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Feeding, Growth, and Food Conversion Rates of Wild Juvenile Saltwater Crocodiles (*Crocodylus porosus*)

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ABSTRACT.—The foods of wild juvenile saltwater crocodiles (*Crocodylus porosus*) are described, and rates of feeding, nutrient intake and growth are quantified. The size of prey eaten is strongly bimodal: large numbers of small prey (mainly crustaceans) and small numbers of large prey (mainly rats). The nutrient intake levels reflect size related changes in diet (more larger prey in larger crocodiles). The average juvenile diet is characterized by 70–71% water, low fat levels (3.0–4.5%), high protein content (12.7–14.7%), and calcium:phosphorus ratios which decline from 7:1 in animals 300–599 mm total length (TL), to 2:1 in animals 900–1200 mm TL. A mean food conversion rate (wet weight to wet weight) of 82.4% is derived, which is appreciably higher than results obtained from captive crocodilians (17–40%). To maintain similar growth rates, a wild juvenile *C. porosus* of 682 mm TL requires food equivalent to 4% of its body weight per week, whereas captive counterparts require four times that amount. The physiological mechanisms associated with digestion and assimilation may not function as efficiently when the stomach is repeatedly filled to capacity, as occurs in captivity.

The development of crocodile and alligator farms around the world (Luxmore et al., 1985) has stimulated research into crocodilian nutrition, feeding rates and growth rates, mainly using crocodilians housed in artificial environments and fed a variety of foods (see for example: Coulson and Hernandez, 1983; Webb et al., 1983a; Garnett and Murray, 1986; Joanen and McNease, 1987; Manolis et al., 1989). However, the degree to which these results apply to wild crocodilians is largely unknown. Growth rates of a number of species in the wild have been quantified (Gorzula, 1978; Chabreck and Joanen, 1979; Webb et al., 1978, 1983b; Hutton, 1984, 1987; Jacobsen and Kushlan, 1989), and there are many studies which describe the prey of wild crocodilians (see reviews by Webb et al., 1982, and Magnusson et al., 1987). However, no studies address the rates of feeding and nutrient intake of wild crocodilians, which is inherently difficult to do at the individual animal level of resolution. As a consequence, we have no information on the food conversion rates of wild crocodilians, and thus no baseline nutritional data to serve as a standard for developing artificial feeds. We also have no information on the biomass of food required to sustain wild crocodile populations, even though food availability appears to limit some populations (Webb,

1985). Competition with people for scarce food resources is perceived as being a "cost" of having depleted populations of crocodiles recover in some countries (Singh, 1987), yet we do not know "how much" crocodiles eat in the wild.

In this study, we describe the foods of wild juvenile saltwater crocodiles (*Crocodylus porosus*) in a tidal river, and quantify the organic and inorganic components of that food. Feeding rates (in terms of prey and nutritive content) and growth rates are quantified, and food conversion rates estimated. The degree to which the results from our study area apply to juvenile *C. porosus* in other tidal rivers is discussed.

MATERIALS AND METHODS

Study Area and Sample Collections.—The study was carried out in the tidal part of the Adelaide River, approximately 50 km east of Darwin, Northern Territory of Australia. The *C. porosus* population in this river was estimated at 1600 individuals in 1986. The river meanders over a black soil floodplain and has muddy banks lined with mangroves and/or floodplain sedges and grasses (Messel et al., 1979). There are two complete tidal cycles each day, with an average of 2.8 m between daily maximums and minimums in the area where crocodiles were caught (65–100 km upstream of the sea).

Ninety-two percent of the 1400 mm annual average rainfall falls between November and April, giving a distinct "wet season" during which saline water is flushed from the river. In the "dry season," a salt wedge moves progressively upstream from the sea (Webb et al., 1983c). Mean monthly minimum air temperatures range from 15.1 to 23.9 C, and maxima from 30.9–35.5 C. Crocodiles in the Adelaide River are essentially exposed to three seasons (Webb and Manolis, 1989; Webb, 1991): a dry-cold season (May to August); a dry-hot season (September to October); and, a wet-hot season (November to April).

Ninety juvenile *C. porosus* (300–1200 mm TL) were caught, 60 (67%) during the wet-hot period when growth is enhanced (Webb et al., 1978), and 30 (33%) during the dry-cold period when growth is retarded. Crocodiles were located at night and caught by hand. Sex was determined, and head length (HL), snout-vent length (SVL; to the front of the cloaca), and total length (TL) were measured. Partly by oversight, body weight (BWT; in g) was only measured on 27 animals. Regression formulae for predicting BWT from SVL, HL and TL were derived from this sample (r² = 0.98 for each), and the mean of predictions from all three formulae was used as the measure of BWT for all animals. This procedure tends to standardize for changes in

BWT attributed to the degree of filling of the stomach.

Within an hour of capture, the stomach contents were removed using the scooping method of Taylor et al. (1978) as modified by Webb et al. (1982). Two or three "scoopings" were necessary before the flushing water was free of food particles. Stomach contents were preserved in 70% alcohol, and were later sorted into what was considered prey and non-prey (vegetation, stones, parasites) items. Prey items were identified and then subdivided (see below) into prey that were fresh (eaten <24 h) and old (>24 h).

Describing, Aging and Assessing Prey Items.— Percent occurrence (the percentage of crocodiles containing a particular prey taxon) and percent composition by both number and mass (the percentage of the total prey number or reconstituted mass accounted for by a particular taxon) were calculated. This allowed comparison with Taylor's (1979) data from other rivers, to determine whether our sample was typical of *C. porosus* in general; it also shed light on the biases associated with the digestibility of parts recovered from crocodilian stomachs (Garnett, 1985a).

