J. Zool., Lond. (1990) **220,** 569–592

Food capture, appetite, digestion rate and efficiency in hatchling and juvenile *Crocodylus porosus*

J. DAVENPORT, D. J. GROVE, J. CANNON, T. R. ELLIS AND R. STABLES

School of Ocean Sciences, University College of North Wales, Marine Science Laboratories, Menai Bridge, Gwynedd LL59 5EY, UK

(Accepted 26 June 1989)

(With 12 plates and 7 figures in the text)

Juvenile estuarine crocodiles captured insects and crabs at or above the water surface by leaps and lunges powered by the hind limbs and tail. The mouth opened as the head cleared the water; most prey were held by sidesnaps of the jaws. Such prey capture was accurate, deliberate and preceded by stalking. In contrast, submerged prey (e.g. prawns) appeared to be detected mainly by touch and detection was followed by undirected, inaccurate 'snapping frenzies' which were usually ineffective. Small prey items were swallowed whole under water. Large dense prey (e.g. crabs) were handled and swallowed on land or in very shallow water; large less dense prey (e.g. cockroaches) were swallowed during vigorous water-treading in deep water, the head being maintained above the water surface.

Young crocodiles ate satiation meals of 9–10% body weight (on a fresh food weight basis) at 30 °C, and appetite returned over about 40 h as the stomach emptied. Total gut clearance time for a meal was 4–5 d. Evidence was obtained which demonstrated that young *Crocodylus porosus* Schneider deliberately eat gastroliths from an early stage. Such gastroliths are retained within the stomach (as were barium/polystyrene spheroids of 1 mm diameter) presumably by the action of the well-developed pyloric sphincter. X-radiographs demonstrated that gastroliths are dispersed throughout the stomach contents after a meal and presumably aid digestion.

Assimilation rates for dry mass (77·5%), energy (85·2%) and protein-N (97·4%) were high in normal juveniles. Animals exhibiting 'runt syndrome' showed strong appetite but slow food processing by the gut, together with poor assimilation, especially of protein (35·7%).

Contents

0952-8369/90/004569 + 24 $03·00

© 1990 The Zoological Society of London

Introduction

Crocodilians are the largest living reptiles and, before Man's intervention, were the top predators of freshwater and estuarine ecosystems throughout tropical and subtropical areas. Effective burst swimming and striking in water, combined with a surprising turn of speed on land (adult crocodiles can gallop at up to 40 km h^{-1} for short distances) allow crocodilians to exploit a wide variety of terrestrial, amphibious and aquatic prey.

Despite the visibility of crocodiles, alligators and caimans, their ferocity and fascination as the sole remnants of the once-dominant archosaurs, it was not until the work of Cott (1961) on the Nile crocodile (*Crocodylus niloticus* Laurenti) that a detailed picture of feeding changes during development was presented for any crocodilian. Cott found that hatchling crocodiles were predominantly insectivorous, progressed through a phase of frog- and fish-eating as they grew during the first few years of life, and only when much larger (2+ m) did they rely heavily upon eating mammals and birds. Similar changes in diet, with minor variations reflecting the available prey organisms, have since been recorded from most other crocodilian species (see IUCN, 1982, for review), although adult slender-snouted crocodilians (e.g. the Australian freshwater crocodile *Crocodylus johnstoni* Krefft and the gharial *Gavialis gangeticus* (Gmelin)) tend to specialize in fish eating.

Studies of the nutrition of wild crocodilians have rarely gone beyond analyses of stomach contents (the studies of Diefenbach (1975*a*, *b*) on gastric function in *Caiman crocodilus* (L.) being the main exception), but the increasing economic importance of crocodile and alligator farming and ranching has generated interest in artificial diets and their adequacy for captive animals. Members of the Family Alligatoridae (alligators and caimans) are now believed to be of wholly freshwater ancestry. They seem to need red meat in their diet, and are apparently adversely affected by the long-chain fatty acids of marine fish flesh (Ferguson, 1981; Lance, 1982). On the other hand, true crocodiles (Family Crocodylidae), which are now thought to be of marine ancestry, following the work of Taplin & Grigg (1981) and Taplin (1984), have a requirement for such long-chain fatty acids, especially in the case of the estuarine crocodile *Crocodylus porosus* Schneider (Garnett, 1985).

From the available literature it was apparent that there were gaps in knowledge concerning food handling and digestion in crocodilians. First, although adult body rolling to tear food from large carcasses had been well known since the 19th century, and Pooley & Gans (1976) reported that *C. niloticus* herded small fish into shallow water with its tail (before striking sideways with the jaws), there had been no published account of details of food capture and subsequent handling, particularly in young crocodilians. Secondly, knowledge of appetite, appetite return, meal residence time in different parts of the gut and digestive efficiency was limited for crocodiles (though some data are available for *Alligator mississippiensis* (Daudin) and *Caiman crocodilus*; Coulson & Hernandez, 1964, 1970; Diefenbach, 1975*a*, *b*). Finally, the long-standing controversy over the function of gastroliths was yet to be resolved. Most workers from the earliest investigations (e.g. Oppel, 1896; Gadow, 1901; Biedermann, 1911: 1272–1282; Friant, 1941) onwards have believed (by analogy with birds) that crocodiles eat stones to help in the digestion of food; the anatomy of the musculature of the gizzard-like fundus of the stomach supports this hypothesis. However, Cott (1961) suggested that the stones swallowed by *C. niloticus* were ingested solely as ballast to allow animals beyond their first year to achieve negative buoyancy, and this concept has been quoted widely. Even the hypothesis that crocodilians deliberately swallow stones has been supported by circumstantial rather than experimental evidence; stone ingestion could be accidental whilst feeding on bottom-dwelling organisms (Brazaitis, 1969), or could be derived from the stomachs of prey (Neill, 1971).

The study described here was designed to fill as many of these gaps in knowledge as possible within the limitations imposed by working in the UK upon a relatively small number of young crocodiles. The investigation was carried out upon hatchling and juvenile *C. porosus*; this species was chosen because it is the mainstay of crocodile farming in South-east Asia and Australasia (so that data ought to be of significance to aquaculture), and because its extensive estuarine distribution (from Sri Lanka in the west to Fiji in the east, and as far south as northern Australia) offers subadult animals an unusually wide range of invertebrate and vertebrate prey, including carabid beetles, sesarmine crabs, prawns of the genus *Macrobrachium*, gobies, rats, fruit bats and dead marsupials (Taylor, 1979). During the course of the study, the opportunity arose to investigate juvenile estuarine crocodiles suffering from 'runt syndrome', a common feature of farmed (and presumably wild) crocodilians of several species. Expressed as a failure to grow despite an apparently adequate appetite, the etiology of this syndrome is obscure. Rate of progress of food along the gut and the efficiency of digestion were investigated in one runt animal for comparison with the normal animals; runts were also dissected and the gut inspected for gross signs of abnormality.

Materials and methods

Collection and maintenance

Twelve hatchling salt-water crocodiles (each about 50 g in weight) were sent from a crocodile farm in Australia (under appropriate CITES permits) to Menai Bridge in May 1987. The animals were held in a mesh-covered holding tank (5 m long × 0·4 m wide × 0·6 m deep) fitted with a feeding platform reached by gently sloping ramps. The holding tank was supplied with recirculating low-salinity water (usually fresh water, but sometimes with added sea water to a maximum of 8‰ as this is known to promote good skin condition (G. C. Grigg, pers. comm.). The water, held at 30 °C, was pumped through a biological filter and header tank; about a third of it was replaced every 2–3 days as faeces and food scraps were siphoned away.

