Parameters Affecting the Growth of the Estuarine Crocodile, *Crocodylus porosus*, in Captivity

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Abstract

The effects of variation in diet, density and handling frequency on the growth, intake and conversion efficiency of immature *Crocodylus porosus* were tested under experimental conditions. The clutch of origin explained most of the variation in all variables. Only after taking clutch into account could it be concluded that diets of pork and beef were superior to fish. Significant interactions between clutch and density and clutch and handling frequency prevented analysis of these treatments: individuals from some clutches responded positively to stress, those from other clutches responded negatively. It was concluded that these clutch-related factors, whether they be genetic or environmental, must be elucidated before the effects of other treatments on crocodile growth can be determined.

Introduction

Captive raising is a major feature of many crocodile management programs (Blake and Loveridge 1975; Bolton and Laufa 1982; Webb *et al.* 1983). General guidelines exist for raising several species (Pooley 1971; Blake 1974; Joanen and McNease 1976, 1977, 1979, 1982; Webb *et al.* 1983), including *Crocodylus porosus* (Yangprapakorn *et al.* 1971; Lever 1975; Bolton 1981; Bolton and Laufa 1982) but details of husbandry such as diet, density and handling frequency have never been examined experimentally.

To address these questions a series of trials were conducted on *C. porosus* at Edward River Crocodile Farm on the west coast of Cape York Peninsula, Qld. The diets tested were those most readily available and shed new light on the debate over the suitability of red meat over fish flesh (Joanen and McNease 1976, 1982; Lance *et al.* 1983). Densities tested covered much of the broad range recommended for crocodilians in the literature (Pooley 1971; Smith 1981). The effects of handling frequency were tested because it has been repeatedly stressed that growing crocodiles should be sorted into size classes (Pooley 1962, 1969, 1971; Higgins 1979; Bolton 1981; Webb *et al.* 1983). It has been demonstrated, however, that frequent handling of farmed green turtles *Chelonia mydas* has a deleterious effect on their health (Garnett and Murray 1981) and the stress of capture (Lhotka 1980) and even human presence (Mackay 1968; Gaunt and Gans 1969; Smith *et al.* 1973) is known to affect adversely the physiology of several reptile species. The sensitivity of *Crocodylus johnstoni* to disturbance was mentioned by Webb *et al.* (1983) but its effects have not been tested experimentally.

Artificial incubation of eggs permitted subsidiary analysis of clutch effects within the experiment. All studies of growth in crocodiles have assumed that each individual is a random representative of the population. This assumption has never been tested and studies of other species with multiple offspring would suggest that the clutch or brood is the basic unit for analysis (Abbey and Howard 1973) as between-clutch variability usually exceeds that within clutches.

Methods

Facilities

Trials were conducted in concrete and fibro-cement pens 1 by 2 m with 1-m-high walls, and including a pool $1 \cdot 5$ by $0 \cdot 95$ m in area and $0 \cdot 1$ m deep. All pens were within an enclosed room under conditions of minimal disturbance. Artificial ultraviolet light was provided daily. Air temperature varied from a mean maximum of 36°C in March to a minimum of 19°C in June. Water, when placed in the pens, was always 30°C throughout the year.

Standard Procedures

Eggs were collected from either the breeding lagoon at Edward River farm (five clutches) or from beside nearby rivers (three clutches) under licence from the Queensland National Parks and Wildlife Service. All eggs were incubated in nests made by females in natural and semi-natural conditions until at least 3 weeks before hatching, when they were moved to an enclosed, insulated box for artificial incubation at about 30°C (± 2°C). Animals were marked individually at hatching by scute-clipping, weighed, measured and assigned to an experimental group. Food, diced into portions 1 by $0 \cdot 5$ by $0 \cdot 5$ cm, was first presented 10 days after hatching. At 1800 h on six days each week a weighed portion of food sufficient to satiate all crocodiles was placed on plates (12 cm diameter) at one end of the pens. At the same time fresh water was added to each pool. Uneaten food was retrieved from the pool between 0600 and 0900 h, at which time the pools were drained and cleaned. Temperature and humidity within the pens were recorded continuously throughout the study.

