

Metabolism and survival of fasting Estuarine crocodiles

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Carbon dioxide production by fasting immature Estuarine crocodiles was between 0.023 and 0.042 ml g⁻¹ h⁻¹. The calculated oxygen consumption was between 46% and 70% of that expected from the crocodiles' weights. The daily percentage weight loss while fasting is given by 0.020 + 0.584 (days without food)⁻¹. Survival time of crocodiles that failed to feed after hatching was related to initial weight, death occurring after 27.4% of the initial weight had been lost. Fat was the principal nutrient catabolized by fasting crocodiles. The results are consistent with those expected of an inactive predator that rapidly lowers metabolic rate to starvation levels when food is unavailable and can thus withstand extended fasts.

Contents

	Page
Introduction	493
Materials and methods	494
Carbon dioxide production	494
Fasting	495
Body composition	495
Chemical analysis	495
Calculations	496
Results	496
Metabolic rate	496
Weight loss and survival	497
Change in body composition	497
Discussion	497
References	500

Introduction

Reptile standard metabolic rate has been defined by Bennett & Dawson (1976) as that of an animal in a fasting state under conditions of minimal disturbance during the period of minimum activity. If four days is taken as the minimum time for gut clearance (Diefenbach, 1975) and 15 h the minimum time for untrained animals to recover from handling (Brown & Loveridge, 1981), then only two measurements have been made of the standard metabolic rate of crocodilians. The measurements of *Caiman crocodilus* (Gatten, 1980) and *Crocodylus niloticus* (Brown & Loveridge, 1981) are about 40% of that predicted from their weight using the equations developed by Bennett & Dawson (1976) to describe the metabolic rate of all reptiles.

An explanation of this discrepancy may be the response of crocodilians to fasting. The definition of fasting is imprecise, particularly the point at which fasting becomes starvation. During starvation, many animals have metabolic rates that are considerably lower than their

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S. T. GARNETT

494

standard metabolic rates (Mann, 1956; Glass, 1968; Marsden, Newell & Ahsanullah, 1973; Anderson, 1974). The time taken by some beetles to attain starvation metabolic rates is related to their ecological strategies (Tanaka & Itô, 1982). This paper examines the fasting metabolic rate of the Estuarine crocodile, *Crocodylus porosus* Schneider and relates it to the effects of starvation on body composition, weight loss, survival and the crocodile's ecological strategy.

Materials and methods

Carbon dioxide production

The amount of carbon dioxide produced by 3 fasting immature crocodiles was measured by recording the dilution of ^{14}C in a closed chamber. All animals had been accustomed to the procedure by twice daily handling for 5 months previous to the experiments and had been kept without food until the initially rapid weight loss levelled out and no faeces had been produced for 5 consecutive days. The experiment was begun at 1800 h when each animal was weighed and placed on a platform in an inverted glass chamber sealed from the external atmosphere by a moat of acidified water. The acidified water also released as gas any CO_2 excreted in the urine (Grigg, 1978). To each chamber was added a small amount of ^{14}C generated from $\text{NaH}^{14}\text{CO}_3$ of known concentration, quantity and activity by the introduction of 1N H_2SO_4 . All gas in the inlet hose was displaced by acidified water. A reading of atmospheric pressure at the start of each experiment was obtained from the Bureau of Meteorology (Garbutt, Townsville). During the course of the next 24 h, a comparative measure of pressure within the chamber was taken using a simple water manometer (diam. 0.5 mm) and maintained at a constant level by the inflation of a butyl rubber balloon (Bennett & Dawson, 1972). A sample of air from the balloon at the end of the experiment contained negligible radiation. The temperature was maintained at 30 °C.