Routine *ad lib.* feeding was upon fish or squid available in the laboratories (mackerel, trout, sprat and whiting figured in their diet on various occasions). Chopped whole food organisms were used to ensure plenty of calcium in the diet. Daily feeding proved to be wasteful, the animals showing a poor appetite and feeding only over a prolonged period. Instead, the animals were fed on every second day; this resulted in rapid consumption of meals. Locusts, cockroaches and shore crabs were also fed to the animals occasionally.

Between May 1987 and September 1987 the animals were not experimented upon, but allowed to become used to laboratory conditions and handling. Eight of the animals grew to about 100 g during this period, one grew to 170 g, while the remaining 3 exhibited various degrees of 'runt syndrome', characterized by negligible or slight growth despite a good appetite; one of the runts died before the end of the period of acclimation and was dissected.

All experiments were carried out between September 1987 and July 1988. One animal continued to grow more quickly than the others and reached 550 g at the end of the experimental period. Most of the others reached 250–350 g, while the remaining runts grew to no more than 75–80 g before losing weight dramatically and dying in March and April 1988.

Filming of feeding behaviour

Feeding crocodiles were filmed with a Panasonic WVP-F10E videocamera fitted with a 'high speed' strobe-effect shutter. This shutter results in information being recorded for only 0·001 s during each video field; effectively a 0·001 s 'still photograph' is taken every 0·04 s. The system allows blur-free recording of reasonably fast movement, but requires strong illumination of the filmed object and some colour information is lost. All filmed action took place in a glass tank (1·2 m long, 0·4 m high, 0·3 m wide) filled to a depth of 0·25 m with fresh water held at 30 ± 0·5 °C, and with a 2 cm square grid drawn upon 3 of its sides to allow distances and directions to be assessed from videotape (Davenport & Sayer, 1989). Movement was analysed by playing videotape through a recorder and monitor with a freeze-field and search facility. Drawings were made from arrested video fields by placing acetate sheets over the screen of the video monitor and using fine fibre-tip pens.

Food capture/handling

Four types of food were offered to the crocodiles to cover the range of food types likely in nature; live cockroaches (*Periplaneta americana*), shore crabs (*Carcinus maenas*) and freshwater prawns (*Macrobrachium rosenbergi*), plus dead fish (*Clupea harengus*) to represent carrion.

To study the responses to cockroaches, 3 crocodiles (120–200 g) were placed in the filming tank and, over a period of several days' filming, offered cockroaches in the following 3 ways. First, a number of full grown cockroaches were allowed to crawl over the dry aquarium walls above the water surface, to mimic the presence of insects on weeds or rocks. Catching, manipulation and swallowing of insects was filmed. Next, live cockroaches of various sizes were placed, one at a time, on the water surface and the crocodiles filmed to determine whether there were differences in food handling dependent on the prey size. Finally, a large number of cockroaches of a variety of sizes were placed on the water surface to see whether the crocodiles would exhibit any preference for particular sizes of insect when feeding.

To investigate feeding upon crabs, a brick feeding platform level with the water surface was built in the tank. Live shore crabs (10–25 mm carapace width) were placed on the platform. Three crocodiles were filmed as they caught, manoeuvred and swallowed the crabs.

Feeding of the same crocodiles on prawns was filmed following the introduction of 3 live *Macrobrachium* into the bare aquarium. The animals' responses to dead prawns were also recorded.

Feeding on carrion (dead herring) was investigated in 2 ways. First, a whole fish was placed on a brick feeding platform, and the crocodiles were observed while they fed upon it. Secondly, to simulate feeding on a large, heavy carcass, a whole herring was firmly tied to a brick and placed under water. The animals were observed as they tore at the food.

Anatomy

The crocodiles which succumbed to 'runt syndrome' were dissected, as was a larger animal (171 g) which accidentally drowned. Particular attention was paid to the gut arrangement (to help in interpretation of X-radiographs); measurements were also made of the sizes of various parts of the gut.

Observations were also made on the appearance of the gut of the 2 crocodiles which were used in studies of the site of assimilation of dry matter, energy and protein (see below).

Gastrolith ingestion

The largest crocodile (weighing about 300 g at the time of the experiment) was used to determine whether gastrolith ingestion was deliberate or accidental. Ten small stones (< 4 mm diameter) were placed in a heavy glass Petri dish under water in the centre of a fenced-off section of the holding tank. The crocodile, which had fed heavily on the previous day, was placed in this section and left undisturbed for 24 h. No food was present; the smooth, heavy glass of the dish could not be manipulated by the crocodile. After 24 h the dish was inspected and the crocodile was X-rayed (see below). Further information about gastrolith ingestion was obtained by dissecting dead animals and opening the stomach. Data concerning movement and position of gastroliths in the stomach were obtained from X-rays taken as part of other trials (see below).

Appetite and appetite return

Four crocodiles (3 normal animals weighing 127, 178 and 233 g, respectively; 1 'runt' weighing 79 g) were deprived of food for 48 h and weighed. They were offered excess food (chopped fish) and left to feed undisturbed for 90 min. They were next reweighed to establish a satiation ration for each animal. After 6 h they were again offered excess food, left for 90 min and reweighed. The whole procedure (food deprivation, satiation meal, period after satiation meal, offer of second meal) was repeated a further 6 times to establish appetite following food deprivation for 12, 18, 24, 48, 72, 75 and 78 h.

Rate of movement of food through the gut

To measure the time taken for food to pass through the gut, crocodiles were fed a diet labelled with chromic oxide (a bright green inert substance not absorbed by the gut). The diet was prepared by mincing fresh fish with chromic oxide (2% by weight). Four crocodiles (one a 'runt') were fed a labelled meal and each was placed in a separate aquarium fitted with a mesh false bottom so that any faeces produced could not be reingested. Normal feeding on unlabelled fish continued after the labelled meal. The aquaria were inspected as often as possible, the first and last appearances of green faeces were recorded.

X radiography

A number of approaches to visualizing the progress of food through the gut were adopted. First, a conventional barium meal (minced fish mixed with barium sulphate (20% by weight)) was fed to animals. This labelled meal was preceded and followed by normal, unlabelled fish meals. X-radiographs were taken before the barium meal, as soon as possible afterwards, and then at intervals until it was expected that all barium-labelled material had been voided. A Chirona KOM 5 X-ray set operating at 70 Kv, 6 ma s^{-1} was employed and a 2 s exposure period was standardized. To make an X-radiograph, a crocodile was placed on top of an X-ray plate in a dry glass tank (the plate being waterproofed by enclosure in a thin plastic bag) at a distance of 65 cm from the X-ray source.

Secondly, a diet labelled with barium sulphate/polystyrene spheroids (ICI Ltd; 1 mm diameter) was used. Such spheroids have been used in the past to provide quantitative information about the rate of movement of material from one part of the gut to another in fish and sea turtles (Grove *et al.*, 1985; Davenport, Antipas & Blake, 1989). A basic diet was prepared by mincing fish with barium sulphate (10% by weight; to give a weak barium shadow to outline the gut). When a labelled meal was to be given to a particular animal, about 100 spheroids were added to 2 g of the basic diet, and this 2 g meal was fed to a crocodile which had just eaten some minced fish. X-radiographs were again taken before the labelled meal, as soon as possible after ingestion and at appropriate intervals thereafter.