Measurements

All animals were weighed weekly on the day of fasting. Total length (snout tip to tail tip) was measured once a month. To measure animal condition the value b in the equation: $\ln W = a + b . \ln L$, where W is weight in grams and L is length in millimetres, was calculated from pooled data from all crocodiles over the 4-month experimental period and used to compute $c = 10^4 (W/L^b)$ for each individual (Le Cren 1951; Taylor 1979). Intake was calculated as the difference between the amount of food presented and the amount retrieved. All food weights were converted to dry matter equivalents. Conversion efficiency was calculated as the ratio between dry matter intake and live weight increase. Sex was determined by cloacal examination at least 1 year after hatching and was confirmed in most individuals after 2 years.

Analysis was conducted on only those animals that demonstrated sustained weight gain, ignoring those that failed to start feeding. All variables were analysed by means of Generalized Linear Interactive Modelling (Baker and Nelder 1978). With time as an integral variable, a model was constructed including time, clutch, one of the three experimental treatments, diet, density or handling frequency, and all possible interactions. For analysis of food intake a variable describing temperature and/or humidity was included in the model. All combinations of variables and their interactions were fitted to the data and the final model was obtained by deleting any that were not significant. Although the same animals were necessarily used at each time interval this would not have affected analysis of the differences between clutches or treatment. The design of the experiment did not permit analysis of possible interaction between treatments.

Diets

The three diets used were pork obtained from the hindquarters of locally shot wild pigs *Sus scrofa*, lean beef, and fillets of threadfin salmon *Nemipterus tolu*. All food was supplemented with $2 \cdot 5\%$ (wet weight) Petvite (IGY Manufacturing Pty Ltd) and 25% dibasic calcium phosphate. Vitamin and mineral supplement contained, in milligrams per kilogram, vitamins A ($42 \cdot 6$), D3 ($0 \cdot 36$), B1 (65), B2 (130), B6 (40), B12 ($0 \cdot 14$), E ($60 \cdot 0$) and K ($42 \cdot 5$), calcium pantothenate (140), niacin (425), folic acid ($2 \cdot 2$), choline chloride ($2 \cdot 85$), sodium chloride (150), calcium (8600), phosphorus (4800), iodine ($11 \cdot 0$), iron (275), cobalt ($2 \cdot 75$), copper ($27 \cdot 5$), magnesium ($262 \cdot 5$), manganese ($37 \cdot 5$), and zinc ($42 \cdot 5$). Analyses of all diets are presented in Table 1.

Diet Analysis

Samples were dried at 80°C to constant weight to give dry matter (DM). DM samples were ashed at 550°C for 5 h (Gorsuch 1970). Organic matter (OM) equals DM minus ash. Whole fat content (F) was determined by 60–80 b.p. petroleum ether extraction under reflux for 12 h in a soxhlet apparatus. Fatty acids were analysed by gas–liquid chromatography. Total nitrogen (N) and phosphorus were determined with a Technicon AA2 autoanalyser. Crude protein (CP) equals nitrogen multiplied by $6 \cdot 25$. Calcium was determined on an atomic absorption spectrometer.

Energy density, in kilojoules per gram organic matter, was determined in a Gallenkamp bomb calorimeter. Glycogen, in grams, was derived by solving the following simultaneous equation: $G + F = \text{OM} - \text{CP}$; $aG + bF = c\text{OM} - d\text{CP}$; where a is $17 \cdot 230$ kJ per gram of glycogen (Blaxter 1967), b is $39 \cdot 375$ kJ per gram of fat (Blaxter 1967), c is kilojoules per gram of OM and d is $22 \cdot 186$ kJ per gram of protein (Schulz 1978).

