HD	Head depth	Top of supra-occipital to base of quadratojugal

TL and SVL were measured on the ventral side of the crocodile and the other measurements were taken dorsally.

Body mass was recorded using a series of spring balances: 0 – 600 g (± 10), 0.5 kg - 1.5 kg (± 0.1 kg), 1.5 kg -25 kg (± 0.5 kg), etc. Body, water and air temperature were recorded using a Batt-12 thermocouple meter (± 0.1 °C). All crocodiles were marked using a scute removal system developed by Leslie (1997), crocodiles > 1m also had a numbered plastic cattle tag attached to the first single scute of the tail (Red for males and yellow for females).

REFERENCES

- Leslie A. J., 1997. The ecology and physiology of the Nile crocodile, *Crocodylus niloticus*, in Lake St Lucia, Kwazulu/Natal, South Africa. Unpublished PhD Thesis, Drexel University, USA

APPENDIX 3

Stomach content collection

Stomach lavage: The Hose-heimlich technique, (Ayarzagüena, 1983; Fitzgerald, 1989)

Prior to securing the jaws, two 'jaw straps' were placed in the crocodiles mouth. The jaw straps were used to prise the jaws apart using a 'jack-system' and allowed a metal 'O' ring to be inserted between the jaws. This was held securely in place by both the crocodiles bite force and tape wound around the jaws and 'O' ring, this allowed the jaws to remain open.

With the crocodile flat on the boat deck and as straight as possible, a lubricated (internally safe lubricating jelly) tygon-tubing pipe was then inserted over the gular fold and into the oesophagus (located just above and behind the larynx opening). The pipe was then gently pushed into the stomach through the cardiac sphincter (the distance was estimated externally and marked on the pipe prior to insertion).

The crocodile was held at a 45° angle, head down to prevent any water entering the larynx. Water was pumped (using a standard water pump connected to a 12v battery) into the stomach until it was bloated (the pressure of the pump could be altered by a valve and over-flow pipe). The stomach was externally hand massaged and water and the stomach contents were then forced back up the oesophagus and collected on a 0.5 mm material mesh secured across the opening of a bucket. This process was continued until the water ran clear. The entire process often took less than two minutes. Particulate matter from the stomach was placed in a storage jar and analysed once back at camp a few hours later.

REFERENCES

- Ayarzagüena, S. J. 1983. Ecología del caiman de anteojos en los llanos de Apure
Venezuela. Donana Acta Vertebrata numero especial. 10: 1 - 136
- Fitzgerald, L. A. 1989. An evaluation of stomach flushing techniques for crocodilians.
Journal of Herpetology. 23 (2): 170 - 172

APPENDIX 4

Prey age assessment

Prey was termed fresh if it had been ingested within twenty-four hours. The criteria used was based on the reference series and photographs from two previous studies (Games 1991, Barr 1997).

Twenty-four hour residency criteria for this study

Insecta:	relatively intact with most of appendages still attached
Arachnida:	main body still intact
Crustacea:	main body intact
Amphibia:	all amphibians found were considered freshly ingested
Pisces:	fish were considered freshly ingested unless only vertebrae were found
Mammalia:	main body intact



Games' (1990) twenty-four hour residence reference series

Insecta:	Gryllotalpidae, Odonata, Gryllidae, Crabidae, Mole cricket, Scarabaeidae, all insects were relatively intact
Fish:	Catfish and Cichlid were still recognisable, with main body intact
Amphibia:	as above
Mammalia:	as above

Barr's (1997) forty-eight hour residency criteria.

Birds:	presence of main body, breast or head
Crayfish:	main body recovered
Salamanders:	main body
Snakes:	large intact pieces of body with attached skin
Turtles:	large pieces of carapace, intact appendages or head

Barr's (1997) forty-eight hour residency criteria continued

Mammals: large pieces of body, skull or other large bones

Snails: soft tissue still attached to operculum

Fish & frogs have gastric residence of less than 48 hours

REFERENCES

Barr, B. 1997. Food habits of the American alligator, *Alligator mississippiensis*, in the Southern Everglades. Unpublished PhD Thesis, University of Miami

Games, I. 1990. The feeding ecology of two Nile crocodile populations in the Zambezi valley. Unpublished PhD Thesis, University of Zimbabwe