Thirdly, crocodiles were offered whole fish (*Sprattus*) of about 1 g individual wet weight, which had been labelled by injecting human barium sulphate into the gut. Finally, crocodiles were fed meals of live crabs labelled with barium sulphate to attempt to assess the period required for food items to be broken up in the stomach (and also, since crab exoskeletons show up well on X-radiographs, to indicate the amount of food movement during digestion). To do this, 0·3 ml of saturated barium sulphate solution was injected into the haemolymph of each crab (through the arthrodial membrane between carapace and abdomen). This volume was found to be enough to label the tissues without causing leakage, and to allow the crabs to survive and show normal movement.

Measurement of assimilation efficiency

To measure the efficiency of assimilation of dry mass, energy (calories) and protein, 3 normal crocodiles and one runt were fed on minced fish labelled with chromic oxide (2% by wet weight). Particular care was taken to ensure that the food and label were thoroughly mixed. The composition of this diet (Diet A) was as follows:

Protein	40% by dry weight
Energy	5·0–5·3 kcal g dry wt^{-1}
Cr_2O_3	35·1 mg g dry wt^{-1}

In a few cases animals were fed a second diet (Diet B) which was similar to diet A but with a lower protein content and gluten added as a binder.

The crocodiles were fed the labelled diet for several days until green faeces had been produced for at least 2 days. At this point faecal collections were made. Food and faecal samples were dried to constant weight in a low-temperature oven (40 °C). Subsamples were weighed and analysed in the following manner. First, the chromic oxide content was determined by the method of McGinnis & Kasting (1964). The chromic oxide was oxidized to sodium dichromate (with concentrated sulphuric acid, sodium molybdate and perchloric acid). The latter was determined spectrophotometrically after dilution following the diphenylcarbizide reaction (Forster & Gabbott, 1971). The method was calibrated with known quantities of chromic oxide.

Next, total nitrogen was measured by digesting subsamples in concentrated sulphuric acid (with selenium dioxide), alkalizing them with sodium hydroxide and, after dilution, determining them spectrophotometrically following the phenolhypochlorite reaction. Ammonium sulphate was used to prepare standards.

Finally, the total calorific content of subsamples was determined by a wet oxidation method. Organic material was oxidized by potassium dichromate in concentrated sulphuric acid; after dilution, the unreduced dichromate was determined spectrophotometrically. The equivalent energy content was calculated from 1 mg $K_2Cr_2O_7 \equiv 0{\cdot}552$ cal, but correction was made on the assumption that only 60% of the protein reacted in this test (Forster & Gabbott, 1971).

At the end of the analytical procedure it was possible to calculate separate assimilation efficiencies for (1) dry mass (i.e. material of dried diet less mass of chromic oxide), (2) protein (assuming a direct relationship between nitrogen and protein contents) and (3) calories, using the following equation:

$$\%\ \text{assimilation efficiency} = 100 \times \left(1 - \frac{(C_1 M_2)}{(C_2 M_1)}\right)$$

where C_1 = chromic oxide content of unit weight of food; C_2 = chromic oxide content of unit weight of faeces; M_1 = dry mass, protein or caloric content per unit weight of food; and M_2 = dry mass, protein or calorie content per unit weight of faeces.

In later studies, protein content of food, gut samples or defecated materials was calculated directly from nitrogen content measured after digestion, distillation in a Kjeltec 1026 Distillation Unit and titration with [illegible] hydrochloric acid following the manufacturers' instructions.

Site of assimilation

To [illegible] about the parts of the gut particularly involved in the assimilation of dry mass, energy [illegible] experiment was carried out. An additional objective was to indicate where uptake of water and nutrients from food occurred in the alimentary canal. Two crocodiles were force-fed daily upon a diet (Diet C) which consisted of casein, fish meal, cod-liver oil and starch. This was bound with egg yolk and carboxymethyl cellulose. It was mixed with Cr_2O_3 (about 1% by weight). This food was dried to form pellets of the following composition:

Protein	37% by dry weight
Energy	5·32 kcal g dry wt^{-1}
Cr_2O_3	11 mg g dry wt^{-1}
Water content	6·5%

Feeding on this diet was maintained until green faeces had been voided for at least 2 days. The animals were then anaesthetized and killed, the heart and lungs removed (for an investigation to be reported upon elsewhere) and samples of material removed from the lumen of the stomach, small intestine, large intestine and rectum. The samples were frozen immediately in covered containers (to avoid water loss) for later analysis. The samples were weighed, dried at 60 °C and reweighed to measure water content. They were then analysed for chromic oxide, calorie and total nitrogen content as described above.

Results

Food capture/handling

Feeding on cockroaches

To capture insects above the water surface (in this case the glass of the tank, but presumably upon rocks or vegetation in nature) the crocodiles showed remarkable jumping ability. A typical sequence is shown in Fig. 1, but hatchling crocodiles (unfortunately not filmed) sometimes jumped almost completely out of water to catch cockroaches (rather than partially as in Fig. 1). In preparation for a jump, the crocodile brought both hind limbs far forward and extended their webs. The tail was bent at right angles to the body axis. To initiate the jump the hind limbs and tail

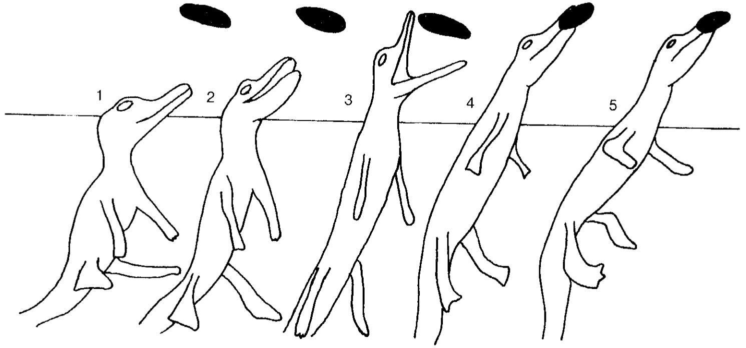

FIG. 1. Juvenile *Crocodylus porosus* leaping out of water to capture cockroach (represented by black ellipsoid). Numerals represent sequence of video fields (0·04 s apart).

were simultaneously driven backwards in a propulsive action lasting about 0·08 s. The head was driven upwards and forwards, the mouth starting to open as the snout cleared the water. The animal accelerated as more of the body left the water, and the mouth gaped wide until it snapped shut on the prey. Before jumping the neck and back were bent; both straightened during the jump.

When crocodiles were offered cockroaches floating on the water surface it was noticed that immobile prey were ignored. Moving cockroaches could be seen from at least 60 cm by crocodiles floating with only the eyes and nostrils exposed. When an insect had been spotted, the crocodile swam quickly towards it using the tail alone with all four hind limbs held against the body (high-speed swimming mode; Davenport & Sayer, 1989). The crocodile stopped abruptly when about 3–5 cm away from the cockroach by spreading the webs of the limbs as brakes. The tail and hind limbs were used to propel the animal forwards and upwards in a weak version of the jump described above. The jaws were snapped downwards and sideways on to the cockroach, taking it below the water surface (Fig. 2). The final lunge was at a speed of about 1 m s^{-1} (3·3 body lengths s^{-1}).

