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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

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Abstract

The stomach contents of 153 *C. johnstoni* were examined by a modification of the method for stomach contents removal described by Taylor *et al.* (1978). Prey are analysed on the basis of taxonomy, although more emphasis is placed on prey equivalents, using a concept termed 'target size'. The relative importance of different taxa and prey equivalents is determined by a number of methods, and a ranking method is preferred. The most important prey are aquatic and terrestrial insects, fish and crustaceans. The most important sized organisms are target size 5, animals presenting a maximum area of 1·0–4·0 cm². With regard to size of prey eaten, three size groups of *C. johnstoni* (16–25, 26–55 and 56–129 cm snout–vent length) were homogeneous within themselves but were significantly different from each other. With increased body size there was a significant increase in the proportion of aquatic prey eaten. Secondary ingestion did not appear a major bias. *C. johnstoni* ate appreciably more during the wet season than during the dry season, although seasonal comparisons were restricted due to the samples not coming from the same pools. Vegetation was found in 39·9% of crocodile stomachs, and its presence varied with season but not with crocodile size. Stomach parasites were present in 43·8% of animals, and the number of infected crocodiles varied with season and size. Stones were present in 88·2% of crocodiles; however, when compared with those of *C. niloticus* the stone loads were relatively small. Most data indicate that *C. johnstoni* is very much an opportunistic predator at the water's edge, which feeds primarily on small aquatic prey, although it may also take substantial numbers of terrestrial prey organisms. During the wet season there is a major shift in the importance of different prey taxa eaten, although the importance of prey equivalents remains largely unchanged.

Introduction

Implicit in the contents of the stomach (or alimentary canal) is information on the foods and feeding strategies of animals—information basic to an understanding of 'niche'. However, the degree to which and ease with which such information can be quantified varies considerably between different animal groups. It may depend for example, on whether the animal is a herbivore, carnivore or omnivore; whether the animal and its prey are large or small; whether foods are soft-bodied and rapidly digested or hard-bodied and slowly digested; whether carrion is eaten; whether the animal masticates its food or swallows it whole; whether the animal is a generalist or specialist feeder, with many or few food taxa. In some cases it is questionable whether the killing of animals to obtain stomach contents can be justified on conservation grounds (Gans and Pooley 1976; Dawson and Ellis 1979).

The above factors also limit the questions about food and feeding habits that can be realistically answered from stomach contents. The fundamental question is: 'what does an animal eat?', and many studies aim to clarify this in broad terms. Examination may be restricted to the maximum number of stomachs available rather than to a predetermined sample size (King and Green 1979), with analyses ranging from simplified summaries (Allen 1974) to more highly quantified breakdowns (Taylor 1979). On the other hand, analyses of stomach contents may be used to test more complex hypotheses about food and feeding; for example, niche separation (Pollard 1973; Cadwallader 1975; Jackson 1978) with the emphasis on specific and often conceptual questions, aimed at examining the fundamental question in more depth.

Most studies on crocodilians have had broad aims. There are many anecdotal lists of food, often from small samples in restricted areas, and detailed quantification of larger samples for *Alligator mississippiensis* (Kellogg 1929; Giles and Childs 1949; O'Neill 1949; Fogarty and Albury 1968; Chabreck 1971; Valentine *et al.* 1972; McNease and Joanen 1977), *Caiman crocodilus crocodilus* (Staton and Dixon 1975; Gorzula 1978), *Crocodylus niloticus* (Welman and Worthington 1943; Hippel 1946; Corbet 1959, 1960; Cott 1961; Graham 1968), and *Crocodylus porosus* (Taylor 1979).

Together, these studies indicate that crocodilians are opportunistic predators, whose prey encompass wide size and taxonomic ranges. They feed mainly in shallow water or at the water's edge, although some prey may be taken on land (Cott 1961). They appear adept at exploiting local abundances of prey, be they insects attracted to lights at night (Whitaker and Whitaker 1977), natural blooms of insect larvae (Taylor 1979), frogs (Gorzula 1978; Medem, personal communication), birds (Attwell 1954), mammals or carrion (Valentine *et al.* 1972; personal observation). Prey may come from the terrestrial, aerial and aquatic environs, and include both permanent and transient residents in those habitats. Most authors suggest that crocodilians may take any suitably sized prey within their feeding area (independent of taxonomy); prey that are large enough to elicit stimuli of sufficient intensity for their presence to be perceived, and not too big to be physically unmanageable. Crocodiles tend to eat smaller prey whole and to tear segments off larger prey, making identification of prey from their stomach contents relatively easy.

The food and feeding habits of the endemic Australian freshwater crocodile, *Crocodylus johnstoni* Krefft, are known only from anecdotal descriptions (Worrell 1952, 1964), and the present study was undertaken with the main aim of determining 'what they eat' in the Mary–McKinlay River system in the Northern Territory. The logistics of sampling prey availability were considered too formidable to undertake at this stage, although some data were collected. Similarly, for logistic reasons the wet-season sample (collected over $1\frac{1}{2}$ months) came from downstream of the dry season sample (the two areas overlapped marginally). This restricts fine interpretation of seasonal trends, although major differences between wet and dry seasons are apparent.

Central to the present study was the aim of enhancing the predictive and comparative value of the data, and towards this end we developed a prey-equivalent approach, termed 'target size', which encompasses aspects of reconstituted prey size and reduces emphasis on the precise measuring of prey. It has limitations in general feeding studies, but appears suited to studies with crocodilians and is amenable to analyses of prey importance.

How important is a particular prey to *C. johnstoni*, and which prey are important and which are not? Both are fundamental questions, yet the methodology of answering them is confusing. The 'importance' of a particular food would seem to refer conceptually to the proportion of the total energy requirements of a population that is supplied by that food source. It is thus affected by the energetic value of the food, the energy expenditure in gaining and assimilating the food, and the proportion of the population utilizing that food. Estimates of importance based on stomach contents usually assume equivalent calorific value and energy expenditure, and as indices of importance use: the proportion of animals utilizing a particular food source (occurrence method); the percentage of the total number of prey items made up by a particular taxon, or sometimes the proportion of the total food volume or weight made up by a particular prey (composition method); the proportion of animals in which a particular food is dominant, as indicated by approximate volumes in the stomach (dominance method); more complex analyses of dominance, in which points are assigned to each food depending on its estimated relative volume in the stomach (points method); analyses based on the ranking of food items on the basis of their approximate volumes in the stomach (ranking method) (Hynes 1950; Pollard 1973; McNease and Joanen 1977; Windell and Bowen 1978). These methods are sometimes combined; for example, Pinkas *et al.* (1971) used occurrence plus both numerical and volumetric measures of composition to form an index for tuna.

In the present study we have compared the occurrence, composition, dominance and ranking methods, with the prey expressed both as prey taxa and target size categories (prey equivalents).

Methods

Study Area

The study was carried out in the Mary–McKinlay River system (131°50′E.,13°0′S.), which drains a large floodplain. During the wet season (November–April) water is abundant, and the plain experiences a bloom of plant and insect growth. During the dry season there is a steady recession of available water, and much of the wet season bloom of plant growth dies or is burnt. By the end of the dry season *C. johnstoni* are congregated in the deeper, larger billabongs (lagoons) and pools, both within and outside the mainstream (Webb *et al.* 1983*b*). The McKinlay River system (the major tributary of the Mary River), and the general weather patterns for the area have been described elsewhere (Webb *et al.* 1983*b*), and additional information is in Story *et al.* (1969).

Data Collection

A total of 153 crocodiles were collected, 101 of them in the Mary R. in the wet season (February–March) of 1978–79, and 52 in the McKinlay R. in the dry seasons (July–September) of 1978 and 1979. They were caught by hand, with a harpoon or with fine nets (Webb and Messel 1977), and were held for between 5 and 18 hours before the stomach contents were removed. In the 1978 dry season some data were obtained from 10 dead *C. johnstoni*. The method described by Taylor *et al.* (1978) was used to remove the stomach contents of all the live-caught animals, but during the course of the study a substantial improvement to that method was made.