Effect of Diet

Each of nine clutches of *C. porosus* was divided randomly at hatching into groups of five hatchlings. Since clutches hatched at intervals over 70 days, they were kept separate, i.e. no group contained hatchlings from more than one clutch. Pork was given to one group of five in each clutch to act as a control. Other groups of five in each clutch were given one of the other two diets. At least three replicate groups of hatchlings were used to test differences between the other two diets. Unfortunately too few hatchlings were available to enable replication of any diet within clutch. Food intake was measured daily, weight and conversion efficiency weekly, and length and animal condition once a month for 4 months.

Table 1. Analysis of the pork, fish and beef diets offered to *Crocodylus porosus* hatchlings

Values are percentages of DM unless otherwise specified. — Not analysed

Nutrient	Pork	Fish	Beef
Energy (kJ g^{-1} OM)	24·01	23·65	23·70
Dry matter (% fresh weight)	31·0	25·5	32·6
Ash	20·7	9·2	19·3
Calcium	3·0	1·0	3·1
Phosphorus	3·9	0·4	3·6
Organic matter	79·3	90·9	81·2
Protein	69·7	76·2	73·4
Glycogen	1·0	5·3	0·8
Fat	8·6	9·4	7·0
Fatty acids (% total fatty acids)			
Saturated	41·00	41·19	—
14:0	1·78	2·28	—
16:0	23·59	22·43	—
18:0	13·79	11·80	—
Monenoic	34·60	19·73	—
16:1	3·62	5·27	—
18:1	30·43	13·44	—
Polyenoic	23·43	38·54	—
18:2	12·06	1·10	—
18:3	5·53	1·39	—
20:4	3·21	8·56	—
20:5	0·00	0·73	—
22:6	0·03	15·61	—

Effect of Density

Six of the nine clutches were also divided randomly into groups of 5, 10 or 20 hatchlings. All were fed pork, so the controls for experiment 1 were also controls for experiment 2. Groups of 10 and 20 were replicated three times, although only one experimental density could be accommodated, other than the control, in each clutch. Measurements were taken with the same frequency and over the same period as experiment 1.

Effect of Handling Frequency

From three of the clutches used in experiments 1 and 2, additional groups of five hatchlings were selected at random. These were caught for weighing once each month instead of weekly, handling frequency being taken as a measurement of stress.

At the end of the three experiments, all crocodiles were combined, then divided according to size into two equal groups which were kept under the same husbandry regime, being fed pork supplemented with insects from a light trap. At intervals of 160, 256 and 516 days all were weighed and measured again, to determine the long-term effects of early treatment. The range of sizes at each interval was such that the body condition factor b could be validly determined on each occasion.

Results

Pertaining to All Experiments

The clutch from which an animal originated accounted for a significant proportion of the variation in initial weight, length and animal condition, and in the same three growth variables throughout all experiments. Clutch characteristics are described in Table 2. Of all parameters measured, clutch alone was still significant among 2-year-old animals. It was also a significant source of variation for intake and conversion efficiency. The amount of variation accounted for by clutch is described in Table 3.