At 1800 h on the second day, 1.00 l of air was sampled from the chamber, after mixing by vigorous pumping at a 20 ml syringe attached to an outlet tube, and the crocodiles were removed from the chamber and weighed. The air was sampled by drawing 1.00 l of acidified distilled water from a flask attached to the outlet tube. To this flask was then added 15 ml of 1N NaOH from which CO_2 had been eliminated. After 12 h, during which all CO_2 in the flask of air was absorbed by the NaOH, 15 ml of 5% NH_4Cl was added to neutralize the hydroxide, followed by 5 ml of 20% BaCl_2 to precipitate BaCO_3 . The BaCO_3 was retrieved, weighed, divided into 2 dry, tared vials, and weighed again. After manual powdering of the carbonate, 'Cab-o-sil' thixotropic gel (Packard Instrument Co. Ltd.), prepared in the manner described by MacRae & Wilson (1978), was added to both replicates and the radioactivity was measured on an LKB 1215 Liquid Scintillation Counter.

Taking into account atmospheric CO_2 and chamber volume, the amount of carbon dioxide produced by each animal during the 24 h was calculated as follows:

Vol. CO_2 produced by a crocodile in 24 h = $abcde/fg$

where:

- a = Wt. BaCO_3 collected from 1.00 l of chamber gas (g/l)
- b = Vol. H^{14}CO_3 solution used to generate $^{14}\text{CO}_2$ in chamber (ml)
- c = Radioactivity of H^{14}CO_3 (Bq/ml) as determined below
- d = Vol. of 1 mole of gas at 30 °C at 1 atmosphere pressure (l/atm.)
- e = Pressure in chamber (atm.)
- f = ^{14}C radioactivity in sampled litre (Bq/ml)
- g = Mol. wt. BaCO_3 = 197.35 g/mol

Radioactivity of the H^{14}CO_3 solution was determined by adding 5 ml 20% BaCl_2 to a measured quantity of $\text{NaH}^{14}\text{CO}_3$ solution which was spiked with a measured quantity of Na_2CO_3 solution, both solutions being of accurately known molarity. The BaCO_3 precipitate was retrieved, measured and its radioactivity counted in the manner described above.

Radioactivity H^{14}CO_3 = $h(i+j)/kl$ where:

h = ^{14}C radioactivity of collected BaCO_3

i = Wt. BaCO_3 expected from Na_2CO_3 spike

j = Wt. BaCO_3 expected from NaHCO_3

k = Vol. H^{14}CO_3 solution

l = Wt. BaCO_3 collected

An error of each estimate of CO_2 production was calculated by taking the square root of the sum of squared coefficients of variation of each variable in the calculation.

Fasting

Three groups of hatchling *C. porosus* were used to determine the degree and duration of the effects of fasting. Of 260 crocodiles used to test the effects of diet, density and handling frequency on growth rates (Garnett, 1985), 54 failed to start feeding on the prepared diet of pork or fish they were offered. The decline in weight of these was recorded weekly. Sixteen of these survived the 4-month duration of this experiment and were stimulated to feed on live insects under a different husbandry regime. After 5 and then 11 months they were compared to their siblings, which had been shifted to the new husbandry regime at the same time but had been feeding on the prepared diets for up to 5 months longer.

The animals that began feeding readily constitute the second group of hatchlings used to test the effects of fasting. Intake of this group was measured on each of the 6 days each week that they were fed and examined for patterns related to the period since the weekly day without food using Generalized Linear Interactive Modelling (GLIM: Baker & Nelder, 1978). At the end of 4 months, 24 of these animals were starved for 3 consecutive days and 22 were starved for 4 days. Weight loss during these periods was recorded but intake afterwards could not be.

The third group consisted of 12 individuals that were weighed twice daily. Six of these were fed every day, the other 6 went unfed for one day each week. Intake and weight were recorded over a period of 10 weeks. Weight loss was then recorded twice daily over a period of 7 days during which no food was provided.

The relationship between time and weight loss was analysed for all groups, while the effect of initial weight and weight loss on survival was examined in only those animals that failed to begin feeding.

All crocodiles were kept in 1 × 2 m pens under conditions of minimal disturbance with access to freshwater and ultraviolet light for 12 h each day.