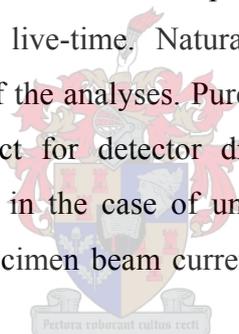


APPENDIX 5

Gastrolith identification

LEO EDS-SEM procedure

Imaging of the samples and analysis of the phase compositions was accomplished using a Leo® 1430VP Scanning Electron Microscope at the University of Stellenbosch. Prior to imaging or analysis the samples are sputter-coated with either gold or carbon depending on the application. Samples were identified with backscattered electron (BSE) and/or secondary electron images, and phase compositions quantified by EDS analysis using an Oxford Instruments® 133 KeV detector and Oxford INCA software. Beam conditions during the quantitative analyses were 20 KV and approximately 1.5 nA, with a working distance of 13mm and a specimen beam current of -3.92 nA. Despite the relatively low energy of the beam, X-ray counts with the set-up used were typically ~ 5000 cps. The counting time was 50 seconds live-time. Natural mineral standards were used for standardization and verification of the analyses. Pure Co, as well as Ti and Fe in ilmenite were used periodically to correct for detector drift. Beam conditions, during semi-quantitative analyses, when used in the case of unpolished samples, were as described above without controlling the specimen beam current and the results were normalised to 100wt%.



APPENDIX 6

Original prey mass

Morphometrics to estimate the original mass of fish were based on measurements taken from specimens that were originally caught in the Okavango Delta and preserved at the South African Institute for Aquatic Biodiversity, Grahamstown, South Africa.

It was assumed that there was a slight underestimation of the original mass estimates, as the fish were all kept in preservative. Ethanol and formalin can cause shrinking (1.8 - 5.6%) and mass loss (1.1 - 8.4 %), which differs between fish species (Buchheister and Wilson, 2005).

When the measurement of standard length was not possible, as in the case of the mochokids and catfish, skull measurements were preferred to those based on spine length, as the spines of mochokids and catfish can vary in length with similar size fish of the same species between populations (pers. comm. R. Bills).

Teleosti

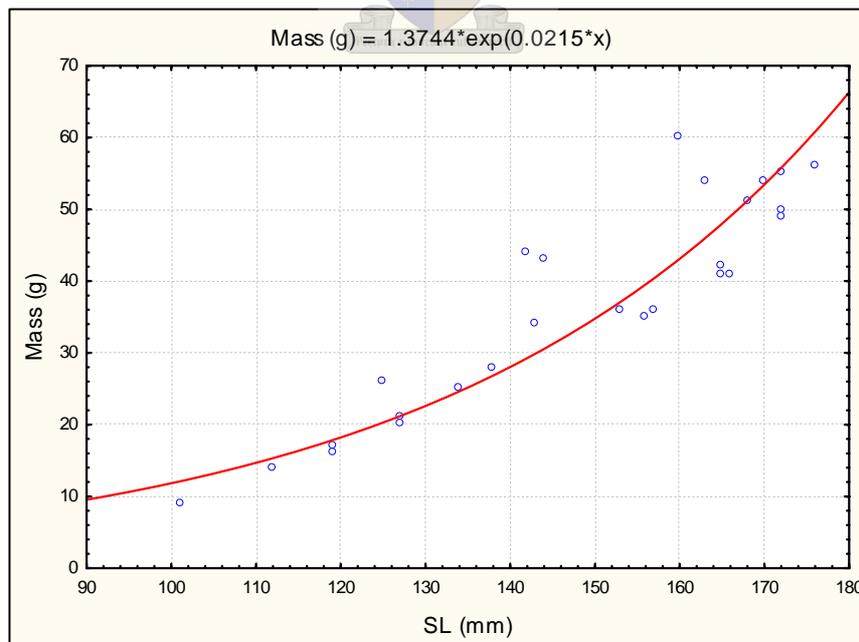


Figure A.6.1 Relationship between standard length and mass for *Hepsetus odoe* (African Pike)