Table 2. Characteristics of the clutches of C. porosus eggs used

Values are means ± standard deviations

(a) **Collection and eggs**

Clutch No.	Collection Place	Date	N	Weight (g)	Eggs Length (mm)	Breadth (mm)
1	Farm Lagoon	22 Jan.	61	$117 \cdot 2 \pm 4 \cdot 2$	$75 \cdot 4 \pm 3 \cdot 1$	$52 \cdot 5 \pm 1 \cdot 0$
2	Farm Lagoon	22 Jan.	62	$116 \cdot 0 \pm 4 \cdot 3$	$79 \cdot 2 \pm 3 \cdot 0$	$50 \cdot 2 \pm 0 \cdot 9$
3	Farm Lagoon	22 Jan.	34	$75 \cdot 2 \pm 1 \cdot 9$	$70 \cdot 5 \pm 2 \cdot 1$	$42 \cdot 5 \pm 0 \cdot 8$
4	Farm Lagoon	22 Jan.	55	$81 \cdot 5 \pm 2 \cdot 7$	$70 \cdot 3 \pm 1 \cdot 8$	$44 \cdot 8 \pm 0 \cdot 7$
5	Farm Lagoon	22 Jan.	39	$65 \cdot 5 \pm 1 \cdot 2$	$65 \cdot 0 \pm 1 \cdot 3$	$40 \cdot 1 \pm 0 \cdot 6$
6	Mitchell R.	29 Apr.	41	$114 \cdot 1 \pm 4 \cdot 3$	$78 \cdot 6 \pm 2 \cdot 8$	$49 \cdot 7 \pm 0 \cdot 8$
7	Chapman R.	17 Apr.	40	$91 \cdot 8 \pm 4 \cdot 2$	$76 \cdot 6 \pm 2 \cdot 6$	$45 \cdot 5 \pm 0 \cdot 8$
8	Munkun R.	19 Apr.	40	$75 \cdot 8 \pm 2 \cdot 9$	$69 \cdot 4 \pm 1 \cdot 6$	$42 \cdot 8 \pm 0 \cdot 7$

(b) **Hatching data**

Clutch No.	Hatching date	No. of hatchlings	Hatching success (%)	Hatchling weight (g)	Hatchling length (mm)
1	11 Apr.	25	41	$78 \cdot 3 \pm 3 \cdot 2$	$32 \cdot 6 \pm 0 \cdot 6$
2	21 Mar.	19	31	$75 \cdot 6 \pm 4 \cdot 5$	$31 \cdot 6 \pm 1 \cdot 3$
3	17 Apr.	22	65	$40 \cdot 0 \pm 4 \cdot 2$	$26 \cdot 0 \pm 1 \cdot 0$
4	13 Apr.	42	76	$56 \cdot 8 \pm 3 \cdot 1$	$29 \cdot 4 \pm 0 \cdot 5$
5	22 Apr.	32	82	$55 \cdot 2 \pm 2 \cdot 5$	$30 \cdot 4 \pm 0 \cdot 5$
6	14 May	38	93	$79 \cdot 6 \pm 5 \cdot 0$	$30 \cdot 8 \pm 0 \cdot 9$
7	19 May	35	88	$61 \cdot 4 \pm 4 \cdot 1$	$30 \cdot 7 \pm 0 \cdot 8$
8	8 June	17	43	$46 \cdot 3 \pm 3 \cdot 2$	$25 \cdot 7 \pm 0 \cdot 7$

An indication of the extent of variation between clutches is described in Fig. 1. All groups for which the mean weights are illustrated in Fig. 1 were kept under standard conditions and fed pork. Clutch numbers are as for Table 2. Because there was such a wide variation between clutches, graphic presentation of results derived from the experiments on diet, density and handling frequency was not possible.

No measured variable accounted for the differences between clutches. Mean weight, length and animal condition for each clutch were tested monthly against initial weight, initial length, measured sex ratio, clutch size, time at which eggs were collected from nest, hatching date, time spent in incubator and hatching success. Several of the clutches that grew particularly fast

in the first 6 months failed to thrive during the next 18 months. However, the pattern was not consistent and the inverse relationship between early and late growth rate was not statistically significant.

Temperature

As different clutches of crocodiles hatched over 2 months between April and June, and growth was measured only weekly, the effects of temperature and humidity on growth could be separated from those of clutch for only those clutches hatching within a few days of each other. No variation in growth rate, that could be attributed to a change in mean weekly temperature or humidity, occurred simultaneously in clutches of similar age.