Taylor *et al.* (1978) described a scoop and pump which were used successfully on *C. porosus* of up to 1·8 m total length (TL). The scoop was a metal rod with a loop at right angles to it at one end, and a small rubber bag sewn on the loop. The pump was essentially a length of PVC tubing. The mouth of a crocodile was held open with a rubber-coated metal cylinder, and the scoop inserted through the oesophagus into the stomach. It was used to remove large items, and the pump, through which water was poured, to flush out small items.

We found that, with *C. johnstoni*, the largest scoop that could be used with a given size of crocodile retrieved only a small proportion of the stomach contents (many of the *C. johnstoni* had very full stomachs and it appeared that the throat region was marginally smaller than in *C. porosus*). Furthermore, after up to eight scoopings, the water flushed through the pump dislodged material which clogged the pump, a particularly serious problem in *C. johnstoni* of under 50 cm TL, for which up to 50 min were needed for each sample. Lubrication with vegetable oil, which was adequate for *C. porosus*, was not so with *C. johnstoni*, and the scoop and pump were difficult to manoeuvre down the oesophagus (the lubricant was wiped off). Furthermore, the scoop was not adequate for removing large food items. Of five animals autopsied after removal of the stomach contents (three fresh dead ones and two which died before release), two had been emptied, one contained three stones (from a total load of five) and two retained large food items, a fish in one and a rodent in the other; the presence of both items was, however, indicated by fragments.

The modified method uses only the scoop. The crocodile's head is tilted to 30° (head up) and water is poured into the throat as the scoop is inserted. The water acts as a lubricant and steadily fills the stomach and oesophagus as the end of the scoop moves posteriorly. The scoop is then moved back and forth about six times to mix the stomach contents, before being pushed posteriorly and extending the bag-like stomach in that direction. The crocodile is then tilted to about 60° (head down) and a flood of water and stomach contents pours out, the scoop being used initially as a pusher to move contents from the stomach into the oesophagus, then as a collector of items in the oesophagus. Rarely are more than two scoops required (5–10 min) before the flushing water is clear of all food particles. In a single dead animal examined, the stomach had been completely emptied and its walls washed clean, although it had originally contained 30 stones, vegetation, nematodes and an assortment of insects and fish.

We used this method on *C. johnstoni* of over 50 cm TL, and Magnusson (personal communication) has since tried it successfully with *Melanosuchus niger*, *Caiman crocodilus* and *Paleosuchus trigonatus*. With *P. trigonatus*, water appeared to enter the trachea and a number of specimens died. His suggestion (personal communication) of a plastic cuff to protect the tracheal opening would be worth investigating.

Stomach contents were collected in squares of cheesecloth (50 by 50 cm) spread over a plastic container. When removal was complete, these were tied shut and immersed in the excess flushing water. They were then removed, lightly squeezed and padded on absorbent paper, and weighed in grams. The volume, in millilitres, of samples was determined by water displacement before preservation in 70% alcohol. A correction for the cheesecloth was later subtracted from the weights and volumes of each sample.

Analysis

Stones of over 1 mm diameter were counted and the mean weight and volume determined; the weight of the largest stone was determined separately. All stone weights and volumes were recorded while they were wet, with free water sponged away.

After the removal of stones, vegetation and parasites, all remaining items were separated into taxonomic groups. The residual fluid, which contained minor pieces of cuticle, flesh and vegetation, was largely ignored, although used to determine whether or not there was evidence, e.g. fish scales and vegetation fragments, of specific prey having been eaten. Most animal remains were identified to family level and some to generic and specific levels. Where possible, prey items were assigned a 'target size' as described below.

The combined volume of whole pieces of vegetation was determined for each animal. The total volume of parasites was measured by displacement.

For categorization of food items into prey equivalents we devised a two-dimensional template (Fig. 1) to which prey items could be rapidly compared. The linear dimensions of each target size category (e.g. TS2, TS3, TS4) are double those of the previous one, so that the area of each TS is four times that of the preceding one. Different-shaped templates are used for different shapes of prey, but each TS category has the same area, and is here considered equivalent, independent of shape.

Prey items were assigned a TS category on the basis of the smallest TS that could accommodate the maximum presentable area of the prey when it was in what was considered a normal posture. As a result of the fourfold increase in each TS category, prey weight and volume increase with increasing TS's; however, it is not mandatory. (Very few prey items in a particular TS category would have a mass and volume overlapping with that of adjoining categories.)

Prey importance was determined by conventional methods and those modified to include target size. These are:

Taxonomic

(1) Occurrence: the percentage of the total number of *C. johnstoni* with a particular prey taxon in the stomach.

(2) Composition (by number): the percentage of the total number of identified prey belonging to a particular taxon.

(3) Dominance: the taxonomic list of prey was grouped into major taxa from essentially aquatic and terrestrial habitats. Dominance was then determined by:

I. Conventional method: each animal with food in its stomach was assigned a taxon category on the basis of the taxon occupying the greatest volume in the sorted stomach contents, as determined by inspection; the data were expressed as the proportion of *C. johnstoni* with that taxon as dominant.

II. Target size: as each TS category is four times the area of the next smaller category, all taxonomic groups in a stomach were given a score relative to the number and TS of prey present; for example, for any one taxonomic group one each TS1, TS2 and TS3 would equal $1+4+16=21$, and two each, $2+8+32=42$; the most dominant taxon was that with the highest score.

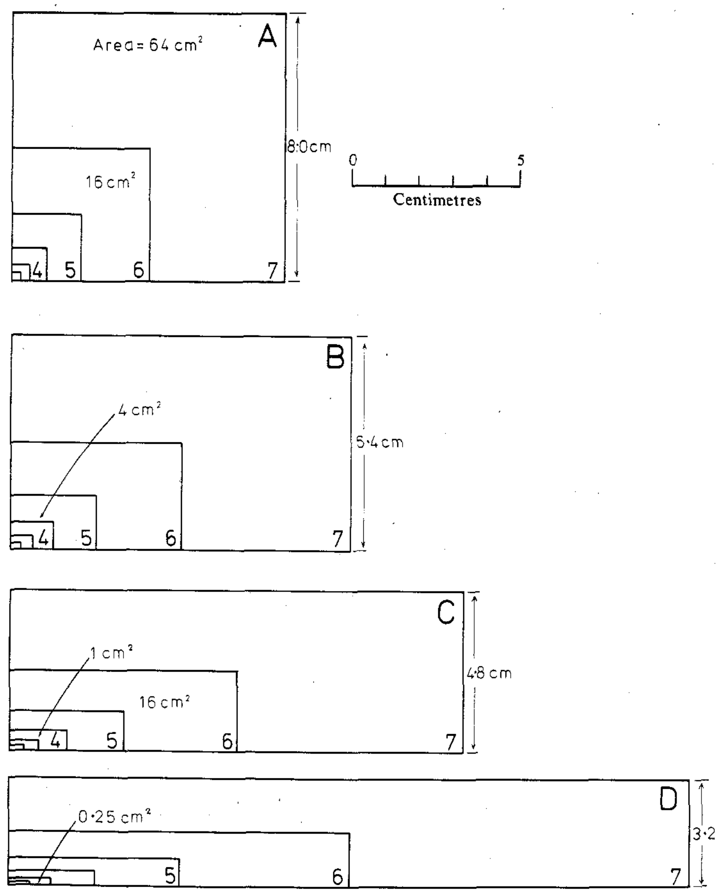

Fig. 1. Templates for assessing the target size of items of prey. Shapes with the same number have the same area and are considered equivalent. The area of each template is four times that of the template with the preceding number.