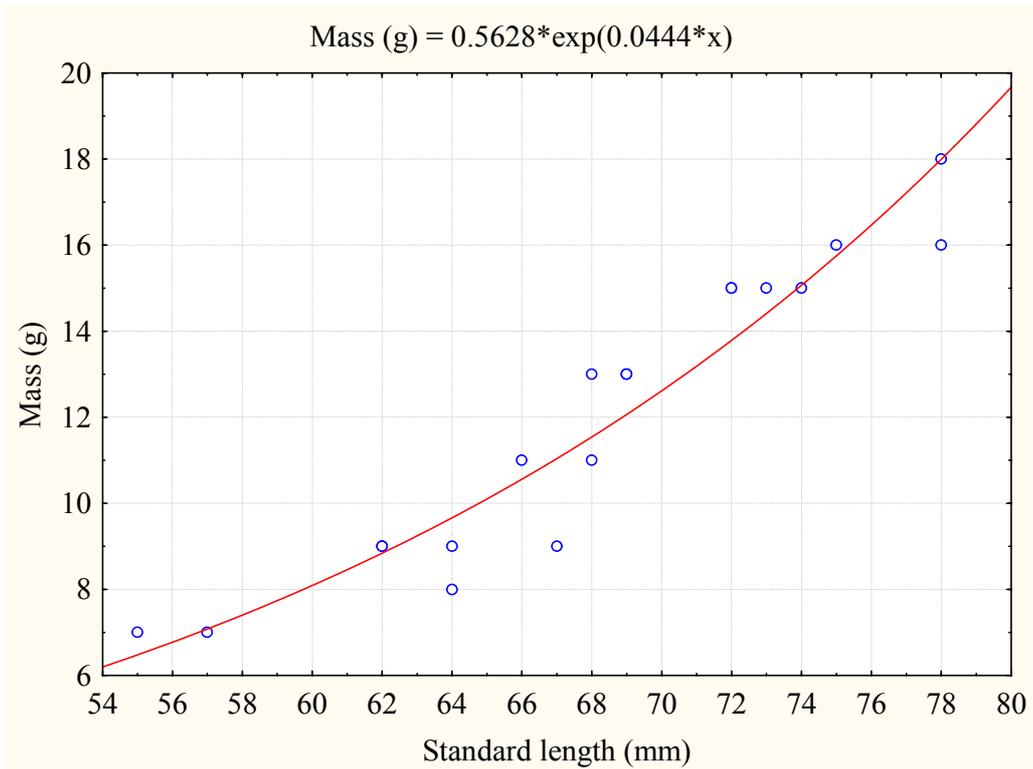


Figure A.6.2 Relationship between standard length and mass for *Tilapia rendalli* (Redbreast tilapia)