Medium-sized and large cockroaches (> 1 cm length) were manipulated wholly in air, the mouth being kept clear of the water. This appears to be necessary because swallowing large items of food under water would involve breaching the seal between tongue and palate, thereby flooding the oesophagus. Each insect was manoeuvred so that its longitudinal axis was directed towards the throat. This was accomplished by small tosses of the crocodile's head accompanied by movements of the tongue. Usually the cockroach was crushed and perforated by the teeth. During final swallowing the jaws were thrown back and the animal trod water vigorously, lifting the angle of the jaws at least 4 cm above the water surface (Fig. 3). Treading water was obviously energy-consuming; when eating medium-sized cockroaches the crocodiles often captured 2–3 insects before starting a bout of water-treading and swallowing, although large animals were dealt with singly.

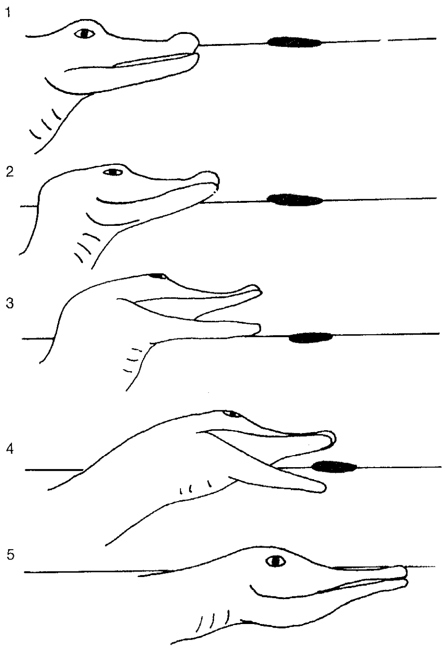

FIG. 2. Juvenile *Crocodylus porosus* catching floating insect. Numerals represent sequence of video fields (0·04 s apart).

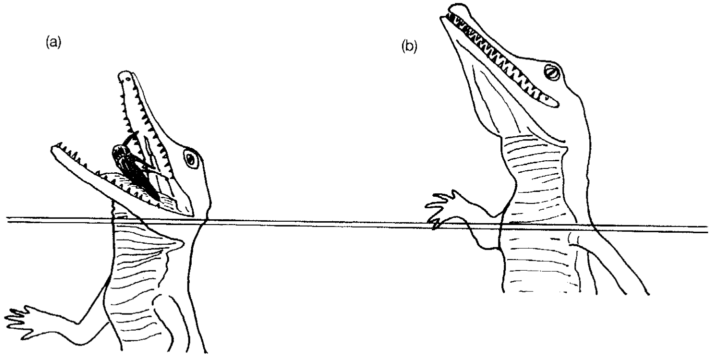

FIG. 3. Juvenile *Crocodylus porosus* handling (a) and swallowing (b) large cockroach.

Small cockroaches (< 1 cm length) were dealt with in an entirely different fashion. All manipulation was carried out under water. Repeatedly the mouth was opened and the snout raised as the cockroach became waterlogged and started to sink. This repetition gradually transferred the insect to the back of the throat. Final swallowing also took place under water in a short space of time (0·08 s), the teeth being held tightly closed and swallowing only being revealed by throat movements.

If a batch of cockroaches of different sizes was introduced to their tank the crocodiles simply attacked the nearest insect and showed no preference for a particular size of prey.

Two qualitative observations were made during the study of feeding on cockroaches. First, it was noticed that drowned cockroaches which sank to the bottom of either the holding or filming tanks were ignored by the crocodiles and not eaten. Secondly, cockroaches (or locusts when available) were always manipulated and swallowed in water, even when captured on the feeding platform; as soon as an insect was caught the crocodile retreated to water (with its jaws firmly closed to prevent escape).

Feeding on crabs

Crabs were always caught on land or in very shallow water. When a crocodile located a crab on

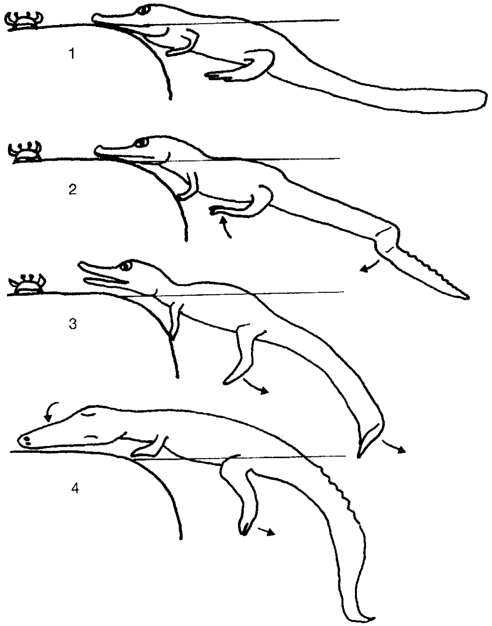

FIG. 4. Juvenile *Crocodylus porosus* stalking and catching crab. Arrows indicate movement of tail and hind limbs. Numerals represent sequence of video fields (0·04 s apart).

the feeding platform it would swim slowly towards it with only the dorsal surface of the head exposed. When the forelimbs grounded, the crocodile would normally pause briefly (<0·5 s) before attacking the crab, although any movement of the latter would precipitate an immediate lunge. As with cockroach-eating, the impetus for an attacking lunge was provided by simultaneous movement of the tail and hind limbs, the forelimbs acting as props to prevent the head and forebody dragging on land (Fig. 4). The crocodile vaulted out of water at about 1 m s^{-1} and the head was twisted to one side as the animal snapped down on to the crab. If the first lunge was ineffective, the crab would be pursued on land by lunges powered by the hind limbs only.

Crabs were always eaten out of water with the crocodile propped up on its forelimbs (Fig. 5). Manipulation and swallowing of crabs took several minutes (rather than the seconds needed to deal with the insects). If the crab was large (*c.* 24 mm carapace width) the swallowing process itself required a considerable effort, involving a wide jaw gape and closure and depression of the eyes (Fig. 6). After swallowing such a large crab the crocodile rested for several minutes with its snout on the ground. In contrast, small crabs were swallowed whole with a closed mouth (Fig. 6). Generally speaking, crabs were damaged either by the initial snap of the jaws during capture o (less often) during subsequent manipulation. Occasionally crabs were sheared in half, but more usually damage was limited to piercing of the arthrodial membranes.

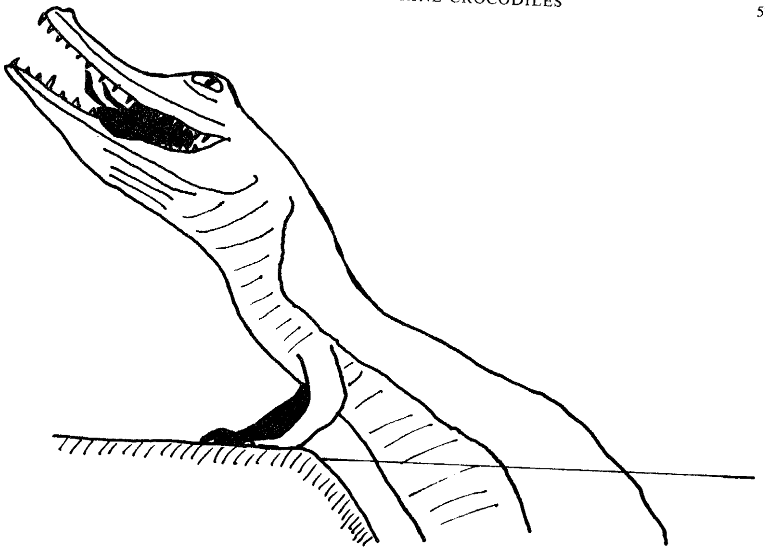

FIG. 5. Juvenile *Crocodylus porosus* handling large crab prior to swallowing.