Table 3. Analysis of the variation in weight, length, condition, intake and conversion efficiency of hatchling and immature *C. porosus* that is explained by clutch of origin

M.S.S., mean sum of squares. NS, not significant

Age class	Variable analysed	M.S.S. (8 D.F.)	M.S.S. (rem.)	D.F. (rem.)	F	P<
1 week	Weight	6·17	0·014	217	427·11	0·001
	Length	2·24	0·037	217	62·78	0·001
	Condition	3·23	0·200	217	26·93	0·001
1–16 weeks	Weight	1·03	0·003	2110	324·70	0·001
	Weight gain (%)	1·60	0·429	2110	3·73	0·001
	Length	3·67	0·025	643	147·96	0·001
	Length gain (%)	1·03	0·094	641	12·99	0·001
	Condition	1·30	0·019	558	68·24	0·001
	Intake	1·24	0·029	256	2·40	0·025
	Conversion efficiency	6·20	2·587	256	2·40	0·025
2 years	Weight	9·91	2·880	147	3·44	0·005
	Length	1·12	0·301	147	3·73	0·001
	Condition	4·44	4·827	147	0·92	NS

Daily measurement of intake allowed comparison with temperature and humidity on a finer scale. Maximum, minimum and mean temperature and humidity were calculated for the night of feeding, the previous day, the previous night, and over the entire period. However, the only measure of humidity or temperature correlated with intake was the maximum night-time temperature. Intake of dry matter, in grams, per gram of live weight increased with maximum night-time temperature at the rate of $0·09\%$ per degree Celsius ($r^2 = 0·655$, 1865 d.f.). Over the range of temperature experienced at Edward River during the experiments, this constituted a maximum variation of $0·62\%$ and was therefore ignored.
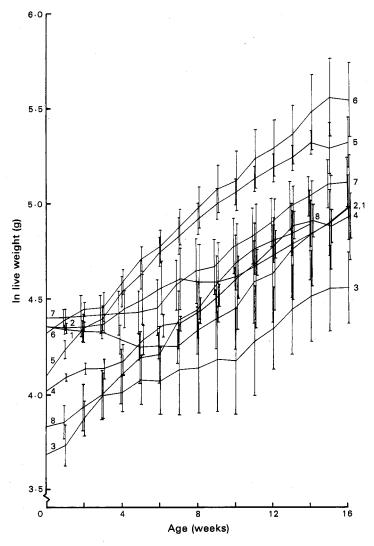
Effects of Diet

A significant proportion of the variation in animal weight, length, condition, intake, and conversion efficiency could be attributed to diet after the effects of age and clutch had been taken into account. For each parameter the fish-fed animals performed differently from hatchlings fed on either beef or pork, between which there was never any significant difference. Fish-fed crocodiles had a higher dry matter intake per gram of live weight but converted it less efficiently, so that they were not only lighter and shorter than their siblings at the same age but, for the first 6 weeks, also in worse condition.

The exponents of time in the relationship between ln (weight) and weeks and between ln (length) and months are given for each diet in Table 4. The intercept in each case is a function

of the variation in initial weights of clutches used to test each diet and does not reflect diet itself.

For weight and length the interaction between diet and time was significant. The analysis of this interaction showed that the difference between fish and the other two diets was significant during the last 2 months but not in the first 6–8 weeks. The disparity, however, appeared gradually; analysis of the variation in rate of weight gain and in rate of length gain showed that the amount explained by diet was insignificant.

Fig. 1. Increase in live weight, expressed as the natural logarithm, of groups of *C. porosus* hatchlings from eight clutches, kept under the same conditions of diet and husbandry, for the first 16 weeks of life. Clutch numbers as in Table 2.

The interaction between condition and time was also significant but the opposite trends were true. After the first week, when all animals were in similar condition, the condition of animals fed fish was less than that of those fed pork or beef until the 6th week, after which it matched that of animals on the other diets.

For intake and conversion efficiency, the interaction between diet and time was not significant: a smaller percentage of the high intake of fish was converted into live weight gain during every week of the experiment.

The effect of diet was consistent for all clutches: there was no interaction between clutch and diet for weight, length, condition, intake or conversion efficiency.