Body composition

During the course of experiments, 5 animals that died were available for whole body analysis, 4 drowned when placed in water when too young and one individual died 58 days after hatching, never having begun feeding. On the assumption that at hatching the animal that starved had a similar composition to the 4 that drowned, it was possible to estimate the changes in dry and organic matter, ash, calcium, phosphorus, protein, fat and fatty acids that occurred during 58 days of starvation.

Chemical analysis

Dry Matter (DM) was obtained by drying at 80 °C to a constant weight. Samples of DM were ashed at 550 °C for 5 h. Organic Matter (OM) was assumed to be DM - Ash. Whole fat content was determined on samples of DM by 60-80 °C BP petroleum ether extraction under reflux for 12 h. Fatty acids in samples of DM were analysed by gas-liquid chromatography using a 20% DEGS column at 190 °C to separate methyl esters. Total Nitrogen (N) was determined on an autoanalyser after Kjeldahl digestion. Protein (CP) was assumed to be 6.25 × N. Calcium was estimated using an atomic absorption spectrometer after digestion in hydrofluoric acid. Inorganic phosphorus was analysed by acid molybdenate reaction using a Technicon autoanalyser.

S. T. GARNETT

Calculations

The weight lost by the fasting crocodiles was averaged over 5 days and assumed to be entirely metabolized organic matter (OMD). The weight of protein (PMD) and fat (FMD) metabolized were derived from the simultaneous equations:

$$\begin{aligned} \text{PMD} + \text{FMD} &= \text{OMD} \\ \mu \text{ PMD} + \Omega \text{ FMD} &= \text{Vol. CO}_2 \text{ produced.} \end{aligned}$$

Values of PMD and FMD were then used to calculate oxygen consumption from the equation:

$$\Psi \text{ PMD} + \Theta \text{ FMD} = \text{Vol. O}_2 \text{ consumed.}$$

Constants were derived as follows:

$\mu = 0.766 = \text{Vol. CO}_2/\text{g PMD} = \Sigma \text{abcd}/e$ for glycine, alanine, glutamine and leucine, the principal amino acids (AA) contributing to the urinary nitrogen in *Alligator mississippiensis* (Coulson & Hernandez, 1959) where:

a = Moles $\text{CO}_2/\text{mole AA}_n$ (assumes all CO_2 from urinary NH_4HCO_3 had volatilized in the acidic environment of the metabolism chamber)

b = Vol. l mole CO_2 at 30 °C, 1 atm. pressure

c = Pressure (atm.) at time of experiment

d = % contribution of AA_n to urinary NH_4^+ in *A. mississippiensis*

e = Mol. wt. AA_n

$\Omega = 1.575 = \text{Vol. CO}_2/\text{g FMD} = \Sigma \text{bcfg}/h$ for all measured fatty acids (FA) where:

f = Moles $\text{CO}_2/\text{mole FA}_n$

g = % contribution of FA_n to total fat change during fasting (Table II)

h = Mol. wt. FA_n

Ψ and Θ were obtained by replacing CO_2 with O_2 in the equations used to derive μ and Ω . Thus $\Psi = 0.700$ and $\Theta = 2.212$.

Results

Metabolic rate

Metabolic rates of fasting crocodiles are summarized in Table I. The oxygen consumption calculated from the CO_2 production was between 46% and 70% of that predicted from the weight

TABLE I
Weight, CO_2 production, O_2 consumption and the weight of protein and fat catabolized by three fasting crocodiles at 30 °C

Metabolic parameter	Animal no.		
	1	2	3
Weight (g)	513.5	306.5	254.5
CO_2 production ($\text{mlg}^{-1} \text{h}^{-1} 10^3$)	22.8	25.6	41.7
O_2 consumption ($\text{mlg}^{-1} \text{h}^{-1} 10^3$)			
calculated from CO_2 production	30.6	35.9	55.0
predicted from weight ($0.278 \text{ wt}^{-0.23} 10^3$) ^a	66.2	74.5	77.8
Protein catabolized ($\text{g h}^{-1} 10^3$)	2.6	0.4	2.0
Fat catabolized ($\text{g h}^{-1} 10^3$)	5.5	5.0	6.5

^a Bennett & Dawson (1976)

using the equation of Bennett & Dawson (1976) for all reptiles at 30 °C. Between 68% and 99% of the carbon dioxide was produced from the catabolism of fat.