Feeding on prawns

The presence of live *Macrobrachium* in the holding or filming tanks elicited behaviour different from that described so far. As soon as the crocodiles were aware of the prawns they became agitated, diving repeatedly to the bottom of the tank with jaws agape, showing virtually continuous swimming and twisting. Almost any stimulus, whether a touch by a prawn or contact with another crocodile, provoked an immediate sideways snap of the jaws. Most snaps were unsuccessful, and in the larger holding tank the crocodiles failed to catch live prawns despite open eyes. After several unsuccessful snaps the crocodiles walked along the bottom of the tank, gaping continuously and snapping sideways and downwards, apparently at random.

Analysis of videotape showed that a sidesnap of the jaws could be accomplished in 0·16 s, the tip of the snout reaching 1·3–1·5 m s^{-1}. However, specimens of *Macrobrachium* accelerated more quickly and reached burst speeds of as much as 1·9 m s^{-1}, so usually evaded capture. If a prawn was caught the crocodile immediately surfaced, trod water, manoeuvred the prawn into a ongitudinal position either head or tail first, and swallowed it. Manipulation of the prawn usually ft debris (limbs, antennae) adhering to the jaws; this material was cleaned off by the claws of the ind limbs.

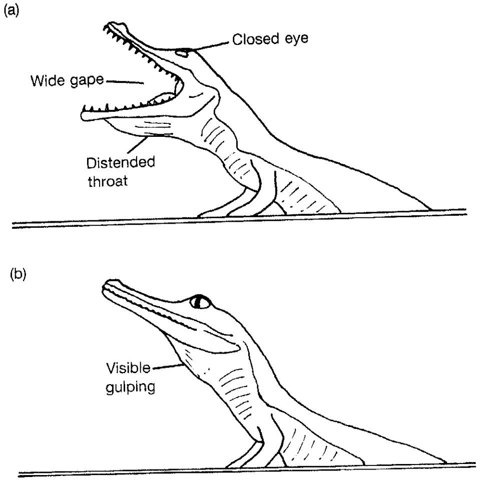

FIG. 6. Swallowing of crabs by juvenile *Crocodylus porosus*. (a) Swallowing of large crab. (b) Swallowing of small crab.

Feeding on carrion

Whether a large fish was placed on the feeding platform or tethered to a brick, the crocodiles fed upon it by biting and then shaking the head vigorously from side to side until a piece detached. At no time were the young crocodiles seen to employ the body-rolling inertial feeding method used by adult crocodiles.

Anatomy

Young salt-water crocodiles have a long, wide oesophagus which opens into a large drum-shaped stomach with no obvious sphincter between them. The stomach occupies about a third of the abdominal cavity and has a thick, muscular wall, especially in the pyloric region which appears to represent the crocodilian 'pyloric gizzard' described by Skoczylas (1978). The stomach leads, via a marked pyloric sphincter, into the duodenum which is wider, but shorter, than the much-coiled ileum. The small intestine as a whole is much longer than the short, simple and straight large intestine (length ratio small : large = 8–10 : 1). There was no hint of a caecum. Crocodiles suffering from runt syndrome had full stomachs, extremely pale livers and enlarged gall bladders.

During collection of material from the gut of newly-killed crocodiles it was noted that both the small and large intestine contained discrete 'slugs' of semisolid material along their lengths. This may indicate that gastric emptying proceeds in bursts, leading to the production of individual boli along the gut.

Gastrolith ingestion and movement

Twenty-four hours after 10 stones had been left in its tank, the crocodile had clearly eaten eight of them, since only two remained in the Petri dish, and X-radiography showed that the gastrolith content of the stomach had increased. This ingestion occurred on a day when food ingestion would not be expected (see appetite section below).

For the Nile crocodile Cott (1961) claimed that stone-eating did not take place in the first year of life. However, the specimens of *C. porosus* reported upon here all had some gastroliths in their stomachs which must have been present when they arrived as recent hatchlings from Australia (since no stones of the type found were ever offered to them in the UK, or were present in their food). This was true even of the 'runt', which died when no more than three months old, but contained three stones of 2–4 mm diameter. As well as this 'Australian' material, all stomachs of dissected animals contained flakes of the non-toxic epoxy paint which coated the plywood of their holding tank. These flakes were hard and thick (< 2 mm); pieces as large as 1 mm × 4 mm had been eaten. Plate I shows the gastrolith content of a single juvenile crocodile (collected on dissection).

In unfed animals gastroliths appeared to be concentrated in a small area at the bottom of the stomach, but as soon as a meal was eaten they were dispersed throughout the stomach. Sequential X-rays from above, together with X-radiographs taken from the side of an animal, demonstrated that hard pieces of inorganic material are moved around the stomach during the digestion of meals and do not remain stationary. They also showed that gastroliths or similar material reach the

PLATE I. Gastrolith material removed from the stomach of a juvenile estuarine crocodile (*c*. 200 g body weight).

dorsal part of the stomach when food is present and do not lie on the ventral stomach wall as envisaged by Cott (1961).

Appetite and appetite return

Despite the relatively simple method of weighing the animals to assess food intake, the results obtained were quite clear (Table I). Six hours after a satiation meal, the crocodiles were only able to consume a fraction (0–32%) of their maximum meal. The X-ray studies described below indicate that, on average, some 4 h must pass before newly-ingested food begins to leave the stomach at 30 °C, thereby allowing the possibility of new food intake. The amount consumed voluntarily increased with deprivation time up to a maximum at 24 h (the largest animal: 226 g body weight) or 48 h (smaller animals: 126–180 g body weight). The 'runt syndrome' animal (76 g body weight) required longer for full appetite return. The maximum meal size (g) increased with body weight, but remained proportionally relatively constant (9–13% body weight) amongst the body sizes available. Table I also shows the return of appetite as a percentage of maximum meal size for each animal at the stated time and, for comparison with the X-ray studies, the estimated amount of food remaining in the stomach after different times had elapsed since feeding. Since only three normal juveniles were tested, and because their sizes differed relatively little, we combined the results displayed in Table I, row d, into a single estimated gastric emptying curve based on the following assumptions:

1. A delay of 4 h occurred before gastric emptying began.
2. The smaller meals (animals 1 and 2) formed later segments of the emptying curve found for the larger animal (3).