(4) Ranking

I. Conventional: following Pollard (1973), each taxon in each stomach sample was ranked according to its approximate volume (highest volume, 1) in that individual sample; a score for each taxon in each animal was then calculated by subtracting the rank of each taxon from the maximum number of taxon categories found in any animal, plus 1. The scores were totalled and the importance of a particular taxon indicated by the percentage of the total score it accounted for.

II. Target size: the taxa present in each stomach were ranked on the basis of the total TS area occupied by those taxa (see above); these ranks were then scored and treated as in the conventional approach.

Size

The taxonomy of prey items was ignored, and each prey item was considered only as a TS.

(1) Dominance: a score was allocated to each TS and habitat category on the same basis as described above, and the most dominant TS for each animal determined on the basis of the highest score.

Table 1. Origin, occurrence and size distribution of 1634 items of prey from the stomachs of 138 *C. johnstoni*

A, aquatic; T, terrestrial. No items of target size 9 were recorded. Because fish were often partly digested, they are not identified to species in the Table, but the following species were identifiable: Plotosidae: *Neosilurus* sp.; Teraponidae: *Leiopotherapon unicolor*, *Syncomistes butleri*; Melanotaeniidae: *Melanotaenia* sp.; Ambassidae: *Ambassis* sp.; Apogonidae: *Glossamia aprion*; Toxotidae: *Toxites chatereus*; Eleotridae: *Oxyeleotris lineolatus*; Ariidae: *Hexanematichthys* sp.

Taxon	Habitat	Percentage occurrence	Percentage composition	Percentage of target size No.: 2	3	4	5	6	7	8
Crustacea										
Decapoda										
Parastacidae										
Cherax quadricarinatus	A	0·7	0·1	—	—	—	—	—	—	100
Palaemonidae										
Macrobrachium tolmerum	A	13·8	1·2	—	—	23·5	41·2	29·4	5·9	—
Atyidae										
Caridina gracilirostris	A	3·6	4·3	—	93	7	—	—	—	—
Undetermined	A	2·9	0·2	—	—	—	—	—	75	25
Insecta										
Coleoptera										
Carabidae	T	27·5	8·3	3·7	33·3	46·7	15·5	0·8	—	—
Dytiscidae	A	37·7	8·0	—	3·1	38·9	46·6	11·4	—	—
Scarabaeidae	T	24·6	5·5	2·3	2·3	17·2	55·2	23	—	—
Undetermined		10·1	2·6	9·7	24·4	41·5	12·2	12·2	—	—
Hemiptera										
Belastomatidae	A	39·8	16·2	—	—	—	100	—	—	—
Corixidae	A	2·9	0·2	25	50	—	25	—	—	—
Gerridae	A	2·2	0·4	—	33·3	—	66·7	—	—	—
Nepidae	A	3·6	0·4	—	—	—	83·3	16·7	—	—
Notonectidae	A	3·6	1·8	82·8	13·8	—	3·4	—	—	—
Odonata										
Anisoptera	A	7·2	1·1	—	—	25	75	—	—	—
Zygoptera	A	1·4	0·2	—	—	66·7	33·3	—	—	—
Undetermined	A	1·4	0·2	—	—	75	25	—	—	—
Orthoptera										
Acrididae	T	11·6	0·9	—	—	8·3	58·4	33·3	—	—
Gryllotalpidae	T	8·0	2·0	—	—	18·2	66·7	15·1	—	—
Gryllidae	T	5·1	0·8	—	7·7	15·4	76·9	—	—	—
Tettigonidae	T	0·7	0·1	—	—	—	—	100	—	—
Undetermined	T	13·0	2·1	—	—	7·7	61·5	30·8	—	—

Hymenoptera										
Formicidae	T	13·0	2·3	37·8	56·8	5·4	—	—	—	—
Sphecidae	T	2·9	0·2	25	75	—	—	—	—	—
Undetermined	T	2·2	0·2	—	66·7	33·3	—	—	—	—
Lepidoptera	T	2·9	0·6	11·1	33·3	44·5	—	—	11·1	—
Mantodea										
Mantidae	T	1·4	0·1	—	—	—	50	—	50	—
Arachnida										
Araneae										
Sparassidae	T	1·4	0·2	—	—	—	33·3	66·7	—	—
Salticidae	T	1·4	0·1	—	—	—	100	—	—	—
Lycosidae	T	1·4	0·2	—	—	33·3	66·7	—	—	—
Araneidae	T	1·4	0·2	—	—	—	33·3	66·7	—	—
Pisauridae										
Undetermined	T	5·1	0·7	—	9·1	9·1	45·5	36·3	—	—
Dolomedes sp.	T	2·2	0·4	—	—	16·7	50·0	33·3	—	—
Undetermined	T	0·7	0·1	—	—	—	100	—	—	—
Scorpionida	T	0·7	0·1	—	—	—	100	—	—	—
Osteichthyes	A	44·2	36·4	—	—	—	47·7	49·9	2·9	0·2
Amphibia										
Leptodactylidae										
Cyclorana sp.	T	0·7	0·1	—	—	—	—	100	—	—
Limnodynastes sp.	T	0·7	0·1	—	—	—	—	100	—	—
Hylidae										
Litoria sp.	T	0·7	0·1	—	—	—	—	100	—	—
Undetermined	T	2·2	0·3	—	—	—	20	60	20	—
Reptilia										
Squamata										
Acrochordidae										
Acrochordus arafurae	A	1·4	0·2	—	—	—	—	—	—	100
Varanidae										
Varanus sp.	T	2·2	0·2	—	—	—	—	—	—	100
Aves										
Undetermined	T	2·9	0·2	—	—	—	—	—	50	50
Mammalia										
Muridae										
Rattus sp.	T	1·4	0·1	—	—	—	—	—	—	100
Microchiroptera	T	1·4	0·1	—	—	—	—	—	100	—
Undetermined	T	2·2	0·2	?	—	—	—	—	—	—

(2) Ranking: the matrix of TS and habitat scores for each animal was ranked according to the scores derived above, and treated as described above.

Although no serious attempt was made to assess prey abundance, in order to gain an indication of whether or not the size of prey taken was random, in the wet season dip-net and sweep-net samples were collected at the water's edge and from amongst semi-aquatic vegetation (where crocodiles were often found); the sizes of items in these samples were compared with those of prey found in stomachs.

Results

Feeding Behaviour

During the present study *C. johnstoni* were often observed feeding in the wild; however, detailed notes were not kept. At night most crocodiles (at least 80% of those sighted) were lying in shallow water on the edge of emergent land, with the cranial platform, eyes and nasal disc above water level. From this position they would strike sideways into the water beside them, and on a number of occasions were seen to grasp small fish, usually pinning them between the most anterior teeth. The fish were shaken with sideways flicks of the head, then manoeuvered posteriorly between the jaws, with vertical jerks of the head.

From the same position at the water's edge, *C. johnstoni* have been observed to snap at and grasp items falling into the water beside them. They have also been seen to submerge from a distance and approach a surface disturbance underwater before emerging and lunging at it. No *C. johnstoni* were observed feeding on land.

Composition of the Diet

Table 1 lists the prey items, with information on whether they are essentially aquatic or terrestrial, the percentage of crocodiles (with food in their stomachs) that contained a particular prey taxon (occurrence), and the percentage of the total recognized prey items belonging to a particular taxon (composition). The target sizes supplied by each taxon are included, but those of vegetation, which is treated separately later, is not.

Clearly, there is a wide taxonomic range of prey, most of which are obtainable at the water's edge. This is consistent with *C. johnstoni* being an opportunistic feeder, especially at the vegetation–water interface.