Table 4. Parameters of relationships for early growth of hatchling
***C. porosus* on three diets**

(a) Weight and age

Weight in grams equals αk_1^β where k_1 is age in weeks

Diet	α	β	ϵ	t	r	D.F.
Pork	83·4	0·0652	0·0023	28·64	0·901	245
Fish	91·8	0·0477	0·0039	12·38	0·800	150
Beef	70·1	0·0534	0·0038	14·29	0·814	128

(b) Length and age

Length in centimetres equals αk_2^β, where k_2 is age in months

Diet	α	β	ϵ	t	r	D.F.
Pork	32·9	0·0537	0·0044	12·11	0·873	66
Fish	33·4	0·0366	0·0075	4·91	0·647	44
Beef	29·9	0·0426	0·0076	5·62	0·675	48

The intake and conversion efficiency are summarized in Table 5. Intake of all diets increased during the first 4 weeks but then levelled out to the asymptote value given in Table 5. Conversion efficiency, however, declined throughout the experiment according to the equation: $w/i = 1\cdot421 - 0\cdot034\,t$, where w is live-weight gain in grams; i is DM intake in grams and t is time in weeks ($r^2 = 0\cdot409$, $P < 0\cdot001$).

The conversion efficiency during the first week was excluded from the analysis because it was greater than any other week by a factor of $2\cdot34 \pm 1\cdot02$.

Thirty-nine hatchlings, $16\cdot8\%$ of the total, did not begin feeding on any of the diets offered. Acceptance varied between diets, pork (90%) being acceptable to a larger proportion of hatchlings than either beef (83%) or fish (77%). The difference, however, is significant at only the 10% level ($\chi^2 = 14\cdot72$, 9 d.f.).

Table 5. Food conversion efficiency of *C. porosus* hatchlings fed three diets

Food intake expressed as mean ± standard deviation

Diet	No. of animals	Intake (percentage live wt per week)	Live weight gain (g) (*L*)	Dry matter intake (g) (*D*)	Conversion efficiency (*L/D*)
Pork	18	5·66 ± 0·52	1755·2	1461·7	1·20
Fish	12	7·02 ± 0·73	734·0	1111·2	0·66
Beef	11	5·67 ± 0·45	716·8	692·0	1·04

Effects of Density

Use of a model in which the effect of density on growth parameters was tested after hatchling age and clutch of origin had been accounted for, demonstrated that groups of 10 outperformed those of either 5 or 20. However, although no interaction with time could be detected, the

significance of the interaction with clutch masked any consistent effects of density (Table 6). The groups of 10 animals from clutch 3 were heavier but not longer than the control, the reverse was true of clutch 4, and neither parameter in groups of 10 from clutch 8 matched the control. A similarly confused pattern exists when groups of 20 are compared to their controls.

Table 6. **Analysis of the interaction between density of** *C. porosus* **hatchlings and their clutch of origin for several growth variables**

$*P < 0·05$

Densities compared	Parameter	F	D.F.	Value of t for clutch No.		
				3	4	8
5:10	Weight	63·74*	4,2106	7·713*	1·189	−6·480*
	Length	12·50*	4,641	1·236	7·126*	−4·158*
	Condition	13·23*	4,554	2·171*	−2·793*	0·334
	Intake	0·61	4,252	0·243	0·508	−0·783
	Conversion efficiency	1·11	4,252	0·335	0·986	0·114
				5	6	7
5:20	Weight			3·795*	−3·016*	0·409
	Length			−9·719*	−3·345*	1·027
	Condition			6·204*	1·921	1·148
	Intake			1·406	−1·061	0·492
	Conversion efficiency			−0·222	1·552	0·141

Effects of Handling Frequency

As for the experiment to determine the effects of density, the interactions between clutch of origin and handling frequency invalidated the conclusions of a simpler model that found frequent handling to be detrimental to growth but ignored interactive effects. In fact, although this was true for crocodiles from two clutches, the opposite was true for those from the third clutch (Table 7). However, all control groups had one hatchling that did not begin feeding whereas all members of groups that were handled monthly began feeding immediately.