Weight loss and survival

The percentage of initial weight lost by fasting crocodiles increased with time according to the following equation:

$$\text{Initial wt. loss (\%)} = 0.752 + 0.00117 \text{ ds} \quad (r = 0.86; \text{d.f.} = 125)$$

where ds = days starvation for ds > 1.

Weight loss was extremely rapid over the first two days but relatively constant thereafter. The rate of weight loss is described by the equation:

$$\text{wt. lost/day (\%)} = 0.020 + 0.584 \text{ ds}^{-1} \quad (r = 0.93; \text{d.f.} = 125)$$

The weekly 48 h fast did not affect weight gain, but weight lost by animals fasting for 72 h was not regained until more than a week later. The weight gains of animals offered food every day were no more rapid than those left unfed for one day out of every seven (one-way ANOVA; $F = 0.73$; $\text{d.f.} = 1/24$). The difference in weight gain of animals starved for 72 h was significantly less than those deprived for only 48 h for the three weeks following the fasting period ($\chi^2 = 27.11$; $\text{d.f.} = 1$). While the food intake of animals fed every day followed no discernible pattern, the daily intake of animals fed six days out of seven was 1.73 times higher on the first day after the weekly fast than on any other. Intake was not measured following longer periods of fasting.

Survival of extended fasting by newly-emerged hatchlings was correlated to initial weight according to the equation:

$$S = 77.56W - 230.0 \quad (r = 0.77; \text{d.f.} = 25)$$

where S = days survival without food after hatching and W = ln (g liveweight).

The percentage of the weight lost before death occurred, however, was constant. Crocodiles that failed to start feeding after emergence from the egg died after they had lost $27.4 \pm 5.5\%$ of their initial weight ($n = 38$).

Change in body composition

The analysed hatchling that died of starvation after 58 days lost 22.7% of its initial weight (Table II). Most of the DM lost was protein but a higher percentage of fat was catabolized, including nearly the entire initial amount of long-chain, polyunsaturated fatty acids. The skeleton was almost unaffected, there being little change in either calcium or phosphorus.

Discussion

In a recent review of American alligator *Alligator mississippiensis* metabolism (Coulson & Hernandez, 1983), discrepancies among published crocodylian metabolic rates (Grigg, 1978; Brown & Loveridge, 1981; Coulson & Hernandez, 1983) are interpreted as differences between individuals and dismissed as irrelevant to a comparison between alligators and homoiotherms. However, such discrepancies, which may equally have arisen from differences between species or between methods, are of interest for comparison of crocodylians with other reptiles, for analysis of ecological strategy and for predicting productivity.

S. T. GARNETT

TABLE II

Analysis of the use of body stores by a *C. porosus* hatchling that died 58 days after hatching, never having fed

Component	Initial weight (g)	Final weight (g)	Loss (%)
Liveweight	46.2	35.7	22.7
Dry matter	10.72	7.07	34.1
Water	35.48	28.53	19.6
Organic matter	9.57	5.98	37.5
Ash	1.15	1.09	5.2
Calcium	0.27	0.26	2.2
Phosphorus	0.09	0.09	1.2
Protein	7.48	4.93	34.1
Fat	2.10	1.05	50.0
Fatty acids			
Saturated			
16:0	0.587	0.390	33.6
18:0	0.412	0.240	41.7
18:1	0.125	0.105	16.0
Monenoic	0.759	0.402	47.0
16:1	0.062	0.024	61.3
18:1	0.637	0.370	41.9
Polyenoic	0.741	0.257	65.3
18:2	0.105	0.089	15.2
18:3	0.036	0.017	52.8
20:4	0.068	0.077	-13.2
20:5	0.163	0.006	96.1
20:6	0.327	0.030	90.8

The fasting metabolic rates of *C. porosus* recorded in this experiment were, like those of *Caiman crocodilus* (Gatten, 1980) and *Crocodylus niloticus* (Brown & Loveridge, 1981), much lower than would be expected from their weights (Bennett & Dawson, 1976). It is suggested here that the discrepancy is a function of a crocodilian's response to lack of food.