Crustaceans were the most common food. Samples of the same crabs and prawns were collected and fed to 18 captive juvenile *C. porosus* (mean TL = 876 ± 26 mm; mean BWT = 1950 ± 102 g) maintained at 31–32 C, which had been fasted for 4 d. The stomach contents of all animals were removed (as described above) after intervals of 6, 12, 24 and 48 h, and the state of the prey items was described. With the exception of some of the smallest prawns (<0.05 g), which contributed little to the diet in the field, all crabs and prawns were recognizable after 24 h. Descriptive criteria for assigning whether crustacean remains from the wild crocodiles were more (old) or less (fresh) than 24 h old were based on these results. The same data were used to age the relatively few fresh insect remains recovered. The few vertebrate remains were assessed individually.

To estimate the reconstituted size of fresh crabs and prawns, regression formulae were derived which predicted fresh weight from the dimensions of parts recovered (mainly carapace, cheliped, and telson segments). Reference series were used to estimate the fresh weight of insect and fish prey recovered and rodent sizes were estimated from a skeletal reference series (at CSIRO, Darwin).

Nutrition.—Samples of crabs, prawns, rats, insects, and fish (mudskippers) were collected, dried (60 C for 72 h), and finely ground. Water content was calculated from the difference in weight between wet and dry samples. Total ni-

trogen was determined by colorimetric reaction with alkaline phenate on an Auto-analyzer (Technicon Instrument Corp., New York) after Kjeldahl digestion with H_2SO_4/H_2O_2 catalyst. Protein content was calculated as $6.25 \times N$ (nitrogen concentration) (Young, 1963). Total fat content was determined by petroleum ether extraction (60–70 C BP) under reflux for 2 h using Soxhlet apparatus. For ash content, samples were ashed in a muffle furnace at 500 C for 5 h. Calcium was determined using an atomic absorption spectrometer (Varian Techtron Pty. Ltd., Springvale, Australia) after samples were digested with H_2SO_4/H_2O_2. Inorganic phosphorus was determined by acid molybdate reaction using a "Technicon" Auto-analyzer.

Rates of Feeding, Nutritional Intake, Growth and Food Conversion.—The 90 animals were subdivided into three groups based on total length: Group 1, 300–599 mm (N = 30); Group 2, 600–899 mm (N = 49); and Group 3, 900–1200 mm (N = 11). The reconstituted mass of all small fresh prey items (crabs, prawns, insects) was used to measure directly the total intake of each prey type (g d⁻¹) by each group in the 24 h prior to capture. With larger fresh prey (rats) that were eaten infrequently, but which provided the bulk of the food, a mean group consumption rate (g d⁻¹) was calculated differently (see Results). The final result was an estimate of the total food consumption, per group, within the 24 h prior to capture (the rate of feeding). As that 24 h was derived from different periods of the year, it is assumed to reflect the average daily feeding rate for crocodiles of that size. The results of the nutritional analyses allowed these estimates to be converted to rates of intake of organic and inorganic components.

Seventeen recapture records from 13 individuals provided data on the mean growth rates of juvenile *C. porosus* in the Adelaide River. These data were compared with juvenile *C. porosus* growth data from other tidal rivers (Webb et al., 1978) as a check that no major bias resulted from the small sample size. Initial and final body weights (BWT$_i$ and BWT$_f$, respectively) were transformed with natural logarithms (lnBWT$_i$ and lnBWT$_f$) and plotted against time in days (0 = initial capture day), for each individual animal. LnBWT at the mean time between captures (lnBWT$_m$) was predicted, and the slope of the line joining the two points was used to estimate the daily increment of lnBWT (growth per day; lnBWT$_{gr}$), at that mean size. As season influences growth rates (Webb et al., 1978), the time interval between captures was transformed into percentage wet season days (%WET), and multiple regression analysis was used to predict lnBWT$_{gr}$ from both lnBWT$_m$ (size) and

ln%WET (percentage wet season between captures). This resulted in an estimate of the mean daily increase in weight, per individual, at the time of capture, which was subsequently used to compute the total increase in BWT per group in 24 h.

Food conversion rates were calculated as the total live weight gain (in g) by a group in 24 h divided by the amount of food (wet weight) eaten by the group in 24 h.

Unless stated otherwise, means are followed by ±1 standard error (SE).

RESULTS

Food and Rates of Feeding.—The mean total lengths and body weights of the *C. porosus* examined in the wet-hot period (N = 60; 677 ± 23 mm TL; 325 ± 102 g BWT) were not significantly different from those from the dry-cold period (N = 30; 690 ± 35 mm TL; 332 ± 104 g BWT: t tests; df = 88; t = 0.019 [TL], t = 0.048 [BWT]; P ≫ 0.50). Of the animals examined, 3.3% had empty stomachs. There were 1.69 fresh prey items and approximately 0.92 old items (total = 2.61 items) per animal; 2.70 items per animal with food in the stomach.

Crustaceans (crabs and prawns) were found in 88.9% of animals and they accounted for 46.3–66.5% of the mass of fresh food eaten (Mass 1 and Mass 2 in Table 1). Insects were found in 40.0% of our animals, but most insect remains were old, accumulated chitin (see Garnett, 1985a); insects only accounted for 2.4–3.5% of the mass of fresh food eaten.