Table 7. **Analysis of the interaction between the frequency with which hatchling** *C. porosus* **were handled and their clutch of origin, for several growth variables**

$*P < 0·05$

Parameter	F	D.F.	Value of t for clutch No.		
			1	5	7
Weight	4·231	1,639	3·102*	2·012*	−25·927*
Length	7·547	1,639	4·163*	8·913*	−14·676*
Condition	0·883	1,639	0·138	1·022	−0·761

Discussion

Effects of Clutch

It is an assumption of evolutionary theory that genotype-by-environment interactions are important perpetrators of spatial phenotypic variability (Powell and Taylor 1979). Nevertheless it is frequently assumed in studies of animal production (Pani 1972; Lasley 1978)

and ethology (Abbey and Howard 1973; Hughes 1979) that these effects are negligible within a given population. This assumption appears to have been made for nearly all studies of reptile growth to date; each individual is assumed to be a random representative of the population. For example, Webb *et al.* (1978) concluded that any variation in initial size would be accounted for by 2 weeks growth. On the basis of the present experiments it would appear that this assumption is questionable, even if used only as a basis for determining the age of young crocodiles, as more of the variability in growth rate was explained by clutch of origin than by any other factor, even among animals over 2 years old.

Two types of genotype-environment interactions were observed in the young crocodiles. Those raised on different diets demonstrated an ordinal reaction (Lubin 1961) in which quantitative phenotypic differences changed but the rank of each clutch remained the same; i.e. some clutches grew faster than others but within each clutch those fed pig or beef grew faster than those fed fish. This is the most frequently encountered type of interaction in animal husbandry (Lasley 1978) and, as the direction of response is consistent between treatments, results can be assessed qualitatively.

Clutches used to test the effects of varying density and handling frequency, however, demonstrated a disordinal interaction (Lubin 1961) in which both phenotypic and rank order differences occur; i.e. some clutches responded to high densities or handling frequency with high growth, others with poor growth. Disordinal reactions are rarely recorded in response to physiological stimuli (Goddard 1979) but they are common in response to psychological stimuli (Erlenmeyer-Kimling 1972). Some strains of mice are particularly sensitive to early stress (Henderson 1967), in others it is the age at which they are stressed that is important (Grosswald and Luttges 1974). In *Drosophila melanogaster* the growth rate of different varieties varies with density (Marks 1982; Taylor and Condra 1983). A U-shaped relationship between stress and behavioural response, in which each genotype has an optimum level of stimulation, has been proposed (Goldman 1969). Such a model would fit the reactions of different clutches to varying density or handling frequency. It is because of the difficulty with which predictions can be made from such a model that genotype-environment interactions are so frequently ignored (Erlenmeyer-Kimling 1972). The results of these experiments show that they should not be, especially in species with multiple offspring.

However, while this conclusion is still valid, it is recognized that the source of the variation between clutches may nevertheless have been environmental. Although conditions in the incubator and during raising were kept as uniform as possible, the nest environments of clutches differed. It has been shown for the American alligator *Alligator mississippiensis* that the temperature of incubation affects not only the sex of the hatchling but the size as well (Ferguson and Joanen 1982). Although neither sex nor initial size explained significant amounts of the variation in growth between clutches, nest environment could have varied considerably (Webb *et al.* 1977; Magnusson 1979). Although a strong genetic base to larval specific growth rates has been proved for the frog *Hyla gratiosa* (Travis 1980) and it is possible to select fish for fast growth rate (Moav and Wohlfarth 1976), it was not possible to separate genetic effects on crocodile growth from those of egg environment.

Diet

The conclusion that red meat from pork or beef is superior to fish as a diet for *C. porosus* is the same as that of Joanen and McNease (1976) for *A. mississippiensis*. Although fish was eaten in the largest amounts, it was converted to growth with least efficiency. The reason for the poor conversion efficiency remains obscure. Fish exceeded red meat in protein content, and fish flesh has been used repeatedly in experiments on *A. mississippiensis* as an example of a complete protein (Coulson and Hernandez 1964; Herbert and Coulson 1975). Both diets were supplemented equally with vitamins and minerals. Of the measured variables, fish differed only in fatty acid composition.