It has been reported that the metabolic rate of *A. mississippiensis* declines by 2% per day when starved (Coulson & Hernandez, 1983). The metabolic rate of the snake *Python* is one third of normal levels after 100 days without food (Benedict, 1932) and that of the turtle *Sternotherus* halved by a fast of similar duration (Belkin, 1965). During four weeks' starvation, the heart rate of the lizard *Calotes versicolor* declined by nearly 40% (Subba Rao & Murty, 1977). In contrast, hatchling *Chelonia mydas* lose weight rapidly during starvation (Bonnet, 1979), which implies a high metabolic rate, and immatures of the same species maintained a constant metabolic rate for two weeks without food (Davenport, Ingle & Hughes, 1982). The lizard *Uta stansburiana* (Roberts, 1968) and tortoises *Gopherus* and *Testudo* (Benedict, 1932) also sustain relatively high metabolic rates when denied food.

The explanation for the variability in response of reptiles to starvation may be ecological, as has been demonstrated for beetles; the herbivorous beetle *Henosepilachna vigintipunctata* remains active throughout a period of starvation and dies within 20 days whereas, in the carnivorous *Coccinella septempunctata*, after an initial rise in activity, metabolic rate was reduced to half that of the herbivore and survival time was quadrupled (Tanaka & Itô, 1982). A similar dichotomy in response to starvation between active and passive feeders appears to exist among reptiles; the low metabolic rate of the crocodile when fasting may thus be a strategy for surviving long intervals between meals. While herbivores such as *Uta*, *Gopherus* and *Testudo* must actively search for food, and it has been argued that herbivory among large lizards is an ecological

necessity (Pough, 1973), sit-and-wait carnivores, such as *Crocodylus*, *Alligator* and *Python*, may regulate their metabolic rate in a manner analogous to *Coccinella*. Such a variation in response to starvation could be another consequence of the dichotomy in foraging mode described for predatory lizards (Huey & Pianka, 1981).

The suggestion that the metabolic response of *C. porosus* to fasting is an adaptation to long periods without food is corroborated by the nature of the weight changes. During the first day, the gut is almost emptied but the lost weight is rapidly recovered at the first subsequent meal. In the relatively cool climate of Louisiana, *A. mississippiensis* actually suffered from gout when fed daily, but thrived when deprived of food for two days each week (Joanen & McNease, 1979). Under the warmer conditions in Darwin, however, *C. johnstoni* both ate more and converted it to body weight more efficiently when fed every day than when offered food on only five days each week (Webb, Buckworth & Manolis, 1983). *Crocodylus porosus* had a similar response in this experiment; by the second day of fasting, body stores were being catabolized and weight loss was less easily redressed. Variation in intake also fits the pattern noted in beetles (Tanaka & Itô, 1982) of initially high but later negligible activity during starvation. The consistently higher intake immediately after a day of deprivation reflects active searching for food. A reduced intake after two days' fasting reported by Webb *et al.* (1983) is probably the response of an animal already adjusting to abstinence.