TABLE I

Return of appetite in juvenile Crocodylus porosus

Animal no.	Body wt. (g)	Max. meal wt. (g)		Deprivation time (h)							
				6	12	18	24	48	72	75	78
1	126·0	14·82	a	0·00	6·95	10·47	6·56	14·82	12·43	3·94	0·87
		(11·8% b.w.)	b	0·00	5·52	8·31	5·21	11·76	9·87	3·13	0·69
			c	0·00	46·89	70·65	44·26	100·00	83·87	26·59	5·87
			d	14·82	7·87	4·35	8·26	0·00	2·39		
2	178·4	19·53	a	4·35	10·47	11·73	11·85	19·53	7·80	3·09	4·05
		(10·9% b.w.)	b	2·44	5·87	6·58	6·64	10·95	4·37	1·73	2·27
			c	22·30	53·61	60·06	60·68	100·00	39·94	15·82	20·74
			d	15·18	9·06	7·08	7·68	0·00			
3	225·9	31·22	a	9·90	17·83	28·90	31·22	28·82	14·72	7·34	8·92
		(13·8% b.w.)	b	4·38	7·89	12·79	13·82	12·76	6·52	3·25	3·95
			c	31·71	57·11	92·57	100·00	92·30	47·15	23·51	28·57
			d	21·32	13·39	2·32	0·00	2·40			
4	75·9	11·08	a	0·00	2·15	2·37	4·25	6·91	11·08	1·49	4·02
		(14·8% b.w.)	b	0·00	2·83	3·12	5·60	9·10	14·60	1·96	5·30
	('runt')		c	0·00	19·40	21·39	38·36	62·40	100·00	13·45	36·28
			d	11·08	8·93	8·71	6·83	4·17	0·00		

a = observed meal size (g); b = observed meal size as % body weight (b.w.); c = observed meal size as % of maximum meal; d = estimated amount (g) of meal remaining in the stomach

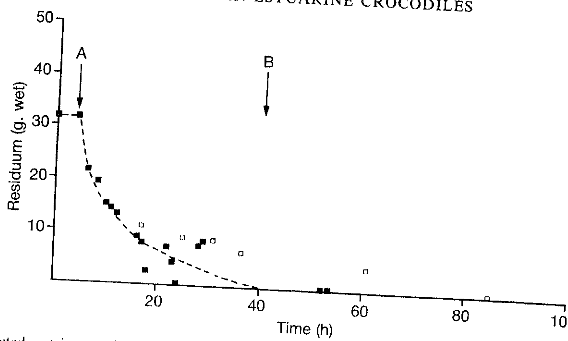

FIG. 7. Predicted gastric emptying curve (solid squares) for juvenile *Crocodylus porosus* (126–226 g body weight) at 30 °C based on return of appetite studies (see Table I). After a delay (see results of X-ray studies) the stomach empties between A and B (arrowed) according to the following equation:

$$\sqrt{R_t} = \sqrt{R_0} - 0{\cdot}137\ t$$

where R_0 = residuum at time 0, R_t = residuum at time t and the slope (0·137) is determined by regression analysis of the square roots of the data presented in row d (Table I) against time.

Also shown are data points (open squares) for a 76 g juvenile exhibiting 'runt syndrome'.

3. Food intake reflected the amount of 'space' available in the stomach.

Figure 7 shows our estimate of the emptying curve for a 31 g meal for young crocodiles (125–226 g body weight). After the initial delay, contents decrease with time in a curve such that more than 90% of the food is emptied within 4 + 36 = 40 h. The fitted curve was drawn on the assumption that emptying follows the 'square root' model found for the lower vertebrates by Jobling (1981). In addition, the figure also demonstrates that return of appetite (and hence the estimated gastric emptying) was noticeably slower in the 'runt' crocodile. The 'runt' ate well, so slow processing of meals may well be a feature of crocodiles suffering from this syndrome. Table I also demonstrates that prolonged deprivation of food led, under the experimental conditions, to a falling food intake after three days, perhaps reflecting a shift in metabolic rate.

Rate of movement of food through the gut

A simple but independent method of checking the gastro-intestinal processing rate was adopted, which also avoided handling of the animals. Under routine feeding conditions one meal was offered which contained chromic oxide as an inert marker. The time from feeding to the first appearance of green faeces was about 68 h. The last faeces were voided 92–113 h (average 97) after the meal. This observation suggests that the total gut clearance time for a meal is 4–5 d, including initial delay in the stomach, gastric emptying processing in the intestine and accumulation in the rectum prior to defecation. However, the time difference between the first and last appearance of labelled faeces is an estimate of gastric emptying time. By this approximation, the emptying process of the stomach requires 24–45 h (mean 29 h) which, when the 4 h delay is added, supports the estimate obtained from the return of appetite studies.

X-radiography

Plates II–VII show X-radiographs of the process of digestion of voluntarily ingested, unfrozen fish (*Sprattus*, *c.* 1 g) which had been injected with barium sulphate. The animal identified with an arrow (body weight 180 g) illustrates the sequence. Plate II shows the stomach contents after several days of food deprivation. Flakes of paint and small stones, subsequently identified *post mortem* during the assimilation studies, are clearly seen. Plate III shows the full stomach 2 h after eating a meal of about 10 fish. Subsequent radiographs (Plates IV–VI) taken 18, 24 and 31 h after the meal show initial transfer of radio-opaque material into the intestine and rectum, with concomitant decrease in stomach volume. After 66 h (Plate VII) most of the meal had reached the rectum and much had been voided; only a few barium-rich boli remained in the large intestine. These observations agree well with the estimates of gastric emptying time (Fig. 7) derived from studies of appetite return, and also with the rate of clearance of chromic oxide in the faeces (described earlier). Examination of these and other radiographs leads us to suggest that the transfer of material through the small intestine is rapid, since this region gave strong images in any X-ray. The later images also suggest that the barium sulphate marker was more concentrated in the last portions of the meal to be released from the stomach.

PLATE II. X-radiograph of juvenile *Crocodylus porosus* taken before consumption of barium-labelled meal. Note gastrolith material in the stomachs. Text description refers to arrowed animal.

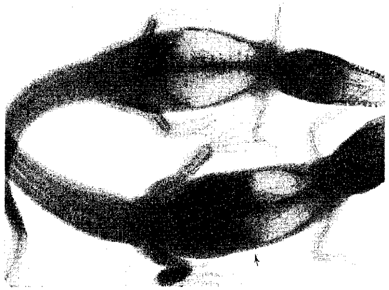

PLATE III. X-radiograph of juvenile *Crocodylus porosus* taken 2 h after consumption of barium-labelled meal. Note large stomach and dispersal of gastroliths. Text description refers to arrowed animal.

In a subsequent study, an attempt was made to follow the gastric emptying process using a diet in which radio-opaque, barium sulphate-labelled polystyrene spheroids were incorporated into the diet at known concentration (Cox & Ennis, 1980; Costal *et al.*, 1983). The assumption behind this approach was that, provided both food and radio-opaque spheroids were emptied from the stomach at the same rate, spheroid counts would confirm the emptying curve shown in Fig. 7. In the event, the results were not as expected. Plate VIII (left) shows a crocodile before feeding, chosen for clarity because this specimen contained no gastroliths to obscure the spheroid images. The remains of a previous barium meal are seen in the rectum. Plate VIII (right) shows the image 30 min after ingestion of a submaximal meal containing the spheroids together with a small amount of barium sulphate to delineate the gut. Subsequent plates (Plates IX–XII) show that, despite subsequent food intake, the spheroids were sorted from the digestible food and most were

PLATE IV. X-radiograph of juvenile *Crocodylus porosus* taken 18 h after consumption of barium-labelled meal. Note that labelled material is present in small and large intestine. Text description refers to arrowed animal.

PLATE V. X-radiograph of juvenile *Crocodylus porosus* taken 24 h after consumption of barium-labelled meal. Note some concentration of barium label in the rectum. Text description refers to arrowed animal.

PLATE VI. X-radiograph of juvenile *Crocodylus porosus* taken 31 h after consumption of barium-labelled meal. Note large amount of material in the rectum. Text description refers to arrowed animal.

PLATE VII. X-radiograph of juvenile *Crocodylus porosus* taken 66 h after consumption of barium-labelled meal. Note empty stomach (save for concentrated gastroliths). Text description refers to arrowed animal.