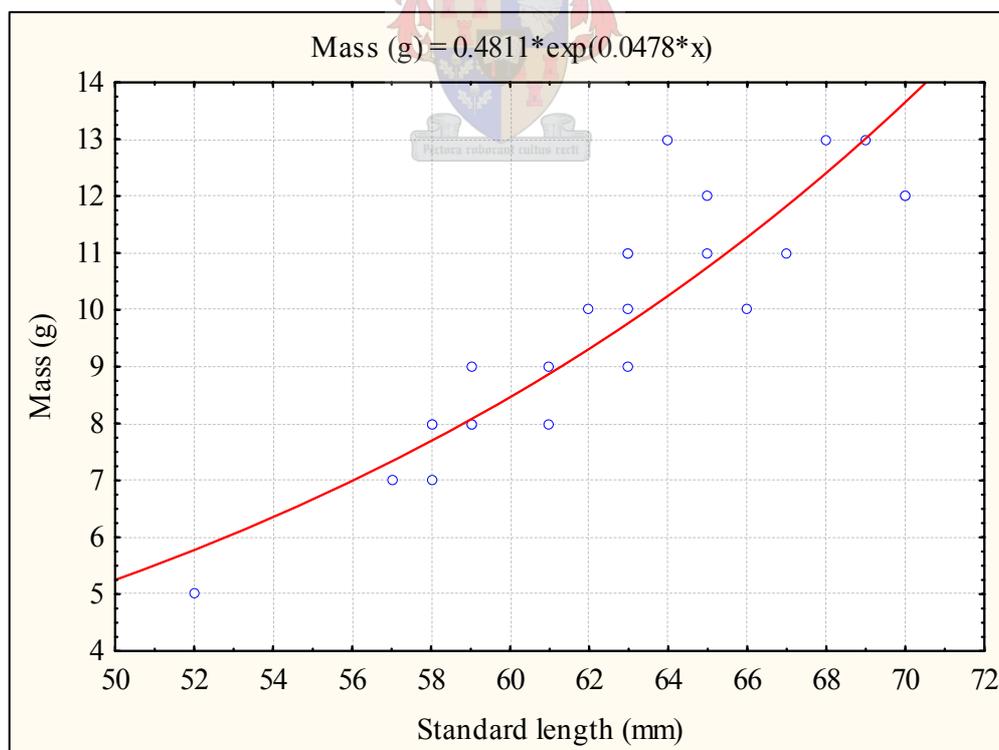


Figure A.6.3 Relationship between standard length and mass for *Tilapia sparrmanii* (Banded tilapia)

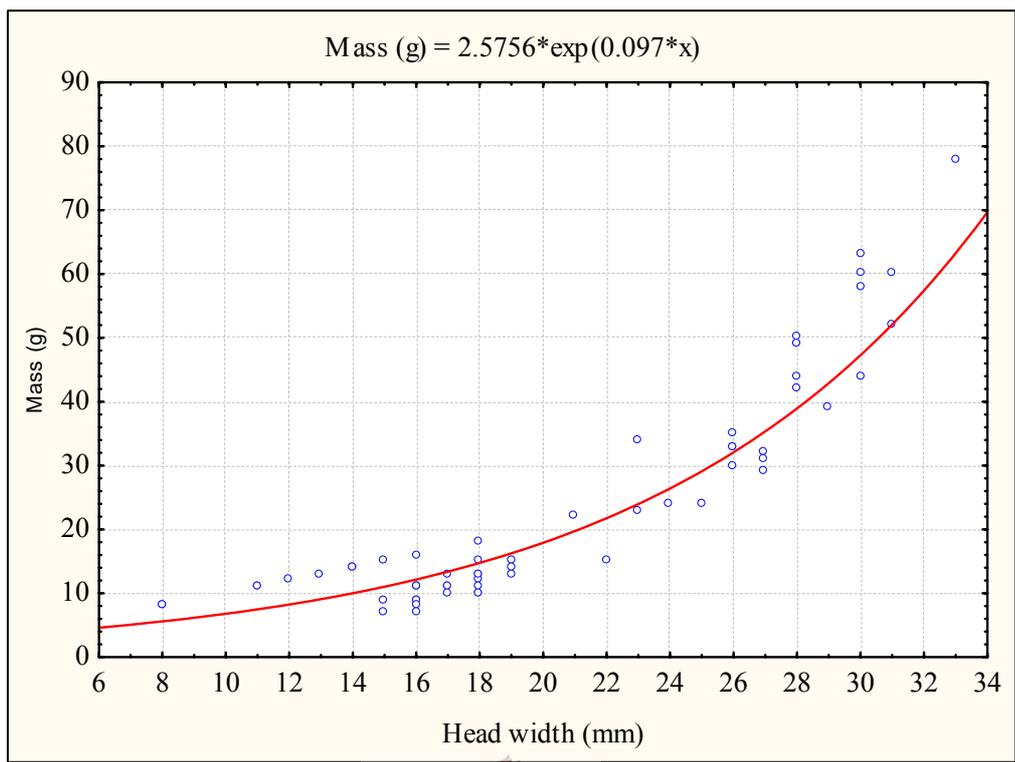


Figure A.6.4 Relationship between head width and mass for *Synodontis sp.* (Squeaker)