Among our sample, 24.4% had been eating vertebrates (old and fresh) which comprised 30.1–51.2% of the mass of fresh food eaten. Stones, vegetation and parasites (mainly the nematode worm *Gedoalstascaris australiensis*) were considered non-food items (Table 1), and are not treated further.

To assess the total daily food consumption by each group, the reconstituted mass of each of the fresh, small prey items (crabs, prawns, insects) was estimated, and allocated to the relevant crocodile size groups. The single small fish found was fresh, and was treated likewise. The total mass of the 147 smaller prey items in the 90 animals was 164 g.

Rats (*Rattus colletti*) were eaten infrequently relative to the smaller prey, but because of their size they contributed greatly to the total mass of food eaten (Table 1). Altogether, 20 animals from all three groups had been eating rats (usually represented by fur), but only two individuals from two groups contained rats that were considered to be definitely fresh. The sizes of five rats (old and fresh) were determined from the remains (16–160 g); their mean size was 80

TABLE 1. Prey items recovered from the stomachs of 90 wild juvenile *Crocodylus porosus*. FRESH refers to that segment of "ALL" prey judged to be less than 24 h old (N = 152 items). Mass 1 = the measured reconstituted mass of all prey types (total = 229.6 g), whereas Mass 2 = the same data adjusted for the corrected mass of rats (total = 329.7 g). "Tr" = trace amounts (<0.1 g).

| | % Occurrence | | % Composition (FRESH only) | | |
	ALL	FRESH	Number	Mass 1	Mass 2
No. of samples (N = 90)	100.0	100.0	—	—	—
Empty (food and non-food)	3.3	7.8	—	—	—
Empty (food only)	3.3	23.3	—	—	—
Vegetation	63.3	—	—	—	—
Stones	4.4	—	—	—	—
Parasites	20.0	—	—	—	—
Prey			—	—	—
All invertebrates	94.4	74.4	98.0	70.0	48.7
Crustacea	88.9	70.0	88.8	66.5	46.3
Decapoda					
Grapsidae	76.7	48.3	44.1	56.0	40.0
Sesarma sp. 1	57.8	42.2	36.2	31.9	22.2
Sesarma sp. 2	27.8	11.1	7.9	24.1	16.8
Palaemonidae	45.6	37.8	44.7	10.5	7.3
Macrobrachium sp.	45.6	37.8	44.7	10.5	7.3
Insecta	40.0	14.4	9.2	3.5	2.4
Coleoptera	36.6	7.8	5.3	1.1	0.7
Cucujoidea	1.1	1.1	0.6	0.1	Tr
Cerambycidae	1.1	1.1	0.6	0.5	0.4
Undetermined	35.6	6.7	3.9	0.5	0.4
Hemiptera	3.3	3.3	2.0	1.7	1.2
Nepidae	1.1	1.1	0.6	1.0	0.7
Fulgoroidea	1.1	1.1	0.6	0.6	0.5
Undetermined	1.1	1.1	0.6	Tr	Tr
Hymenoptera	3.3	1.1	0.6	Tr	Tr
Formicoidea	1.1	1.1	0.6	Tr	Tr
Undetermined	2.2	0.0	0.0	0.0	0.0
Orthoptera	1.1	1.1	0.6	0.6	0.5
Acrididae	1.1	1.1	0.6	0.6	0.5
Mantodea	1.1	1.1	0.6	0.6	0.5
Mantidae	1.1	1.1	0.6	0.6	0.5
All vertebrates	24.4	3.3	2.0	30.1	51.2
Pisces	1.1	1.1	0.6	1.3	0.9
Teleostomi	1.1	1.1	0.6	1.3	0.9
Periophthalmidae	1.1	1.1	0.6	1.3	0.9
Mammalia	22.2	2.2	1.3	28.7	50.3
Muridae					
Rattus colletti	22.2	2.2	1.3	28.7	50.3
Aves	1.1	0.0	0.0	0.0	0.0
Undetermined	1.1	0.0	0.0	0.0	0.0

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g, which is consistent with an estimated mean of 70–80 g for the "average" size of *R. colletti* in the area (Hertog and Corbett, pers. comm.).

Notwithstanding the limited data, we derived an estimate of fresh rat intake per group, in a way that reduced the emphasis on the exact size of the two fresh rats found, and their chance distribution between the three groups. A predictive relationship between rat size and crocodile size was derived from the 5 rats referred to above. This relationship was not statistically significant ($r^2 = 0.25$; $P = 0.39$), but its positive

slope was considered biologically significant: the smallest crocodile (249 g) eating rats would have been unlikely to eat the largest rat (160 g). This formula was used to predict a mean rat size for each crocodile known to be eating rats (old or fresh), and that weight was reduced by 90% based on the probability of finding a fresh rat in any animal (2 out of 20).

This crude adjustment gave a net increase (100.1 g) in the total mass of fresh rat consumed and allocated the new total between the three groups, according to the frequencies with which

TABLE 2. Percentage occurrence (% of the total number of crocodiles containing a particular taxon) and percentage composition by number and mass (% of the total number and/or reconstituted mass of prey made up by a particular taxon) of fresh prey recovered from the stomachs of wild juvenile *Crocodylus porosus* in the three size groups. Mass 1 = the measured reconstituted mass of all prey types; Mass 2 = the measured mass for all prey corrected for rats.