Partly digested fish proved difficult to identify, and all fish are therefore lumped in Table 1. By matching a reference series of scales to those found in the stomachs, and by recognizing the shapes of some fish, it was possible to determine that some species had been very commonly eaten (*Melanotaenia* sp. and *Ambassis* sp.), others much less so (*Neosilurus* sp. and possibly *Hexanematichthys* sp.), and others only rarely (*Glossamia aprion*, *Leiopotherapon unicolor*, *Oxyeleotris lineolatus*, *Syncomistes butleri* and *Toxotes chatareus*). It is likely that other fish had been eaten but were not recognized (for example, *Fluvialosa erebi* is reasonably common, but its scales are indistinct when partly digested). It is worthy of note that the two most common fish found in the stomachs are both species which school and which were abundant at the water's edge during the latter half of the wet season.

Table 2 contains the relative importance of major taxonomic groups as indicated by different methods. The rankings which resulted from all methods were significantly correlated with each other (Kendall's rank correlation; Siegel 1956), although some pairs of rankings were much more highly correlated than others (Table 3). The two ranking methods (volume and target size area) gave perfect rank correlations, which supports the use of TS for indicating prey importance. These methods ranked aquatic insects as most important, followed by terrestrial insects, fish, crustaceans and spiders. The two dominance methods tested were not as highly correlated with each other, although that using TS was marginally more highly correlated with the ranking method than was that using volume. The dominance methods *per se* tended to reduce the importance of prey items such as spiders, which

Table 2. 'Importance' of taxa and habitats as food sources for *C. johnstoni*, as indicated by different methods of analysis

A, aquatic; T, terrestrial. Under 'Occurrence', as each animal may contain a number of taxa, the total of percentages exceeds 100

Taxon	Ranking		Dominance		Occurrence (%)	Composition (%)
	Target size (%)	Volume (%)	Target size (%)	Volume (%)		
Insecta (A)	30·4	30·5	29·7	32·6	64·5	28·7
Insecta (T)	27·7	27·4	20·3	17·4	65·9	25·5
Osteichthyes (A)	20·4	21·3	29·3	34·1	44·2	36·4
Crustacea (A)	7·9	8·1	8·0	8·7	18·8	5·8
Arachnida (T)	5·4	5·2	0·4	0·0	15·2	1·8
Amphibia (T)	2·6	2·5	2·9	2·9	5·8	0·7
Mammalia (T)	1·8	2·1	2·9	1·4	5·1	0·4
Aves (T)	1·5	1·4	2·9	2·2	2·9	0·2
Reptilia (T)	1·5	0·9	2·2	0·0	2·9	0·2
Reptilia (A)	0·8	0·6	1·4	0·7	1·4	0·2
Total scores	1856	1897	138	138	138	1634

Table 3. Kendall's rank correlation coefficients for comparing importance as indicated by different methods of analysis

All values of *P* are two-tailed

	Ranking by volume		Dominance By TS area		Dominance By volume		Occurrence		Composition	
	τ	$P<$	τ	$P<$	τ	$P<$	τ	$P<$	τ	$P<$
Ranking										
By TS area	*1·00*	6×10^{-7}	*0·69*	5×10^{-3}	*0·63*	9×10^{-3}	*0·94*	3×10^{-5}	*0·90*	$1·2\times10^{-4}$
By volume	—		*0·69*	5×10^{-3}	*0·63*	9×10^{-3}	*0·94*	3×10^{-5}	*0·90*	$1·2\times10^{-4}$
Dominance										
By TS area	—		—		*0·88*	4×10^{-4}	*0·65*	9×10^{-3}	*0·70*	5×10^{-3}
By volume	—		—		—		*0·59*	$2·8\times10^{-2}$	*0·73*	5×10^{-3}
Occurrence	—		—		—		—		*0·86*	4×10^{-4}

were often present (15·2% occurrence) but rarely dominant, and tended to enhance the importance of items such as fish that, when eaten, were usually taken in large numbers (44·2% of animals ate fish, and in 34·1% of animals fish were dominant). The occurrence method was highly correlated with the ranking methods, but tended to enhance items which were commonly eaten but were of small size (terrestrial insects), whereas the composition method, like the dominance method, tended to enhance items which when available were eaten in large numbers.

Of the six methods, we feel the ranking methods give the most realistic indices of importance because they account for both prey size and the proportion of crocodiles eating a particular prey.

Table 4 summarizes the information on target sizes given in Table 1. Prey ranged from TS2 (area of 0·0625 cm^2) to TS8 (area of 256·0 cm^2), the modal size being TS5 (area of 4·0 cm^2). Smaller prey tended to be crustaceans, insects and spiders; intermediate prey were crustaceans, insects, spiders, fish and amphibians; and larger prey mainly vertebrates.

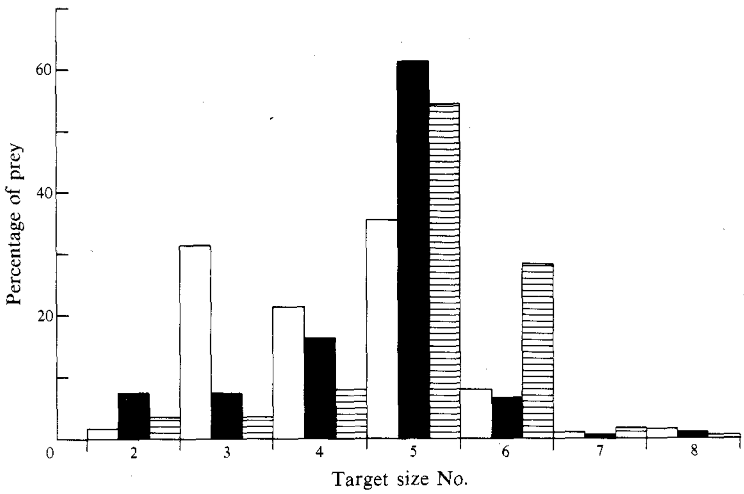

Fig. 2. Distribution according to target size of 1488 items of prey in stomachs of *C. johnstoni* in the wet season. Open bars, prey from stomachs without fish; hatched bars, from stomachs containing fish; solid bars, from stomachs containing fish, but with the fish itself omitted.

Some of the fish eaten (at least *Toxotes chatareus*) also feed on small insects, and ants' heads in some of the samples suggest that secondary ingestion could bias the sample towards small prey. To determine whether or not this bias was important, the distributions of different-sized prey in the stomachs of crocodiles with and without fish were compared (Fig. 2), with the 'with fish' category subdivided so that the fish themselves (TS4–TS8; Table 4) were either included or excluded. Clearly, there was a greater proportion of small prey in the crocodiles which had not been eating fish; secondary ingestion as a source of error was subsequently ignored.

Prey sizes in the samples taken by sweep- and dip-net near the water's edge in the wet season were compared with those in stomach contents in the same season. The distribution of TSs among 335 items from sweep nets and 1488 items from stomachs was:

Target size	In sweep sample (%)	In stomach sample (%)	Target size	In sweep sample (%)	In stomach sample (%)
2	36·7	3·1	6	3·0	23·0
3	28·4	10·8	7	0·6	1·5
4	20·9	11·4	8	0	0·7
5	10·4	49·4			

The difference between the two was highly significant (χ^2; $P<0\cdot001$), indicating that an abundance of smaller items was not being utilized.