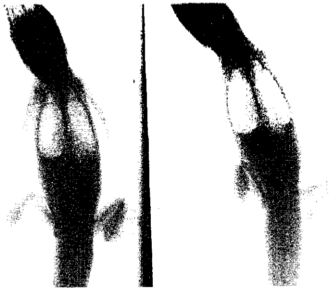

PLATE VIII. X-radiograph of a juvenile *Crocodylus porosus*. Left: unfed. Note barium shadow in rectum (from earlier meal). Right: taken 30 min after consumption of barium- and barium spheroid-labelled meal.

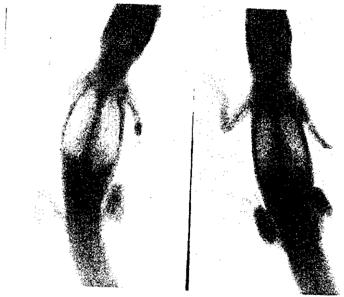

PLATE IX. X-radiographs of a juvenile *Crocodylus porosus*. Left: six days after barium- and barium spheroid-labelled meal. Right: seven days after meal.

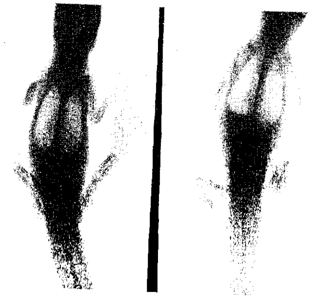

PLATE X. X-radiographs of a juvenile *Crocodylus porosus*. Left: nine days after barium- and barium spheroid-labelled meal. Right: 11 days after meal (blurred by movement of animal).

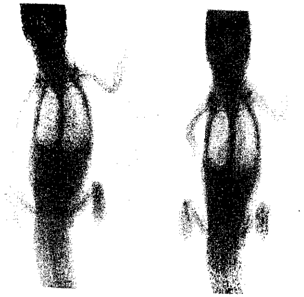

PLATE XI. X-radiographs of a juvenile *Crocodylus porosus*. Left: 14 days after barium- and barium spheroid-labelled meal. Right: 15 days after meal.

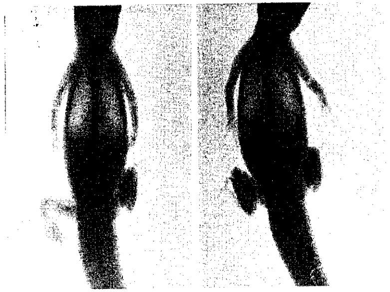

PLATE XII. X-radiographs of a juvenile *Crocodylus porosus*. Left: 20 days after barium- and barium spheroid-labelled meal. Right: 24 days after meal.

still in the stomach 24 days later, long after the digestible food and barium meal had been eliminated. Spheroids of this size are not processed with the main meal, presumably because they, like gastroliths, are held back by the pyloric sphincter. In the sequence displayed in Plates VIII–XII the distribution of spheroids changes as the stomach is distended by subsequent radio-transparent meals (and the spheroids are dispersed through the food).

X-radiographs of crocodiles which had eaten crabs were difficult to interpret because of the presence of gastroliths. However, X-rays taken shortly after meals demonstrated that crabs remained in the oesophagus for several minutes after ingestion. Carapaces and chelipeds could only be distinguished for about 8 h.

Assimilation efficiency and site of assimilation

In the main assimilation study, crocodiles were offered a minced fish diet (A), a similar diet which was bound together with gluten (B) or a dry diet based on casein and fish meal (C). Diets differed in protein content (40, 14 and 37% of dry weight, respectively). Table II shows the chromic oxide, energy and protein nitrogen content per unit dry weight of the feeds and the faeces collected from the tanks. Diet A was processed efficiently by the test animal, so that the assimilation efficiencies were as follows:

Dry mass	77·5%
Energy	85·2%
Protein-N	97·4%

Two further crocodiles were fed with diet C for four consecutive meals (over 48 h) before being examined for changes in gastrointestinal blood flow after feeding (Nilsson *et al.*, In prep.). The animals were killed 18 h after their last meal and food samples removed from different segments of the gut for analysis (Table II). As the food passed along the gut, a dramatic rise in water content occurred in the stomach; this presumably reflects both gastric secretion and drinking. This water content rise was consistently lower in animal 1. Chromic oxide levels rose four-fold between ingestion and the posterior intestine, but some retention of the marker may have occurred since rectal faecal levels were not as high as those in the intestine. In comparison, faeces collected from animals fed regularly on labelled material for a week or more showed marker levels between four and ten times greater than in the food. The energy content of the gut contents fell progressively along the tract, with no indication of a specific zone where most of the food energy was absorbed. The sample sizes were too small to allow protein nitrogen analysis at every site, but there was some evidence that protein nitrogen continued to be absorbed even in the rectum before defecation.

TABLE II

Assimilation efficiencies in juvenile ***Crocodylus porosus***

(a) Faecal collection from free-swimming animals

Diet	Body weight (g)	Food			Faeces		
		Cr_2O_3 mg g^{-1}	Energy cal mg^{-1}	Protein-N mg g^{-1}	Cr_2O_3 mg g^{-1}	Energy cal mg^{-1}	Protein-N mg g^{-1}
A	126	15·62	5·04	64·10	65·95 (77·5%)	3·15 (85·2%)	7·1 (97·4%)
B	140	44·85	5·48	22·36	359·95 (91·7%)	5·35 (87·8%)	—
	178				445·76 (94·2%)	2·51 (95·4%)	—
	76[a]				107·07 (60·8%)	3·08 (76·5%)	34·3 (35·7%)

(b) Post-mortem collection from stated area of the gut, 18 h after last meal (Diet C)

Gut site		% water	Cr_2O_3 mg g^{-1}	Energy cal mg^{-1}	Protein-N mg g^{-1}
	Diet C	6·5	12·0	4·5	59·3
	Animal no.				
Stomach	1	62·7	27·9	3·8 (62·2%)	59·1 (57·0%)
	2	78·4	13·5	2·8 (41·5%)	48·8 (26·8%)
Small intestine	1	42·0	32·8	3·5	—
	2	—	—	—	—
Large intestine	2	88·8	37·5	2·3	—
	2	78·1	43·6	1·9	—
	1	34·0	23·3	3·4	—
Rectum	2	82·1	28·4	2·2 (79·3%)	29·3 (79·1%)
Faeces	1+2	—	29·5	2·1 (82·7%)	14·0 (90·4%)

Values in parentheses denote assimilation efficiencies

[a] Animal exhibiting 'runt' syndrome

Diet B contained lower protein levels than the other diets but, when compared with diet A, both dry material and energy were assimilated by normal animals at equally high rates. When this diet was offered to a 'runt' crocodile, all assimilation efficiencies recorded were lower than those characteristic of normal animals, but protein assimilation was especially poor (35·7%).

Discussion

Crocodilians are relatively slow and inefficient swimmers which do not rival the capabilities of fish, aquatic birds or marine turtles (Davenport & Sayer, 1989). For a great deal of their food capture juvenile *C. porosus* must rely on the acceleration produced as much of the body moves from water to air during jumps or lunges. The acceleration depends upon the body moving into a medium of low viscosity (air) while the propulsive organs (tail and hind limbs) remain in a medium of low compressibility (water). This behaviour allows young salt-water crocodiles to catch animals living at or near the air : water interface readily. The crocodiles' binocular vision, focusing ability in air (Fleishman *et al.*, 1988), cryptic floating posture, powerful broad-webbed hind limbs and strong tail all contribute to hunting success.