	% Occurrence			% composition by number			% composition by Mass 1			% composition by Mass 2		
	1	2	3	1	2	3	1	2	3	1	2	3
No. of crocodiles	30	49	11	30	49	11	30	49	11	30	49	11
No. of prey and mass (g)	—	—	—	51	94	7	56.9	110.3	62.6	70.0	155.6	104.1
Crab	50.0	51.0	36.4	49.0	40.4	57.1	81.2	63.6	19.5	66.0	45.1	11.7
Prawn	46.7	36.7	18.2	49.0	43.6	28.6	18.6	11.9	0.6	15.1	8.4	0.4
Insect	3.3	24.5	0.0	2.0	13.8	0.0	0.1	7.2	0.0	0.1	5.1	0.0
Rat	0.0	2.0	9.1	0.0	1.1	14.3	0.0	14.5	79.9	18.7	39.4	87.9
Fish	0.0	2.0	0.0	0.0	1.1	0.0	0.0	2.7	0.0	0.0	1.9	0.0

each group was known to eat rats. It suggested that the two fresh rats recovered were small relative to the size of rat normally eaten by the crocodiles from which they were recovered.

With these corrections (Table 1; Mass 2) it became apparent that although 98.0% of fresh prey were invertebrates, they accounted for only 48.7% of the mass of fresh food. Only 2.0% of the fresh prey were *R. colletti*, but they accounted for 50.3% of the mass of fresh food eaten.

Effects of Body Size.—Excluding the single fish (Table 2), contingency table analysis (df = 6) indicated significant differences in the frequencies of major prey types in the three size groups of crocodiles, regardless of the index used (% Occurrence: $\chi^2 = 12.6$; $P = 0.049$; % Composition by number: $\chi^2 = 16.8$; $P = 0.01$; % Composition by Mass 1: $\chi^2 = 120.4$; $P < 0.001$; % Composition by Mass 2: $\chi^2 = 102.0$; $P < 0.001$). The larger crocodiles tended to eat different prey than the smaller ones, namely more vertebrates and less invertebrates. Of the fresh food eaten by Group 1, 81.2% was invertebrates and 18.7% vertebrates, whereas in Group 3, 12.1% was invertebrates and 87.9% vertebrates.

Nutritive Content of Prey.—The mean fat content (Table 3) we derived for *R. colletti* (4.8%) was below the levels reported by Williams (1987) for this species at different times of year (6.3 to 23.3%). Ash contains the inorganic components, particularly minerals, and includes both calcium and phosphorus. The "unknown" component refers to organic components other than fat and protein (for example, carbohydrates). Calcium and phosphorus were the only minerals assessed independently.

Consumption of Inorganic and Organic Components.—The nutrient consumption rates, in terms of the dry weights of different inorganic (mineral) and organic components per day, reflect the swing away from invertebrates and towards vertebrates with increasing crocodile size (Table 4). Protein, fat and phosphorus content tended to increase with increasing size whereas calcium and ash content decreased, particularly with the shift away from crabs. Calcium to phosphorus ratios declined sharply, from 7.3:1 in Group 1 to 1.8:1 in Group 3.

Growth and Food Conversion Rates.—The 17 recaptures spanned 27 to 517 days (mean = 226

TABLE 3. The percentage composition of the major prey items eaten by wild juvenile *Crocodylus porosus* expressed as wet and dry weights. N = sample sizes; "mean insect" refers to the mean value for all insect groups; "Terr." = terrestrial; "Unk." = unknown; "Ash" = total ash content, which includes both calcium and phosphorus. Totals exceed 100%.

		Wet weight							Dry weight					
	N	Prot.	Fat	Ash	Water	Unk.	Ca	P	Prot.	Fat	Ash	Unk.	Ca	P
Crab	10	11.6	2.4	12.2	67.9	5.9	3.9	0.4	36.2	7.5	38.0	18.3	12.0	1.2
Prawn	15	14.9	3.4	6.3	73.6	1.8	1.7	0.3	56.6	12.7	24.0	6.7	6.5	1.2
Mudskipper	12	14.6	3.1	5.1	74.5	2.7	1.2	0.7	57.4	12.0	20.0	10.6	4.6	2.7
Rattus colletti	4	15.1	4.8	3.9	71.8	4.4	0.7	0.6	53.4	17.0	13.8	15.8	2.6	2.1
Grasshopper	4	23.7	7.0	1.4	61.0	6.9	0.04	0.2	60.8	18.0	3.6	17.6	0.1	0.4
True bugs	17	19.8	6.9	2.1	61.5	9.8	0.1	0.2	51.3	17.8	5.4	25.5	0.3	0.5
Aquatic beetle	12	27.7	12.2	2.7	51.9	5.6	0.1	0.2	57.5	25.3	5.6	11.6	0.3	0.4
Terr. beetle	8	26.1	3.7	1.9	61.3	7.0	0.1	0.2	67.5	9.6	4.8	18.1	0.3	0.6
Mean insect	4	24.3	7.5	2.0	58.9	7.4	0.1	0.2	59.3	17.7	4.9	18.1	0.3	0.5

TABLE 4. The source and daily intake of different inorganic and organic components of the diet (grams of wet and dry matter per crocodile) of wild juvenile *Crocodylus porosus* in three size categories. "Corr. rat" = the corrected intake of rat; "Unk." = unknown; "Tr" = trace amounts only (<0.001 g). The calcium and phosphorus components are also contained within the "Ash" component, so percentages do not add to 100%.