Of the 153 *C. johnstoni* examined, 39·9% contained vegetation, and as only one animal had that and no other food, vegetation was in 43·5% of 138 animals with (non-vegetation) food in their stomachs. Vegetation was found almost exclusively in animals caught in the wet season (53 of 101), being present in only 8 of 52 dry-season animals (Fisher's test; $P<0\cdot001$). There was no significant difference in the

Table 4. Percentages of major taxa among 1561 items of prey from the stomachs of *C. johnstoni*, according to target size

A, aquatic; T, terrestrial. Values in parentheses are the percentages of each TS group in each major taxon. No target size could be assigned to 73 prey items

Taxon	*N*	Percentage of target size No.: 2	3	4	5	6	7	8
Crustacea (A)	93	—	39·8	4·8	0·9	1·4	14·3	14·3
		—	*(71·0)*	*(9·7)*	*(7·5)*	*(5·4)*	*(4·3)*	*(2·1)*
Insecta (A)	467	48·1	7·2	35·1	45·9	4·5	—	—
		(5·3)	*(2·6)*	*(14·1)*	*(74·5)*	*(3·4)*	—	—
Insecta (T)	386	51·9	52·4	58·5	15·8	11·3	7·1	—
		(7·0)	*(22·5)*	*(28·5)*	*(31·1)*	*(10·4)*	*(0·5)*	—
Arachnida (T)	30	—	0·6	1·6	2·1	2·8	—	—
		—	*(3·3)*	*(10)*	*(53·3)*	*(33·3)*	—	—
Osteichthyes (A)	559	—	—	—	35·1	77·5	60·7	7·1
		—	—	—	*(47·6)*	*(49·2)*	*(3·0)*	*(0·2)*
Amphibia (T)	11	—	—	—	0·1	2·5	3·6	—
		—	—	—	*(9·1)*	*(81·8)*	*(9·1)*	—
Reptilia (A)	3	—	—	—	—	—	—	21·4
		—	—	—	—	—	—	*(100)*
Reptilia (T)	4	—	—	—	—	—	—	28·6
		—	—	—	—	—	—	*(100)*
Aves (T)	4	—	—	—	—	—	7·1	14·3
		—	—	—	—	—	*(50)*	*(50)*
Mammalia (T)	4	—	—	—	—	—	7·1	14·3
		—	—	—	—	—	*(50)*	*(50)*

proportions containing vegetation of the three size groups (see later) (χ^2; $P>0\cdot5$). In Table 5, vegetation is included as a category and its importance indicated by the ranking method using volume (compare with Table 2, where vegetation is excluded). The reasonably high value for importance of vegetation in the dry season results from the general lack of other prey items in the stomach contents in this season.

In Table 6, the importance of TS and habitat categories, as indicated by different methods, is listed. The preferred ranking method indicates aquatic TS5 prey as the most important, its score being almost twice that of the next most important, aquatic TS6, which is close to terrestrial TS6. The occurrence and composition methods give similar values for the major items, although they tend to weight small abundant items heavily. Conversely, the dominance method indicates aquatic TS6 as being marginally more important than aquatic TS5 and, in general, weights the large prey as being more important than small prey.

Variation in Diet with Body Size

To determine whether or not different-sized *C. johnstoni* eat different-sized prey, contingency tables were constructed for 5-cm increment categories of snout–vent

Table 5. Seasonal variation in the importance as food for *C. johnstoni* of major taxa, with vegetation included

Importance is estimated by the ranking method using volume of prey items; target size could not be applied to vegetation

Taxon	Wet season (%)	Dry season (%)	Total (%)
Insecta (A)	23·9	33·9	25·8
Insecta (T)	22·1	26·0	22·8
Osteichthyes (A)	21·4	4·7	18·3
Vegetation	16·7	12·4	15·9
Arachnida (T)	5·1	0·0	4·2
Crustacea (A)	4·1	18·3	6·8
Amphibia (T)	2·3	1·7	2·2
Mammalia (T)	2·1	0·0	1·7
Aves (T)	1·1	1·7	1·2
Reptilia (A)	0·6	0·0	0·5
Reptilia (T)	0·6	1·2	0·7
Total scores	1768	404	2172

Table 6. Relative importance in the diet of *C. johnstoni* of foods grouped according to target size and habitat, as estimated by four different methods

Each animal may contain a number of different taxa, so the percentages under 'Occurrence' add up to >100

Target size and habitat	Ranking (%)	Dominance (%)	Occurrence (%)	Composition (%)
5A	24·6	24·6	66·4	39·8
6A	14·8	26·9	38·1	19·0
5T	12·5	8·2	35·8	8·8
4T	9·7	3·7	28·4	7·2
4A	8·4	5·2	29·1	4·8
6T	8·3	4·9	19·4	3·8
7A	6·2	11·2	14·9	1·3
3T	5·4	1·5	26·1	5·6
8T	2·7	6·0	7·5	0·7
2T	2·3	0·7	11·2	1·7
7T	2·1	4·1	3·7	0·4
3A	1·8	0·7	7·5	5·0
8A	0·9	2·2	1·5	0·2
2A	0·2	0·0	1·5	1·6
Total scores	2582	134	134	1561

length (SVL), and the range of prey TSs. By isolating subsets of this table it was possible to show that three size groups were homogeneous within themselves, but were significantly different from each other at the 5% level. Prey size (Table 7) clearly increased between groups 1 (16–25 cm SVL) and 2 (26–55 cm SVL), and only marginally increased between groups 2 and 3 (56–129 cm SVL). TS4 was the most abundant prey in group 1, and TS5 in groups 2 and 3.

With increasing body size there is a shift from terrestrial to aquatic prey: nine group 1 crocodiles contained 55 aquatic and 75 terrestrial items, 51 group 2 contained 524 and 255, and 78 group 3 contained 581 and 144, respectively (χ^2; $P<0\cdot005$).

In Table 8 the TS categories are listed according to their importance as indicated by the ranking method for TS; indices of dominance, occurrence and composition are included. TS5 was the most important prey size in all crocodile size groups, even though TS4 was most abundant in group 1 (Table 7).

Table 7. Distribution of target size of prey items from *C. johnstoni* of different sizes

Wet and dry seasons combined. Total prey items 1561; five animals each contained one item of indeterminable TS

Group No.	SVL (cm)	Number of: Croco-diles	Prey items	Percentage in target size No.: 2	3	4	5	6	7	8
1	16–25	9	128	1·6	15·6	40·6	35·2	7·0	—	—
2	26–55	50	740	5·3	13·4	11·7	47·6	20·3	1·3	0·4
3	56–129	74	693	1·6	6·8	7·1	52·1	28·3	2·6	1·6

Table 8. Relative importance of different-sized prey to small, medium and large *C. johnstoni*, as estimated by four different methods

Each animal may contain a number of different taxa, so the percentages for 'Occurrence' add up to >100

SVL (cm)	Method	Percentage in target size No.: 2	3	4	5	6	7	8	Total score
16–129	Ranking	2·9	9·5	18·1	32·8	22·6	9·4	4·8	1612
	Dominance	0·7	1·5	10·8	33·2	30·6	14·2	9·0	134
	Occurrence	11·2	29·9	44·0	76·1	47·8	17·9	9·7	134
	Composition	3·3	10·6	12·0	48·6	22·7	1·8	0·9	1561
16–25	Ranking	3·5	14·9	26·6	35·5	19·5	0	0	141
26–55	Ranking	2·1	7·8	21·3	31·9	24·8	8·5	3·6	660
56–129	Ranking	3·3	10·0	13·9	33·0	21·5	11·7	6·5	811

Variation in Diet with Season

Of the 101 *C. johnstoni* examined during the wet season, 5·9% had empty stomachs, compared with 19% of 52 caught in the dry season (χ^2; $P<0\cdot001$). In the wet-season sample there was an average of $16\cdot2\pm22\cdot9$ (SD) prey items per crocodile, compared with $1\cdot8\pm1\cdot0$ in the dry season. TS5 items were the most important in both seasons, as follows:

Target size	Wet season (%)	Dry season (%)	Target size	Wet season (%)	Dry season (%)
2	2·4	4·9	6	23·3	19·7
3	10·1	6·9	7	9·3	9·9
4	16·5	24·7	8	4·5	5·9
5	33·9	28·0	Total score	1308	304

Table 9 shows that there was significantly more food in the stomachs of groups 2 and 3 in the wet than in the dry season (group 1 animals were not caught in the dry season). In groups 2 and 3 it was also possible to investigate differences in the proportions of aquatic and terrestrial prey eaten. In group 2 there was no significant difference between the seasons (dry: 9 aquatic, 6 terrestrial; wet, 515 aquatic, 249 terrestrial); this could reflect the small dry-season sample. In group 3, however, significantly more aquatic prey was eaten during the wet season (dry: 40 aquatic, 22 terrestrial; wet: 541 aquatic, 122 terrestrial; χ^2; $P<0\cdot005$).