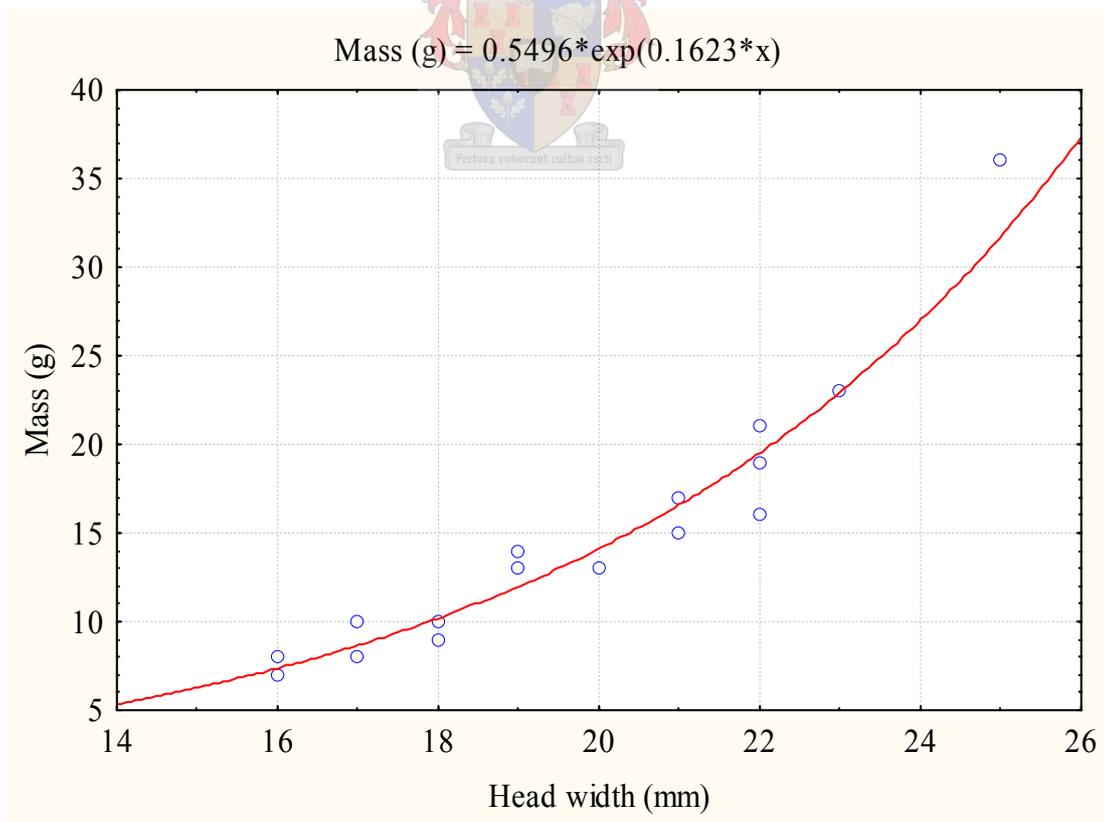


Figure A.6.5 Relationship between head width and mass for *Catfish sp.*

Due to the similar sizes of all the Mormyridae (Snoutfishes), they were allocated an original mass of 2 g each and *Aplocheilichthys johnstoni* (Johnston's topminnow) was allocated an original mass of 0.1 g each.

Invertebrata

The masses of invertebrates were based on field measurements. Many of the smaller invertebrates could be only given a mass of 0.1 g when they occurred in sufficient numbers.