| Group	Food	Dry matter						Wet matter						
		Protein	Fat	Ash	Unk.	Ca	P	Protein	Fat	Ash	Unk.	Water	Ca	P
1	Crab	0.557	0.116	0.585	0.282	0.185	0.018	0.179	0.037	0.188	0.091	1.046	0.060	0.006
	Prawn	0.199	0.045	0.085	0.024	0.023	0.004	0.052	0.012	0.022	0.006	0.259	0.006	0.001
	Insect	Tr	Tr	Tr	Tr	Tr	Tr	Tr	Tr	Tr	Tr	Tr	Tr	Tr
	Corr. rat	0.233	0.074	0.060	0.069	0.011	0.009	0.066	0.021	0.017	0.019	0.313	0.003	0.003
	Total	0.991	0.235	0.730	0.375	0.219	0.032	0.298	0.070	0.227	0.117	1.620	0.069	0.010
	%	42.7	10.1	31.3	16.1	9.4	1.4	12.8	3.0	9.7	5.0	69.4	3.0	0.4
2	Crab	0.518	0.107	0.544	0.262	0.172	0.017	0.166	0.034	0.175	0.084	0.972	0.056	0.006
	Prawn	0.151	0.034	0.064	0.018	0.017	0.003	0.040	0.009	0.017	0.005	0.196	0.005	Tr
	Fish	0.035	0.007	0.012	0.006	0.003	0.002	0.009	0.002	0.003	0.002	0.045	0.002	Tr
	Insect	0.668	0.213	0.173	0.198	0.033	0.026	0.189	0.060	0.049	0.055	0.898	0.009	0.008
	Corr. rat	0.096	0.029	0.008	0.029	Tr	Tr	0.039	0.012	0.003	0.012	0.095	Tr	Tr
	Total	1.468	0.390	0.801	0.513	0.225	0.049	0.443	0.118	0.247	0.158	2.207	0.070	0.015
	%	46.2	12.3	25.2	16.1	7.1	1.5	13.9	3.7	7.8	5.0	69.5	2.2	0.5
3	Crab	0.401	0.083	0.421	0.203	0.133	0.013	0.128	0.027	0.135	0.065	0.752	0.043	0.004
	Prawn	0.021	0.005	0.009	0.002	0.002	Tr	0.006	0.001	0.002	0.002	0.028	Tr	Tr
	Corr. rat	4.442	1.414	1.148	1.314	0.216	0.175	1.256	0.399	0.324	0.366	5.973	0.058	0.050
	Total	4.864	1.502	1.578	1.519	0.352	0.188	1.390	0.427	0.462	0.432	6.752	0.102	0.054
	%	51.4	15.9	16.7	16.1	3.7	2.0	14.7	4.5	4.9	4.6	71.4	1.1	0.6
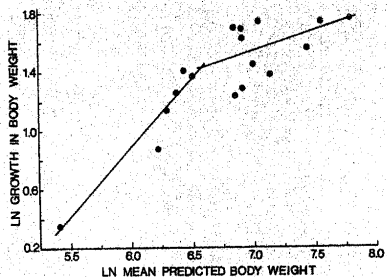
FIG. 1. Relationship between growth (g d^{-1}) and mean body weight (g) for two size classes of juvenile *Crocodylus porosus* (greater and less than 735 g; lnBWT = 6.6) captured in the Adelaide River, Northern Territory, as predicted from 17 recaptures.

± 30.4 d). To obtain the lowest errors when predicting daily growth increments from size, two regression formulae were used (Fig. 1):

<735 g BWT; lnBWT$_{gr}$ = −4.908 + 0.963 lnBWT$_m$ ± 0.13

$$(r^2 = 0.92, P = 0.003);$$

>735 g BWT; lnBWT$_{gr}$ = −3.154 + 0.532 lnBWT$_m$ + 0.256 ln %WET ± 0.10

(Total r^2 = 0.92; r^2 due to lnBWT$_m$ = 0.20, P = 0.17; r^2 addition due to ln%WET = 0.72, P = 0.006)

The formula for smaller animals was highly significant and was not improved with the addition of %WET or ln%WET. The formula for the larger animals was greatly improved with the addition of ln%WET, although the "size" variable (lnBWT$_m$) was forced into the relationship first. The low statistical significance of the size variable is assumed to reflect statistical rather than biological problems (small sample size and limited size range).

The two regression models were used to predict a daily increment in BWT, at the time of capture, for each individual animal, with season

of capture being taken into account with the larger animals. These predicted growth increments were then added, giving a total crocodile growth (g d^{-1}), for each of the three size groups (Table 5). These were then divided by the total daily food consumption (with measured and corrected input of rats) for each group, giving estimates of the food conversion rates (wet weight) for each group. The overall mean corrected conversion rate for the complete sample of 90 crocodiles was 82.4%; 329.7 g of food consumed in 24 h by 90 animals, for a total predicted increase in body weight of 271.6 g. The mean food conversion rate from Groups 1, 2 and 3 was 78.9 ± 8.7% (N = 3).

DISCUSSION

Feeding, Growth and Food Conversion Rates.—The extent to which our feeding results can be considered typical of juvenile *C. porosus* in tidal rivers can be gauged by comparison with Taylor's (1979) results. The mean TL (681 ± 19 mm; range 316 to 1180 mm) of our sample was similar to that of Taylor's (approximate mean = 708 mm; N = 289), although about 17% of her sample were larger than our largest animals. In our sample, 3.3% of animals had empty stomachs, whereas Taylor (1979) reported 15.6% as being empty (Contingency table; χ^2 = 9.45; df = 1; P = 0.002). Using only animals with food in their stomachs, she reported 2.60 prey items (fresh and old) per animal, and we found 2.70 items. Crustaceans (crabs and prawns) were found in 88.9% of our animals and 70.2% of those examined by Taylor (χ^2 = 1.38; df = 1; P = 0.24). Insects were found in 40.0% of our animals and 20.4% of Taylor's animals (χ^2 = 9.27; df = 1; P = 0.002). Among our sample, 24.4% had been eating vertebrates (old and fresh) which was significantly more than the 12.1% reported by Taylor (1979) (χ^2 = 5.39; df = 1; P = 0.02).