Table 9. Weights and volumes of stomach contents of *C. johnstoni*

Weights of stones in the stomachs are not included. Means are ± standard deviations. Significance tested by *d*-statistic (Bailey 1974)

SVL (cm)	Wet season Mean	Range	*N*	Dry season Mean	Range	*N*	Significance
			Weight (g)				
16–25	8·3±4·3	2·7–15·9	9	—	—	0	—
26–55	24·4±17·0	2·1–66·6	37	4·0±3·5	0·7–9·6	8	$P<0\cdot001$
56–115	34·7±45·5	2·3–158·6	45	5·7±6·5	0·6–27·1	20	$P<0\cdot001$
			Volume (ml)				
16–25	6·6±3·6	3·5–15·6	9	—	—	0	—
26–55	21·9±16·3	0·1–65·4	37	5·88±3·83	0·8–12·6	8	$P<0\cdot001$
56–115	29·9±38·9	2·0–171·1	45	8·3±7·1	0·6–28·5	20	$P<0\cdot001$

Table 10 demonstrates the importance of different taxa and target size categories from the first and second halves of the wet-season sampling period. Clearly, fish became far more important in the second half, replacing mainly aquatic insects. TS5 was the most important size of prey in both periods, although there was a substantial increase in the importance of TS6 during the second period, reflecting the generally larger size of fish (Table 4).

Stomach Stones

Of the 153 *C. johnstoni* examined, 88·2% contained stones in the stomach. Regression analyses were used to indicate basic trends, and to allow stone loads to be predicated for comparison with other species. These analyses indicated that:

(1) Total stone weight (S, in grams) increased with increasing body weight (B, in grams) ($\ln S = -5\cdot7382+0\cdot8906\ \ln B \pm 1\cdot2411$; $r^2=0\cdot38$; errors are the standard error of estimates; Zar 1974);

(2) Total stone weight as a proportion of body weight ($r^2=0\cdot03$) showed no significant increase or decrease with increased body weight; mean value of this proportion was $0\cdot0022\pm0\cdot0020$ (SD);

(3) Mean stone weight S_x increased with increasing body weight ($\ln S_x = -6\cdot0927+0\cdot4790\ \ln B\pm0\cdot5629$; $r^2=0\cdot46$);

(4) Number of stones (N_s) increased with increasing body weight, but was extremely variable ($r^2=0\cdot14$) ($N_s=-148\cdot81+28\cdot03\ \ln B\pm76\cdot41$). Mean N_s was $78\cdot50\pm82\cdot00$ (SD);

(5) The weight of the largest stone S_L increased with increasing body weight ($\ln S_L=-6\cdot3520+0\cdot7111\ \ln B\pm0\cdot6491$; $r^2=0\cdot59$).

Together, these data indicate that the weight of stones in the stomach increased with increased body weight of *C. johnstoni*, and that this increase was primarily due to increasing size of the stones, although there was a slight increase in their number. The relationship between number of stones and body weight was extremely variable, as was that between total weight of stones (as a proportion of body weight) and body weight.

Table 10. The importance of taxon and target size of prey in the first and second halves of the wet season, as estimated by the ranking method using target size

	First half (%)	Second half (%)	Total (%)
Taxon			
Insecta (A)	41·5	19·6	28·3
Insecta (T)	22·4	30·6	27·4
Osteichthyes (A)	14·5	30·5	24·2
Arachnida (T)	5·9	7·2	6·7
Amphibia (T)	5·5	0·9	2·8
Crustacea (A)	4·2	5·3	4·8
Mammalia (T)	3·5	1·4	1·4
Reptilia (A)	1·8	0·8	0·9
Aves (T)	1·2	1·5	1·4
Reptilia (T)	0	2·2	1·3
Total scores	597	912	1509
Target size No.			
2	1·7	2·8	2·4
3	11·7	9·1	10·1
4	14·8	17·6	16·5
5	39·5	30·2	33·9
6	17·3	27·2	23·3
7	9·2	9·3	9·3
8	5·8	3·7	4·5
Total scores	519	789	1308

Analysis of covariance (Snedecor and Cochran 1972; Bailey 1974) was used to determine whether or not the parameters associated with stomach stones were independent of wet and dry seasons, although seasonal effects may be confounded by differences between areas sampled in the two samples. Equivalent ranges of *C. johnstoni* size were selected (37–115 cm SVL), because the wet-season sample contained more smaller animals. In addition, SVL rather than body weight was used as the independent variable, because during the dry season some *C. johnstoni* lose weight (Webb *et al.* 1983*a*). These comparisons indicated that:

(1) Total stone weight as a function of SVL (L, in centimetres) increased at the same rate in both wet and dry seasons; however, the 48 dry-season stone weights were significantly greater than the 66 wet-season weights (intercepts, $F = 5\cdot33$; 1,110 d.f.; $0\cdot025 < P < 0\cdot01$) (dry: $\ln S = 0\cdot0786 + 0\cdot0323L \pm 1\cdot027$; wet: $\ln S = -0\cdot7784 + 0\cdot0375L \pm 1\cdot292$).

(2) Mean stone weight increased, with increasing SVL, significantly faster during the wet than the dry season (slopes: $F = 14\cdot16$; 1,110 d.f.; $P < 0\cdot001$) (dry: $\ln S_x = -3\cdot238 + 0\cdot0148L \pm 0\cdot5102$; wet: $\ln S_x = -4\cdot0836 + 0\cdot0354L \pm 0\cdot4168$).

The two lines intersect at 41 cm SVL, indicating that in animals below this size mean stone weights are highest in the dry season, but in those above this length weights are highest in the wet season.

(3) The above trend was also evident with the weight of the largest stone, where the two regressions were significantly different (slopes, $F = 4 \cdot 36$; 1,110 d.f.; $0 \cdot 05 > P > 0 \cdot 025$) (dry: $\ln S_L = -1 \cdot 6866 + 0 \cdot 0231L \pm 0 \cdot 6821$; wet: $\ln S_L = -2 \cdot 8589 + 0 \cdot 0388L \pm 0 \cdot 5878$). The size at intersection was 75 cm SVL, indicating that in *C. johnstoni* below this size the largest stone tended to be smaller during the wet than the dry season, whereas above this size it was smaller during the dry season.

(4) During the wet season the number of stones and SVL were not significantly correlated (*F* test: $P = 0 \cdot 64$, mean value $52 \cdot 6 \pm 43 \cdot 8$ (SD). During the dry season, the regression slope was significant, with the number of stones increasing markedly with increasing SVL (dry: $N_s = -18 \cdot 94 + 2 \cdot 36\, L \pm 44 \cdot 04$).

Together, these data indicate that total stone loads for crocodiles of a given size were higher in the dry than in the wet season. The increased load resulted primarily from an increase in the number of stones, as mean stone weight and size of the largest stone tended to be higher in the wet than in the dry season.