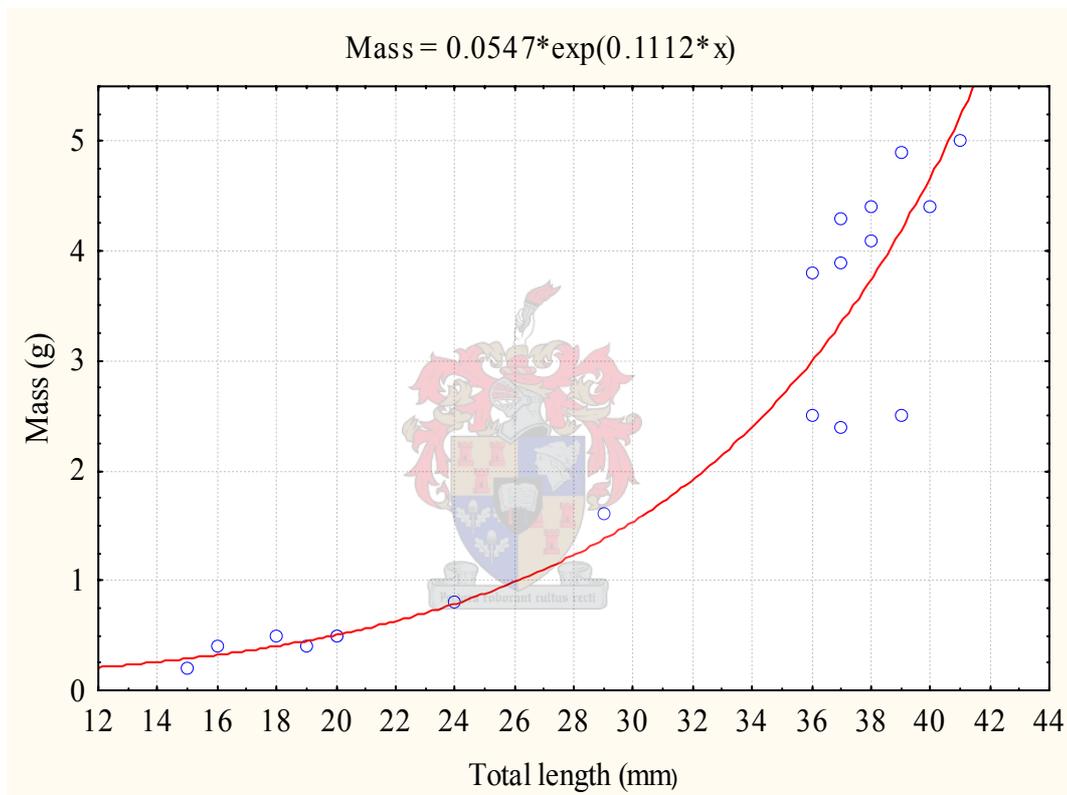


Figure A.6.6 Relationship between total length and mass for Dytascidae *sp.* (Water beetles), no distinction was made between species

Mammalia

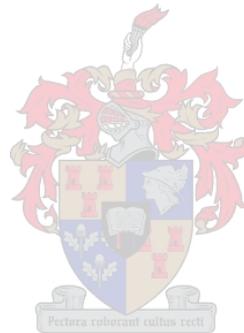
The original mass for the recently ingested small mammals was estimated using the Field Guide to Mammals of Southern Africa (Stuart and Stuart, 2001). *Crocidura mariquensis* (Swamp shrew) were allocated an original mass of 10 g as all they were all adult and of a similar size. The unidentified small mammals were allocated an original mass of 15 g each, being of similar sizes.

Amphibia

The reed frog, *Hyperolius marmoratus* was allocated an original mass of 1.2 g (\pm 0.2 S.E.) each based on a series of field measurements.

REFERENCES

- Buchheister, A. and Wilson, M. T. 2005. Shrinkage correction and length conversion equations for *Theragra chalcogramma*, *Mallotus villosus* and *Thaleichthys pacificus*. *Journal of Fish Biology*, 67, 541 - 548
- Stuart, C. and Stuart, T. 2001. *Field guide to Mammals of Southern Africa*. Struik Publishers (Pty) Ltd. Cape Town. South Africa



APPENDIX 7

Prey Species

Table A.7.0 Identified prey species recovered from stomachs (all species were adult, unless otherwise stated)

Scientific name	Common name
HEMIPTERA	BUGS
Hydrophilidae	Water scavenger beetles
<i>Hydrochara sp.</i>	
<i>Hydrophilus sp.</i>	
<i>Hydropilus aculeatus</i>	
Nepidae	Water scorpions
<i>Ranatra sp.</i>	Stick water scorpions
<i>Laccotrephes sp. *</i>	Common water scorpions
Belastomatidae	Giant water bugs
<i>Appasus sp.</i>	Brooding water bugs
<i>Apasus grassei</i>	
<i>Limnogeton fiebberi</i>	Fiebbers giant water bug
<i>Hydrocyrius longifemorata*</i>	
Gerridae	Pond skaters, water striders
<i>Limnogonus capensis</i>	Striped pond skater
Hydrometridae	Water striders
<i>Hydrometra sp.</i>	
COLEOPTERA	BETLES
Dytisidae	Water beetles
<i>Cybister sp. Unk</i>	
Gyrinidae	Whirligig beetles
Cleridae sp.	Chequered beetles
Curculionidae sp.	Weevils, snout beetles
Carabidae sp.	Ground beetles
DERMAPTERA	EARWIGS