The higher proportion of empty stomachs recorded by Taylor (1979) could reflect the improved method of removing contents that we used (Webb et al., 1982), or perhaps a shorter time delay (<1 h) between capture and stomach

TABLE 5. The estimated food intake and increase in body weight (BWT) over 24 h, for three groups of wild juvenile *Crocodylus porosus*. Food conversion rates (CR) are calculated (wet weight to wet weight). "TL" = total length; "Meas." = measured mass of food eaten; "Corr." = mass of food eaten corrected for rat intake.

| Group | TL (mm) | N | Food eaten (g) | | BWT increase (g) | CR (%) | |
			Meas.	Corr.		Meas.	Corr.
1	300–599	30	56.9	70.0	50.2	88.2	71.7
2	600–899	49	110.3	155.6	149.7	135.7	96.2
3	900–1200	11	62.6	104.1	71.7	114.5	68.9
1–3	300–1200	90	229.8	329.7	271.6	118.2	82.4

contents removal. However, neither explanation seems likely to account for the full difference observed. Regardless, the results of this study, and those of Taylor (1979) and Allen (1974) are consistent in indicating that crustaceans are a base diet of juvenile *C. porosus* in tidal habitats. Why our animals were eating significantly more vertebrates than those of Taylor (1979) is unknown. The availability of *R. colletti* in the Adelaide River, although highly variable from year to year (Williams, 1987), was unusually high during the period of our study (Williams, 1987; Corbett and Hertog, pers. comm.). As most crocodilians are adept at exploiting local "blooms" of prey (Attwell, 1954; Valentine et al., 1972; Whitaker and Whitaker, 1977; Gorzula, 1978; Taylor, 1979; Webb et al., 1982), it is possible that the *C. porosus* we examined were eating more rats throughout the period of study than would normally be the case. It is worthy of note that the animals Taylor (1979) studied had similar growth rates to those sampled here (see below), and that they ate similar amounts of crabs and prawns. The extra amounts of rat being eaten by our animals does not appear to have been reflected in increased growth.

Under controlled-environment conditions, juvenile *C. porosus* within their first month of life have food conversion rates of 28% if fed daily and 40% if fed every two days (Webb et al., 1990). Garnett and Murray (1986) estimated food conversion rates of captive juvenile *C. porosus* under a variety of feeding regimes as 17–37%. Estimates derived for other captive crocodilians under two years of age are similar: *Alligator mississippiensis*, 25–40% (Coulson et al., 1973; Joanen and McNease, 1987); *C. johnstoni*, 22.3% (Webb et al., 1983a); *C. niloticus*, 24–36% (Foggin, unpubl.). The overall food conversion rate derived for wild juvenile *C. porosus* in this study (82.4%) is thus appreciably higher than all the estimates derived from captive crocodilians to date. For the reasons outlined below, we consider this to be a real reflection of the situation in the wild, and not an artefact of the techniques used and assumptions involved in deriving the estimate.

If the high food conversion rates reported here are spurious, food consumption rates would need to have been underestimated, growth rates overestimated, or both. With regard to underestimating food consumption rates, three of the four main possibilities can be rejected.

The scoop and pump developed by Taylor et al. (1978) completely emptied the stomachs of three *C. porosus* she sacrificed as a check. The technique has been significantly improved since then (Webb et al., 1982), partly to account for species-specific differences in its application. We used that improved method in this study, and are confident that few fresh items would have

escaped detection, even if all parts of all prey items had not been removed completely (Fitzgerald, 1989).

A further possible underestimating bias lies with the smallest prawns, which may not have been recognizable after 24 h. However, prawns of this size make up a negligible component of the total mass of prawns eaten, and as such, could not be a serious bias.

The method used to age crustaceans and insects, if significantly in error, would also tend to result in an overestimate of feeding rates and thus an underestimate of food conversion rates. The reference material was derived from captive animals maintained at 31–32 C, whereas animals in the wild were subjected to lower water temperatures (especially in the dry-cold period), which could be expected to reduce rates of digestion (Diefenbach, 1975).

The scant data used for estimating the consumption of rats are an obvious area where error could be introduced. The corrections resulted in more fresh rat being added to the diet than was actually measured from the contents, suggesting that errors would be in the direction of having overestimated the contribution made by rats. In addition, *R. colletti* was unusually abundant during the period of study and the crocodiles may have been eating more rats during the period of sampling than would normally be the case; this is certainly suggested by Taylor's (1979) data.

Nevertheless, with so few fresh rats detected, the contribution of a single rat is very significant. If digestion rates were able to proceed at the rate described by Delany and Abercrombie (1986) in *A. mississippiensis*, we considered it possible that one large rat (160 g), which we considered old here, may have been assigned to within 24 h. Using this as the worst case scenario, the measured mass of food (Mass 1) would be increased by 70% and the corrected mass (Mass 2) by 32%. This would reduce food conversion rates (Table 5) to 69.7% for the measured food and 65.9% using the corrected mass of food.