Capture of prawns (and presumably small fish) in water is accomplished in a very different manner. Detection of prey appears to be by touch rather than sight, and triggers snapping behaviour which has a distinctly random, undirected element. This is consistent with the findings of Fleishman *et al.* (1988) that crocodilians are unable to focus under water, and of Fleishman & Rand (In press) that spectacled caimans can capture fish in total darkness. While this behaviour was generally unsuccessful under the experimental conditions employed (clear water; few prawns), presumably because of the vision and speed of the prawns, it is feasible that snapping frenzies are effective in killing members of schools of prey, particularly in the turbid water of estuaries.

The way in which food items were handled after capture depended on two characteristics of the item concerned: its size and density. Small items (e.g. small insects, small pieces of carrion) were swallowed whole under water. This took place with the jaws tightly closed and was accomplished quickly (presumably to minimize intake of water). The handling of larger items was prolonged and took place during water-treading episodes if they were of relatively low density (insects, prawns), or on land if they were dense (crabs, pieces of fish, squid). This difference in approach probably lessens the chance of prey escaping (prawns, insects) or sinking into deep water (carrion, crabs). All large items were manipulated in the jaws and were punctured or crushed by the teeth. Puncturing of the exoskeleton will speed the digestion of arthropod prey, so the somewhat laborious water-treading episodes probably have two functions rather than simply orientating the prey in the mouth prior to swallowing.

Young *C. porosus* possess a long and broad oesophagus. From several X-radiographs inspected it may be seen that large, hard food items (such as crabs) may take several minutes to reach the stomach. As the oesophagus passes between the lungs, the distortion of the former by such prey must press upon the latter, restricting ventilatory capacity. This probably explains why young salt-water crocodiles usually rest immobile for several minutes after ingesting a crab, yet resume activity immediately after eating softer cockroaches.

The results of this study demonstrate that young salt-water crocodiles deliberately ingest small stones and other hard material. Taken with the observations that such objects disperse throughout the stomach after a meal is eaten, that the stomach wall is thick and muscular, and that small hard objects (e.g. barium spheroids) are sorted and retained by the stomach, this finding strongly suggests that gastroliths are involved in breaking down ingested prey, perhaps helping to squeeze fluids out of punctured arthropods.

Young crocodiles are capable of eating rather large satiation meals (*c.* 10% body weight), but the somewhat long period taken to recover full appetite has implications for commercial rearing. Since the stomach does not empty until about 40 h after a satiation meal it would appear that daily feeding of large rations to captive animals would be wasteful and counterproductive, even at this early stage of growth.

The assimilation efficiencies recorded in normal animals were high, particularly for protein nitrogen (97·4%), confirming the general impression of estuarine crocodiles as highly efficien carnivores. *A priori* it had been expected that most assimilation, particularly of protein, would hav occurred by the time that the end of the small intestine had been reached. Instead, it is evident tha the large intestine (and probably the rectum) are also implicated in assimilation of both energy and protein.

The 'runt' syndrome of poor growth appears from our studies to lie not in the lack of appetite, but in slow rates of food processing and poor digestion and absorption, especially of protein.

The authors gratefully acknowledge the financial support of a grant from the Nuffield Foundation which allowed this work to be carried out.

REFERENCES

Biedermann, W. (1911). Die Aufnahme, verarbeitung und Assimilation der Nahrung—XII. Die Ernährung der höheren Wirbeltiere. In *Handbuch der vergleichenden Physiologie* **2**(1): 1116–1492. Winterstein, H. (Ed.). Jena: Fischer.

Brazaitis, P. J. (1969). The occurrence and ingestion of gastroliths in two captive crocodilians. *Herpetologica* **25:** 63–64.

Costal, B., Gunning, S. J., Naylor, R. J. & Simpson, K. H. (1983). The central site of action for metoclopramide to facilitate gastric emptying in the guinea pig. *Br. J. Pharmac.* **80:** 191.

Cott, H. B. (1961). Scientific results of an enquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *Trans. zool. Soc. Lond.* **29:** 211–356.

Coulson, R. A. & Hernandez, T. (1964). *Biochemistry of the alligator: A study of metabolism in slow motion.* Baton Rouge: Louisiana State University Press.

Coulson, R. A. & Hernandez, T. (1970). Protein digestion and amino-acid absorption in the cayman. *J. Nutr.* **100:** 810–826.

Cox, B. & Ennis, C. (1980). Apomorphine and gastric emptying in the guinea pig. *Br. J. Pharmac.* **70:** 104.

Davenport, J., Antipas, S. & Blake, E. (1989). Gut function in young green turtles (*Chelonia mydas* L.). *Herpet. J.* **1:** 336–342.

Davenport, J. & Sayer, M. D. J. (1989). Swimming in young salt-water crocodiles (*Crocodilus porosus*). *Herpet. J.* **1:** 356–361.

Diefenbach, C. O. da C. (1975*a*). Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia)—I. Rate of gastric digestion and gastric motility as a function of temperature. *Comp. Biochem. Physiol. (A)* **51:** 259–265.

Diefenbach, C. O. da C. (1975*b*). Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia)—II. Effects of temperature on pH and proteolysis. *Comp. Biochem. Physiol. (A)* **51:** 267–274.

Ferguson, M. W. J. (1981). The value of the American alligator (*Alligator mississippiensis*) as a model for research in craniofacial development. *J. craniof. Genet. devl Biol.* **1:** 123–144.

Fleishman, L. J., Howland, H. C., Howland, M. J., Rand, A. S. & Davenport, M. L. (1988). Crocodiles don't focus underwater. *J. comp. Physiol.* **163A:** 441–443.

Fleishman, L. J. & Rand, A. S. (In press). *Caiman crocodilus* does not require vision for underwater prey capture. *J. Herpet.*

Forster, J. R. M. & Gabbott, P. A. (1971). The assimilation of nutrients from compounded diets by the prawns *Palaemon serratus* and *Pandalus platyceros*. *J. mar. biol. Ass. U.K.* **51:** 943–961.

Friant, M. (1941). La trituration des aliments par l'estomac chez les crocodiles. *Bull. Mus. natn. Hist. nat. Paris.* (2) **13:** 405–407.

Gadow, H. (1901). *Amphibia and reptiles.* London: Macmillan and Co.

Garnett, S. (1985). Fatty acid nutrition of the estuarine crocodile *Crocodylus porosus*. *Comp. Biochem. Physiol.* **81B:** 1033–1035.

Grove, D. J., Moctezuma, M. A., Flett, H. R. J., Foott, J. S., Watson, T. & Flowerdew, M. W. (1985). Gastric emptying and the return of appetite in juvenile turbot, *Scophthalmus maximus* L., fed on artificial diets. *J. Fish Biol.* **26:** 339–354.

IUCN (1982). *The IUCN Amphibia-Reptilia red data book, Part 1. Testudines, Crocodylia, Rhynchocephalia.* Gland, Switzerland: IUCN.

Jobling, M. (1981). Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. *J. Fish Biol.* **19:** 245–257.

Lance, V. (1982). Trace elements, vitamin E, and glutathione peroxidase in the American alligator, *Alligator mississippiensis*. *Proc. a. Alligator Prodn Conf.* **2:** 17–30.

McGinnis, A. J. & Kasting, R. (1964). Comparison of gravimetric and chromic oxide methods for measuring percentage utilization and consumption of food of phytophagous insects. *J. Insect Physiol.* **10:** 989–995.

Neill, W. T. (1971). *The last of the ruling reptiles: Alligators, crocodiles, and their kin.* New York & London: Columbia University Press.