Scientific name	Common name
Earwig	
DIPTERA	FLIES
Tabanidae (larvae)	Horse flies
ODONATA	DAMSELFLIES AND DRAGONFLIES
Libuellulidae <i>Orthetrum sp.</i> (nymph) <i>Trithemis sp.</i> (nymph) <i>Phyllomacromia sp.</i> (nymph)	Skimmers
LEPIDOPTERA	MOTHS AND BUTTERFLIES
Lepidoptera sp. Noctuidae (Agrotidae)	Owlet moths
ARACHNIDA	SPIDERS
Araneidae <i>Neoscona subfusca</i> <i>Pararaneus cyrtoscapus</i>	Orbweb spiders
Pisauridae <i>Dolomedes gracilis</i> <i>Thalassius marginatus</i>	Fish-eating spiders
Lycosidae Tetragnathidae <i>Tetragnathidae angolaensis</i> <i>Tetragnathidae boydi</i>	Wolf spiders Long-jawed orb-weavers
BIVALVES	
Mussel sp. *	
TELEOSTI	FISH
Cyprinidae <i>Barbus multineatus</i>	Cyprinids Copperstripe barb
Characidae <i>Rhabdalestes maunensis</i> unk sp.	Characins Slender robber

Scientific name	Common name
Poeciliidae <i>Aplocheilichtys johnstoni</i>	Topminnows Johnston's topminnow
Mormyridae <i>Pollimyrus castelnaui</i> unk sp.	Snoutfishes Dwarf stonebasher
Hepsetidae <i>Hepsetus odoe</i>	African pike African pike
Catfish	Catfishes
Mochokidae <i>Synodontis sp.</i>	Squeakers, suckermouth catlets Squeakers
Cichlidae <i>Tilapia sparrmanii</i> <i>Tilapia rendalli</i> unk sp.	Cichlids including tilapia Banded tilapia Redbreast tilapia
MAMMALIA <i>Crocidura mariquensis</i> <i>Dasymys incomtus</i> unk small mammal	Water rat Swamp shrew
AMPHIBIA <i>Hyperolius marmoratus</i> unk frog sp.	Reed frog
Scientific name	Common name
AVES Unk bird *	BIRDS
REPTILIA unk snake unk turtle *	REPTILES

* Denotes old remnants found only, digested prior to 24h of capture.

APPENDIX 8

Captive digestion rate study

The experiment took place at the Samochima ‘Krokovango’ crocodile farm, Botswana, in a quiet secluded area. Due to the experiment being outside, the crocodiles were subject to a natural diurnal cycle and a temperature range of 19 °C – 29 °C.

Holding cages for the crocodiles were constructed from 45° angle iron with 5mm vertical round bar supporting rods, chicken mesh (to prevent crocodile jaw injuries from penetrating the larger diamond mesh, biting and twisting) with an external covering of diamond mesh fencing around the sides and roof. Rigid expanded metal floors allowed faeces to drop through onto the faecal collection trays below (Table A.8.0). Faecal collection trays were made from corrugated tin cut to the dimensions of the cage.

Table A.8.0 Number and dimensions of crocodile holding cages

Size class	n	Length (cm)	Width (cm)	Height (cm)
Yearling	8	100	65	50
Juvenile	8	150	90	70
Sub-adult	3	200	120	100

A 10m long, 4 m wide, 0.5 m deep pool was excavated and concrete lined. The longitudinal sides sloped to a central 0.5 m wide flat bottom. The entire area (12 m long x 8 m wide), was longer and wider than the pool to ensure the cages were shaded during

phase II of the experiment. The pond was covered with 40 % shade cloth held up by gum poles and cross bars. Surrounding trees and vegetation also provided additional shade.

The cages were arranged along the longitudinal sides of the pool and placed at an angle allowing access to water (enough to completely submerge) and a dry basking area.

Two garden sprinklers, one at either end of the pool, provided a fine mist to assist in cooling the crocodiles and a garden hose with a nozzle was used to provide the crocodiles with drinking water during phase II of the experiment.

Only two people were allowed access to the area once the experiment began. Crocodiles were offered food on feeding trays *ad libitum*. During this time period they were observed to ensure that all the food was eaten. Excess food was then removed.

Crocodiles could possibly have eaten anything additional that came into the experimental area, such as aquatic insects. However, the crocodiles were kept under constant observation by the two observers and no additional feeding was seen.