Taken together, there are a number of avenues through which the estimated food consumption rates could be biased, but we have no data suggesting any large or consistent bias occurred. However, the sensitivity of the analysis to the frequency with which fresh rats were eaten is such that this possibility cannot be rejected.

We consider it unlikely that growth rates were significantly overestimated. A number of independent estimates of growth rate have been reported for wild juvenile *C. porosus*. Between hatching (310–320 mm TL) and 52–69 days (360–410 mm TL) of age, Webb et al. (1977) reported mean growth rates between 0.5 and 0.7 g d^{-1}. Magnusson and Taylor (1981) reported means between 0.5 and 1.7 g d^{-1} between hatching and

3 months of age (370–430 mm TL). In this study, *C. porosus* of 350, 450, and 500 mm TL would have had growth rates of 0.6, 1.2, and 1.6 g d^{-1} (Fig. 1), which is consistent with these independent estimates.

As a check on whether the growth rates recorded in this study were consistent with those described previously (Webb et al., 1978) for juvenile *C. porosus* (the same individuals that Taylor [1979] studied), data from this study were analyzed in an identical fashion to the previous study. The mean-sized animal in our study (681.5 mm TL) had a predicted instantaneous head length growth rate of 0.160 mm d^{-1} using the previous data, and 0.154 mm d^{-1} using these data.

Webb et al. (1978) also found an effect of season on growth in *C. porosus* greater than 670 mm TL, as was found here; the larger animals grew faster in the wet-hot season than in the dry-cold season. Whether or not any biological significance can be attributed to the intersection of the two regression lines used to predict growth (Fig. 1) is unknown. Webb et al. (1978) described a similar change in the growth rate to mean size relationship within juvenile *C. porosus* but it occurred around 700 mm SVL (lnBWT = 8.8; Fig. 1), which was beyond the size range of animals sampled in this study.

Thus the data on food consumption and growth rates obtained in this study are consistent with independent data on juvenile *C. porosus*. The estimated food conversion rate, although high relative to captive crocodilians, is accepted as being real. Using the worst case scenario (underestimating the age of a large rat), food conversion rates would still be much higher than reported for captive crocodilians. Juvenile *C. porosus* appear to be much more efficient at converting food to body tissue in the wild than they are in captivity.

No consistent trend between food conversion rates and size was demonstrated here, although this may reflect the method used and the limited data. Newly hatched *A. mississippiensis* in captivity have about 25 times the metabolic rate of grown adult male alligators, and require 25 times as much food per unit body weight for maintenance and growth; they also digest food many times faster (Coulson and Hernandez, 1983). Coulson et al. (1973) report that alligators within their first year have food conversion rates of around 40%, but that these are reduced to 25% by 1–3 years of age.

In captivity, the daily intake of food by juvenile *C. porosus* is much higher than that of their wild counterparts. A sample of juvenile *C. porosus* raised from 2 to 4 mo under a controlled-environment raising regime consumed 15.1 g d^{-1}, or approximately 25.5% BWT per week (unpubl.).

From 4 to 6 mo (mean TL = 633 mm; mean BWT = 697.5 g at 6 mo) they consumed 20.7 g d^{-1}, or approximately 20.7% BWT per week, and from 6 to 8 mo 26.5 g d^{-1}, or approximately 17.7% BWT per week. Garnett (1983) reported food consumption rates for hatchling *C. porosus* of 27.5% BWT per week.

In contrast to captive *C. porosus*, the wild ones sampled here (682 mm TL, 688 g BWT) consumed only 3.66 g d^{-1}, or approximately 4% BWT per week. Yet the average wild *C. porosus* attains 730 mm TL and 870 g in one year (Webb and Manolis, 1989), whereas the average animal raised under farm conditions attained 750 mm TL and 1360 g BWT in a year (unpubl.; they are heavier per unit length).

The reasons why food conversion rates in the wild are much higher than those reported in captivity are unknown. Conditions in captivity could be far more stressful than is generally recognized, although corticosterone levels in captive *A. mississippiensis*, maintained at low densities, suggest that this is not the case (Elsey et al., 1989, 1990). In the wild, *C. porosus* do not appear to have the opportunity to fill their stomachs each time they feed, which usually occurs in captivity. This raises the possibility that the physiological mechanisms associated with the digestion and assimilation of food may not function as efficiently when the stomach is repeatedly filled to capacity. Captive hatchling *C. porosus* fed daily have food conversion rates (28%) that were appreciably lower than those fed every two days (40%; Webb et al., 1990).

Nutritional Considerations.—Juvenile *C. porosus* in tidal rivers obtain large amounts of calcium from crabs. Calcium and phosphorus are two dietary minerals involved in a wide range of physiological and biological processes (Robbins, 1983), and the higher intake of calcium by the smaller animals is consistent with their immediate need to enhance skeletal development. Yet whether or not juvenile *C. porosus* need such high levels of calcium in their diet is unclear. Hatchlings also survive and grow in freshwater swamps (Webb et al., 1983d) without access to crabs and quite possibly with a much reduced calcium intake.

Calcium and phosphorus supplements (wet weight) in captive *C. porosus* diets have ranged from 0.9% calcium and 0.5% phosphorus (Garnett and Murray, 1986) to 2% calcium and 1% phosphorus (Manolis et al., 1989). These are not dissimilar to the absolute levels in the wild diet (Table 4; wet weights), although calcium:phosphorus ratios are much lower than we found in the smaller *C. porosus* (7:1). For *A. mississippiensis*, 1% calcium and 0.5% phosphorus (dry weight) was recommended to improve growth (Staton et

al., 1988), which is less than what is being eaten by wild juvenile *C. porosus* (Table 4; 3.7–9.4% calcium, and 1.4–2.0% phosphorus).