After two days' fasting, the rate of weight loss declined so dramatically that large, newly-emerged hatchlings were able to survive at least 18 weeks on their vitelline stores alone. After only short periods without food, most fish (Weatherly & Gill, 1981) and mammals (Anderson & Volpenheim, 1979) lose weight rapidly and die (Bilton & Robbins, 1973). If the relationship between time and weight loss were to hold for adult *C. porosus*, a 1000 kg animal could survive 16 months without eating. In fact, it is likely that crocodiles can survive a good deal longer, and the weight loss in these experiments was more rapid than it would have been under less stressed conditions. Evidence for this lies in the difference in body condition between the newly-hatched and the starved hatchlings. Although in *Caiman crocodilus* resorption of liver cells for gluconeogenesis occurs after only 20 days without food (Gist, 1972), the loss of protein appears excessive since the stores of saturated fatty acids that remained were much higher than usually present in starving animals (Johnson & West, 1973). Turtles use over 60% of stored fat before death (Belkin, 1965) and the lizard *Takydromus tachydromoides* routinely uses over half its fat stores during winter dormancy (Telford, 1970). Catabolism of amino acids is characteristic of the later stages of starvation (Woo & Fung, 1981); in fish, fat stores usually stabilize at about 15% of their original level (Hegarty & Kim, 1981). Death after losing only 30% of the initial liveweight is also uncommon for an animal that can fast for so long. The frog *Rana esculenta* can fast for over 20 months for the loss of a similar proportion of its mass but still show no ill effects (Grably & Piery, 1981).

Two metabolic factors may have contributed to early death with fat stores largely intact:

(i) Phosphorus was retained to a greater degree than other body components. Unavailability of phosphorus may have inhibited β -oxidation of the fatty-acids (Takeuchi & Nakazoe, 1981) which would in turn have resulted in the observed conservative use of $C_{18:0}$ fatty acid.

(ii) The almost complete catabolism of $C_{20:5}$ and $C_{20:6}$ fatty acids is also surprising (Murata & Higashi, 1980). Since *C. porosus* appears to have a dietary requirement for these long-chain fatty acids (Garnett, 1985), a high turnover rate of long-chain membrane phospholipids such as demonstrated in trout (Castledine & Buckley, 1982) may have accelerated as a result of stress, causing reserves of these acids to reach fatally low levels before other fatty acids could be used.

Finally, the rapid growth of hatchlings that began feeding after several months of abstinence suggests that extended starvation has no lasting ill-effects. Like several species of fish (Bilton & Robbins, 1973; Weatherly & Gill, 1981), *C. porosus* hatchlings demonstrated a remarkable compensatory growth, surpassing their siblings in their rate of weight increase. So rapid and complete was this compensatory growth that the reluctant feeders had weights and lengths indistinguishable from their more voracious siblings after only 11 months.

The metabolism of *C. porosus* is therefore adapted for patient opportunism rather than active predation. Exceptionally long periods without food can be withstood, even by newly-emerged hatchlings. When the opportunity to eat arises, much of the food is converted with great efficiency (Coulson, Coulson & Hernandez, 1973; Joanen & McNease, 1976; Webb *et al.*, 1983) into energy-dense fat (Garnett, 1985) with which the crocodile can survive another period of deprivation. Such a strategy is a luxury that can be afforded by few other vertebrates. Homoiotherms must sustain a high metabolic rate to maintain body temperature; fish expend much energy in obligatory swimming (Nijkamp, van Es & Huisman, 1974). Such short-term lipid cycling in response to irregular food availability is a third alternative to the negligible and seasonal variation of lipid storage in lizards considered by Derickson (1976).

The obvious disadvantage of such a strategy is that growth may be retarded and that little of the growth which does occur is somatic. To compensate, crocodiles can survive in an environment of temporally patchy food abundance; individuals can continue to reside in seasonally favourable sites during periods of low food availability. The considerable homing ability and site fidelity of many crocodilians (Webb & Messel, 1978; Grigg, Taplin, Harlow & Wright, 1980) attests to this. The fidelity of hatchlings to precise resting sites (Garnett, 1985), that are not necessarily determined by temperature (Lang, 1981), may also be a function of an exceptionally low metabolic rate. It enables the young to remain in a safe site until the arrival of food allows the expenditure of energy in exploration.

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