The principal difference between the fatty acids of fish and those of pork is their level of

saturation. The high levels of polyunsaturated fatty acids in fish are particularly liable to autocatalytic peroxidation (Christie 1973), a process initiated by ultraviolet light and pro-oxidant metal ions such as cobalt, manganese, iron and copper (Fogerty 1971). All four metal ions were present in the mineral supplement that was added to each diet before feeding, and the diets were prepared in a room illuminated, in part, by ultraviolet light. Dietary oxidized fatty acids have led to pathology resembling vitamin E deficiency in fish (Watanabe 1982) and poultry (Voreck and Kirchgessner 1981), but rancid fats fed to poultry can also result in a subclinical reduction in growth rate (Toscano and Tartari 1979) caused by reduced accessibility of both fat and protein (Opstvedt 1974). Autoxidation of the fatty acids in the fish would explain not only the lower growth rates of the fish-fed animals but also why, if the fats were indeed rancid, more hatchlings failed to start eating fish. Long-term detrimental effects of a marine fish diet on the reproductive potential of alligators have been suspected (Lance 1982) but have not, as yet, been demonstrated (Lance et al. 1983). Certainly no long-term effect on growth rates was detected after all crocodiles were switched to a diet of pork and insects.

Density

When the area of land within a pen is used as the basis for comparison, since that is where the hatchlings form their highest concentrations, the densities tested in this experiment ranged from $0 \cdot 025$ to $0 \cdot 1$ per square metre of land area per animal. This encompasses the range of densities that have been used for newly hatched C. porosus, C. novaeguiniae and C. siamensis on farms (Yangprapakorn et al. 1971; Blake 1974; Bolton 1984) and for A. mississippiensis in environmental chambers (Joanen and McNease 1976). It is less than that employed by Smith (1981) on a commercial alligator farm and greater than that recommended by Pooley (1971) for C. niloticus. Yet within the range tested, there were no differences between densities that could not be accounted for by variation between clutches and, even when 20 crocodiles clustered in a corner, none suffocated. Nor was there any skew in size frequency distribution, even among the 2-year-old animals, that would suggest the territoriality observed among slightly older C. porosus (Bustard and Kar 1980).

Density as a function of land area, however, may not be the appropriate measure. Given the propensity of the hatchlings to huddle it may be more appropriate to measure density in terms of the number of animals per pen. The highest densities reported (Yangprapakorn et al. 1971; Smith 1981) used groups of 20 or fewer per pen, whereas larger overall numbers in a pen have had to be kept at lower densities.

Handling Frequency

Studies of wild crocodiles suggest that growth rate may be affected for up to 6 months from the time of initial capture (Webb et al. 1978) but differences in response of individuals to stress have frequently been encountered in studies of crocodilians (Coulson and Hernandez 1983). The evidence from this experiment suggests that the clutch of origin is an important factor in this variation. As in other species with multiple offspring (Abbey and Howard 1973), it is the clutch, not the individual, that should be used as the unit for examining variation within the species. There is some evidence that variation in glandular secretion by A. mississippiensis may also be explained by clutch of origin (Johnsen and Wellington 1982).

Overall, most of the experimental crocodiles habituated rapidly to repeated handling, to the extent that all those handled twice daily continued to feed and grow well. These, however, had already been feeding for several months and it is perhaps telling that there were no runts among those not handled in the first month whereas there were in each of the control groups. If stress does indeed affect the growth rate of young C. porosus it would seem that it is in the first month that it will do so most dramatically.

In conclusion it would appear that factors relating to the clutch, whether they be genetic or related to the incubation environment, are the most important determinants of early growth

by *C. porosus*. Although the crocodiles in these experiments performed similarly to the *C. porosus* described by Bolton (1984) and demonstrated levels of efficiency like those of other crocodilian species (Joanen and McNease 1979; Coulson and Hernandez 1983; Webb *et al*. 1983), more detailed comparison with the measurements of other workers is not possible without elucidation of those clutch-related factors.

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