If crocodilians are fed a high fat diet (48%, wet weight), the absorption of both calcium and phosphorus may be affected by the formation of insoluble calcium soaps (Garnett, 1988), and protein digestion may be adversely affected by the fat physically blocking access to proteins by the enzymes (Garnett, 1988). With *A. mississippiensis*, amino acids were assimilated approximately 50% faster with fat-free diets relative to diets which included fat (Coulson et al., 1987). Staton et al. (1987) demonstrated that alligators which ingested high levels of fat put on less weight than those with low levels. According to Garnett (1988) the fat content in the diet of captive hatchling *C. porosus* should be less than 9% (wet weight); this is still almost double what they are eating in the wild (3.0–4.5%), which is essentially a low fat diet.

Composition of the fat is clearly an important aspect of nutrition. Garnett (1983, 1985b) suggested that *C. porosus* may require particular long-chain, polyunsaturated fatty acids which are in high concentrations in marine animals. Crabs and prawns contain a significant proportion of polyunsaturated fatty acids of the linolenic (n^3) series (Reddy et al., 1981; Naughton et al., 1986).

The "unknown" content (4.6–5.0%) in the diet of wild *C. porosus* may reflect a carbohydrate portion, which is probably not assimilated. Crocodilians seem unable to digest either vegetable proteins or polysaccharides (Coulson and Hernandez, 1983).

"Importance" of Different Prey.—Insects account for a very small portion of the mass of fresh food eaten daily, but because some parts of insect exoskeletons (particularly mandibles and elytra) are retained in the stomach for long periods (Garnett, 1985a), they may appear far more "important" than they really are. Percentage composition by mass of fresh prey is a direct measure of the daily intake of nutrients, and it is perhaps the "best" importance index for evaluating nutrition. However, even this index is not sufficient when assessing the "importance" of large prey eaten irregularly.

Predator and Prey Sizes.—The size of the prey eaten by wild juvenile *C. porosus* was strongly bimodal, with larger prey being eaten more frequently by larger crocodiles. Shifts in prey size with increasing predator size presumably reflect an energetic advantage. The average *R. colletti* (80 g) eaten in this study had the equivalent mass of 39 mean-sized crabs, or 185 prawns, or 160 insects. Although a shift to larger prey with increasing body size is common amongst crocodilians, some species, such as *C. johnstoni* (Webb

et al., 1982) specialize on smaller prey, whereas others seem to specialize on larger prey (Magnusson et al., 1987).

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Tooth Number in the Scincid Lizard Genus *Ctenotus*

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ABSTRACT.—The relationship between the numbers of premaxillary, maxillary and dentary teeth and head size is examined between the sexes in one species (*Ctenotus essingtoni*) and among single, unsexed adult specimens of 25 species of the Australian scincid lizard genus *Ctenotus*. The number of premaxillary teeth is constant in all cases except in males of *C. essingtoni*, where it increases slightly with size. The numbers of maxillary and dentary teeth increase with size in all cases. The slopes of the regressions of the number of maxillary teeth and the number of dentary teeth on size do not differ significantly between the sexes of *C. essingtoni*, but males have a higher intercept for maxillary teeth. The number of dentary teeth exceeds the number of maxillary teeth in all cases; within female *C. essingtoni* this difference increases with size. Comparisons are made with the limited data available from other lizard species.

Much has been written on tooth replacement in squamates (Edmund, 1969; Kline and Cullum, 1984, 1985, for review and references), but little has been reported on the relationship between the number of teeth and body size. This is unusual for as animals change size in ontogeny and phylogeny, tooth number would be one aspect of dentition that might also change. However, despite the potential significance of this relationship there are only four studies, involving eleven species in four squamate families (iguanids—Ray, 1965, Montanucci, 1968; gekkonids—Kluge, 1962; Thorpe, 1983; scincids—Arnold, 1980; teiids—Dessem, 1985), that specifically relate the number of teeth to body size. These primary sources are only meagerly supplemented by three types of secondary sources providing potentially useful data or insights into the relationship between the number of teeth and body size: morphological works reporting "raw" data on tooth number in various species (e.g., Siebenrock, 1892, 1894, 1895; Mertens, 1942; Edmund, 1969); tooth replacement studies recording, among other things, changes in the number of teeth during growth

(Cooper, 1966; Cooper et al. 1970; Cooper and Poole, 1973; Kline and Cullum, 1984); and taxonomic works using the number of teeth as a major group character (e.g., Greer, 1979 for lizards; many works on snakes).

The purposes of the present study are two: (1) to determine the relationship between head size, and the number of premaxillary, maxillary and dentary teeth within one population of one species of the scincid lizard genus *Ctenotus*; and (2) to evaluate the same relationships among species of *Ctenotus*. A more general purpose of the study is to extend earlier analyses of the relationship between the number of teeth and body size in squamates to help establish some general trends.

MATERIALS AND METHODS

The genus *Ctenotus* consists of about 80 species of terrestrial, generally diurnal, oviparous skinks endemic to Australia and southern New Guinea. The species range from 41–123 mm in maximum snout–vent length (SVL). They are active, searching predators (generally on arthropods) operating at relatively high body