Parasites

Of the 153 *C. johnstoni* examined, 57 contained nematode worms in the stomachs. There were significantly more animals with nematodes during the wet season ($49 \cdot 5\%$; $n = 101$) than during the dry season ($13 \cdot 5\%$; $n = 52$) (χ^2; $P < 0 \cdot 001$), although this could in part reflect the differences in area. Volumes of parasites, when present, ranged from less than $0 \cdot 1$ ml to $2 \cdot 0$ ml during the wet season (mean, $0 \cdot 301 \pm 0 \cdot 38$). During the dry season, six *C. johnstoni* had less than $0 \cdot 2$ ml, and one had 5 ml.

Identification of the parasites in 50 samples indicated that the most predominant species was *Dujardinascaris* sp. (96% of samples), followed by *Eustrongylides* sp. (14%), *Contracaecum* sp. larvae (6%), *Physaloptera* sp. (2%) and *Goezia fluviatilis* (2%).

In the wet-season sample, there were significant differences in the proportion of different-sized *C. johnstoni* that contained parasites: group 1 (11%; $n = 9$) and group 3 (32%; $n = 50$) were not significantly different from each other (Fisher's test; $P > 0 \cdot 05$), but both had significantly fewer infested animals than group 2 (79%; $n = 42$; $P < 0 \cdot 001$).

Discussion

Taxonomic and Prey Equivalents

The taxonomic range of prey eaten by *C. johnstoni* and other crocodilians is extensive (for example, see lists in: Corbet 1960; Cott 1961; Fogarty and Albury 1968; Graham 1968; Valentine *et al.* 1972; Staton and Dixon 1975; McNease and Joanen 1977; Gorzula 1978 and Taylor 1979), and includes invertebrates and vertebrates from both terrestrial and aquatic environs. In general terms, insects and crustaceans appear the most common prey of smaller crocodilians, fish being eaten by crocodiles from intermediate to large size. Birds and mammals appear a more important food source for larger crocodilians. Amphibians and reptiles, although important to a wide range of sizes in some areas (e.g. Gorzula 1978) are less important in other areas (e.g. *C. johnstoni* in this study).

Other than these general trends, the literature contains a large amount of information on what particular species in specified areas were eating at specified times. It clearly demonstrates that the taxonomic suite of prey items varies with size of the crocodile, habitat, season and geographic region (see, in particular: Graham 1968; McNease and Joanen 1977; Gorzula 1978), and there are virtually no data showing marked preferences for specific prey which cannot be interpreted as simply the availability of that prey. The conclusion reached by most authors—that crocodiles eat anything available to them within acceptable (but usually unspecified) size limits—is difficult to challenge.

Similarly, *C. johnstoni* appears to be an opportunistic feeder. Towards the end of the wet-season sampling period, for example, fish replaced insects as the most important food item; at that time fish were noticeably abundant as the floodplains drained back into more permanent pools. The overall impression created in this study was that an abundance of any suitable-sized prey at the water's edge is reflected in the diet, and the taxonomic list was a list of potentially important prey, dependent on availability.

The use of prey equivalents based on size and area of origin overcomes some of the variability, associated with prey taxonomy, that makes comparative studies difficult. The range of different-sized prey available must ultimately determine what can be eaten. However, that the size of *C. johnstoni*'s prey increases with the size of individual suggests that a wide range of prey sizes is available, if all crocodiles are equally equipped to feed on them. From the point of view of quantifying diet, we believe it may often be more informative to emphasize prey equivalents, and discuss prey taxonomy within that framework. For example, the size of prey eaten by *C. johnstoni* between 26 and 55 cm SVL is homogeneous, and consists of prey between TS2 and TS8, the most important prey being TS5. The prey comes primarily from the water's edge, and in the Mary–McKinlay system is composed of 32·7% terrestrial fauna (mainly insects) and 67·3% aquatic fauna (fish and insects).

Clearly, there are often instances where specific predator–prey relations need to be examined and the taxonomic listing is critical (e.g. where parasite life cycles may be under study; *A. mississippiensis* feeding on fur-bearing animals and sporting fish; McNease and Joanen 1977). However, if the aim is to quantify diet in a manner amenable to intraspecific predictions and interspecific comparisons, such precision may often be redundant.

The criterion of target size is a workable form for assessing prey equivalents, but is also limited. It would be difficult to account for carrion with such a measure (although carrion feeding was not indicated by the stomach contents of *C. johnstoni* in this study). Vegetation poses similar problems, and has been treated separately here.

Schooling by small prey also creates difficulties in the application of the target size concept. A single shrimp (of, say, TS2) may not induce a feeding attack, whereas the stimulus of a dense school (with an apparent TS5) may. On the basis of stomach contents data alone, no decision can be made as to whether single animals or a school evoked the feeding response, and thus the smallest TS categories may be over-represented in any analysis.

Secondary Ingestion

The suggestion that insects are usually obtained by secondary ingestion (Neill 1971), and are not primary food items, is simply not substantiated by the mass of data available (Schmidt 1924; Kellogg 1929; Smith 1931; Giles and Childs 1949; Corbet 1959, 1960; Cott 1961; Pooley 1962; Modah 1967; Chabreck 1971; Powell 1972; Staton and Dixon 1975; Blomberg 1975, 1977; Gans and Pooley 1976; McNease and Joanen 1977; Taylor 1979). Insects are quite probably the most important prey item of small crocodiles. As pointed out by Jackson *et al.* (1974), and found in the present study, *some* insect remains may be acquired through secondary ingestion, but in most feeding situations this proportion is probably insignificant.

Relative Importance of Prey

(i) *Taxonomic*

As stated previously, it is generally assumed that the calorific value of prey and the metabolic costs of obtaining and assimilating it remain relatively constant, such that importance can be estimated on the basis of the numbers or amount of a particular prey eaten, and the proportion of the population eating it. Although we recognized that the above assumptions need testing, we examined indices of importance with the dual aims of identifying a suitable method for crocodilians and testing whether or not the data scored in terms of target size gave results equivalent to those of more conventional approaches.

The literature contains a diverse range of computations which have been used to assess importance of crocodilian prey. The most common approach has been by way of occurrence, the percentage of crocodilians eating a particular prey taxon (Kellogg 1929; Giles and Childs 1949; Corbet 1960; Cott 1961; Graham 1968; Valentine *et al.* 1972; Staton and Dixon 1975; Blomberg 1977; McNease and Joanen 1977; Taylor 1979). This has usually been combined with extremely variable measures of composition. Some authors have presented composition by numbers (Kellogg 1929; Cott 1961; Staton and Dixon 1975; Gorzula 1978), whereas others have used volume or weight of prey, both as found in the stomachs (Fogarty and Albury 1967; Valentine *et al.* 1972; McNease and Joanen 1977) or when reconstituted (Chabreck 1971; Valentine *et al.* 1972 (his 1964 data); Staton and Dixon 1975; Taylor 1979). In presenting data, some authors give percentages of the total sample, others exclude empty stomachs and others both empty stomachs and those with fragments. Vegetation, parasites and stones have similarly been excluded or included by different authors. Indications of 'importance' have usually been derived by comparing the values for occurrence and composition, only Staton and Dixon (1975) combining them in a single importance index (following Pinkas *et al.* 1971). As a generalization, the variation in methodologies restricts comparisons to broad trends in the most important food items.

One advantage of a single importance index lies in the objective ranking of importance, in a form amenable to comparative studies. Percentage occurrence and percentage composition (by numbers) both give valuable data, but as importance indices *per se* (Table 2) do not account for prey size. Percentage composition by volume or weight is far more meaningful, although it still does not account for the number of animals eating a particular prey. The dominance method underestimates prey which are always present but rarely dominant. We feel that the ranking method (Pollard 1973) gives the most realistic compromise of the methods we tested; the results achieved by using volume of food in the stomach and target size areas were almost identical (Table 2). The argument of whether reconstituted size of prey or actual volume in the stomachs should be used (Taylor 1979) can be avoided by using target sizes; however, if a choice between the two were necessary, actual volume (or weight) would appear to give a more realistic value from which to discuss importance. Reconstituted size of prey overestimates the importance of large food items, which take longer to digest. The target size method weights large food items on the basis of area rather than volume, and thus substantially reduces the full weighting of reconstituted volume or mass.

(ii) *Prey equivalents*

By the same arguments as stated previously, reliance on the taxonomy of prey rather than prey equivalents detracts from the broad comparative value of the data. The listing of importance by the ranking method based on target sizes (Table 6) gives an objective ranking of prey equivalents which should be comparable with data from other species in other areas.

Size of Prey versus Size of Crocodile

Although it is generally recognized that size of prey increases with size of crocodilian, the relationship has usually been inferred from taxonomy (Cott 1961) and has seldom been quantified. Taylor (1979) found no significant change in prey size of *C. porosus* up to 90 cm SVL, although wide variances may have masked more subtle differences. Crocodilians tend to maintain their ability to eat small prey while the maximum size of their prey steadily increases (Gans and Pooley 1976; Valentine *et al.* 1972).

C. johnstoni showed a significant increase in maximum size of prey with increased body size, although the size of prey most commonly eaten changed only marginally. With few data available for comparison, *C. johnstoni* cannot be compared with other species in this respect, but from the literature it would appear that *C. johnstoni* feeds on smaller prey than do most other crocodilians.

Seasonal Changes in Diet

The most dominant seasonal changes which affect crocodilian feeding appear to be temperature and, indirectly, rainfall. In the analysis of factors affecting growth in *C. porosus*, it was found that during the wet season growth was greater than in the dry season, and that in the coolest part of the year (early dry season) the growth of larger crocodiles was more impaired than was that of smaller ones (Webb *et al.* 1978). In *C. johnstoni*, growth in the dry season appears negligible in animals of all sizes (Webb *et al.* 1982*a*).

These same trends, to a greater or lesser extent, appear to affect most species. *A. mississippiensis* ceases feeding in the winter, although smaller individuals may remain active on warm days (Chabreck 1966). *C. johnstoni* in the McKinlay River system take little food in the dry season (independent of temperature cycling), which may reflect prey availability more than low temperatures. *C. niloticus*, larger animals in particular, reduces food intake in cold weather, and may utilize concentrations of food as water levels recede during the dry season (Pooley 1962; Gans and Pooley 1976). *Caiman crocodilus* isolated in Llanos pools may have an abundance of food available during the dry season (Staton and Dixon 1975; Gorzula 1978), whereas in many *C. johnstoni* dry-season refuges food seems wanting, with the wet season bloom of insects and fish appearing to be the major source of food.

Vegetation

The importance of vegetation in crocodilian diets remains something of a mystery. On the basis of volume in *C. johnstoni* stomachs, vegetation was important (Table 5), and was particularly so during the wet season. This is consistent with accidental ingestion, as much more food was eaten during the wet season. If it were a food, one would expect it to be available during the dry season, when normal prey appears scarce. On the other hand, a captive *A. mississippiensis*, held in a large pool in Louisiana, which was not fed for a week to facilitate capture, was found to have its stomach packed full of *Phragmites* roots and stems, and in fact most crocodilians which have been studied have had from small to substantial amounts of vegetation in their stomachs: *A. mississippiensis:* Kellogg 1929; Chamberlain 1930; Giles and Childs 1949; Fogarty and Albury 1968; Valentine *et al.* 1972; McNease and Joanen 1977; *Caiman crocodilus:* Staton and Dixon 1975; *Crocodylus niloticus:* Corbet 1959; Blomberg 1977; *Crocodylus porosus:* Taylor 1979.

Stones

The load of stones carried in the stomachs of crocodilians varies considerably. In *C. johnstoni* some 88·8% of animals had stones, which are readily available in the study habitat. In contrast, Taylor (1979) found stones in only 0·4% of juvenile *C. porosus* examined in the essentially stoneless, muddy, tidal rivers of Arnhem Land. Cott (1961) demonstrated very clearly that whether or not juvenile *C. niloticus* contained stones was dependent on the availability of stones in the environment in which they were found; however, all larger *C. niloticus* had them independent of environment. This clearly indicates travel from the stoneless sites, though not necessarily for the reason of picking up stones. As with *C. niloticus*, most adult *C. porosus* contain stones (personal observations), even though the area they live in may be stoneless. Cott (1961) discussed the theories related to stomach stones: namely, that they were of gastrolithic value, hydrostatic value, or functioned to keep the stomach expanded during times of fasting. None of these functions need be mutually exclusive, and it would seem likely that the stones fulfil at least gastrolithic and hydrostatic functions to some degree.

Cott's (1961) arguments for a hydrostatic function seem sound for *C. niloticus*. Stone loads of up to 2·7% of body weight would effectually increase weight in the water by nearly 25%, their position on the ventral surface giving stability. The hunting strategies of larger crocodiles appear to involve more deliberate attacks on single prey items, often after a submerged approach (Abercromby 1913; Cott 1961; Pooley 1962; Gans and Pooley 1976). In contrast, smaller crocodiles are eating smaller prey, which can usually be obtained from a resting position at the water's edge; the hydrostatic value of stones would not appear to be as important.

The stone loads of larger *C. niloticus* are much greater in proportion to body weight than are those of *C. johnstoni* (Table 11). If the hydrostatic function is a major one, it would appear less important in *C. johnstoni* than in *C. niloticus*, which is consistent with larger individuals of *C. johnstoni* continuing to eat mostly small prey from the water's edge. The *C. niloticus* studied by Cott (1961) were in good condition (compared with those from Lake Rudolph; Graham 1968) and could be expected to have large amounts of low-density (buoyant) body fat; the stone load could well have been compensating for the effect of the fat.

Regardless of hydrostatic function, the stones must play some gastrolithic role

(Diefenbach 1975). The mean number of stones in *C. johnstoni* was 79, providing a substantial surface area for the breakdown of food.

The degree to which stones could keep the stomach expanded is unknown, and whether or not such a function is important remains to be tested. However, we noted in the field that the stomachs of animals examined during the dry season had thick walls and much reduced volumes, in comparison to those examined in the wet season (when substantially more food was being consumed), which were thin-walled and expanded. Chabreck (1971) reported similar alterations in the stomach volume of *A. mississippiensis* from saline and freshwater marshes, and it would appear that fasting or reduced food intake results in a contraction of the stomach. The increased stone loads in the dry-season sample were significant and are consistent with the above theory; however, because our samples were not from exactly the same area, this difference could be geographic rather than seasonal. If compensation for the effect of fat by the stone load were important, one would expect *C. johnstoni* to enter the dry season with relatively large loads.

Table 11. Body weights and gastric stone weights of *C. johnstoni* and *C. niloticus* compared

Values for *C. niloticus* from Cott (1961)

Crocodile body wt (kg)	*C. johnstoni*		*C. niloticus*	
	Stone wt (g)	Percentage of body wt	Stone wt (g)	Percentage of body wt
0·22	0·00	0·00	0·00	0·00
1·60	2·30	0·14	1·65	0·10
4·57	5·85	0·13	12·94	0·28
17·20	19·06	0·11	105·7	0·62
40·87	41·20	0·10	270·7	0·66

The question of purposeful or accidental ingestion is far from clear. The relationship between mean (and maximum) stone size and body size indicates that there is a definable threshold at which stones are not swallowed, which increases with increased body size. The size of stone actually swallowed is, however, well below the size of prey that can be eaten, which is consistent with accidental ingestion. On the other hand, if the weight of stones in the stomach was not controlled by a feedback mechanism, crocodiles in stony areas would tend to gradually fill up with stones, which has not been found in *C. johnstoni* or reported in other species. It would appear that observations and experiments with captive animals (Brazaitis 1969) may give some insights into the many questions about crocodilian stomach stones yet to be satisfactorily answered.

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