

# Thermoregulation in the Nile Crocodile, *Crocodylus niloticus*

J. P. LOVERIDGE

Department of Zoology, University of Zimbabwe,  
P.O. Box M.P. 167, Harare, Zimbabwe

## SYNOPSIS

Thermoregulation in wild and captive Nile crocodiles was studied in Zimbabwe. Whilst basking in the sun, juvenile crocodiles of 0.5-1.5 kg body weight had mean body temperatures ( $T_b$ ) in the range 29.7-33.4°C. Biotelemetric studies suggest that basking temperatures of 32-34°C are also maintained by crocodiles up to 38 kg body weight. Crocodiles of body weight above 90 kg had mean  $T_b$ s of 25.1-28.4°C.

Juvenile crocodiles caught on land during the night had  $T_b < T_w$  (water temperature) and  $T_b > T_a$  (air temperature) during the cold months but  $T_b < T_a$  during the hot months. Those caught in the water had  $T_b = T_w$  at all seasons of the year.

In the absence of radiant heat, crocodiles in the weight range 75 g-4 kg did not heat significantly faster than they cooled. When heated by two 1000 W lamps the relationship between thermal time constant ( $\tau$ ) and body weight in the range of 0.22-314 kg was  $\log_{10} \tau = 0.3259 + 0.4479 \log_{10}$  body weight (g). The aquatic weed *Salvinia molesta* affords a substantial insulation when draped on the backs of crocodiles. Windspeeds in the range 1.0-4.5 m s<sup>-1</sup> significantly shortened the time constant for heating under two 1000 W lamps.

Although mouth gaping did not always occur in circumstances where there was need for cooling of the body, laboratory experiments showed that the oral mucosa (tongue and roof of the mouth) was a site of evaporative cooling. Tongue temperatures were about 5°C lower than back temperatures when a crocodile was heated from a  $T_b$  of 16°C to 34°C. Evaporative water losses in the range 2.8-21.2 mg cm<sup>-2</sup>h<sup>-1</sup> were measured by means of ventilated capsules on portions of the oral mucosa.

## INTRODUCTION

Despite the obvious importance of thermoregulation in the lives of crocodylians, it has been studied in only a few species. The American alligator, *Alligator mississippiensis*, has received most attention (Colbert, Cowles & Bogert, 1946; Spotila, 1974; Smith, 1975; Lang, 1979a). The Australasian crocodiles, *Crocodylus novaeguineae* and *C. porosus* have been studied by Johnson (1974), Johnson, Webb & Tanner (1976), Lang (1981) and *C. johnstoni* by Grigg & Alchin (1976). Aspects of thermoregulation in *C. acutus* have received attention from Lang (1979a), and in *Caiman crocodylus* from Diefenbach (1975).

Thermal preferences and behavioural thermoregulation of crocodylians have been studied in a number of species (Spotila, 1974; Smith, 1975; Diefenbach, 1975; Johnson, Webb *et al.*, 1976; Lang, 1981). Heating and cooling rates in *A. mississippiensis* (Smith, 1976a; Johnson, Voigt & Smith, 1978; Smith & Adams, 1978) and in *Crocodylus johnstoni* (Grigg & Alchin, 1976) have been measured, and mechanisms for differences in heating and cooling rates investigated (Smith, 1976b; Grigg & Alchin, 1976). Lang (1979a) has reported on the thermophilic behaviour after feeding in *A. mississippiensis* and *C. acutus* and Spotila, Terpin & Dodson (1977) have studied the effect of mouth gaping on heating rates in *A. mississippiensis*.

The Nile crocodile, *Crocodylus niloticus*, has not received the same attention as North American and Australasian species. Cott (1961) reported on behavioural studies of diurnal activity rhythm, thermoregulation and gaping of adult animals. Cloudsley-Thompson (1969) measured evaporative water loss of hatchling animals when heat-stressed and Diefenbach (1975) observed the effect of gaping in young *C. niloticus*. There have been no studies of the body temperatures of Nile crocodiles during thermoregulation or of heating and cooling rates in this species. Lang (1979b) has suggested that alligators, living in temperate climates, are thermoregulators and attempt to maintain high, stable body temperatures. By contrast, crocodiles living in tropical climates are thermoconformers, avoiding rapid heating during the day. In view of these possible differences it is important to extend our knowledge away from alligators towards the more tropical crocodiles.

In nearly all the work mentioned above, the size range of animals studied has been in the range of 60 g to 14 kg. As has been pointed out by Gans (1976) and by Smith (1979), very large animals should be included to confirm the validity of extrapolation of work done on hatchlings and juveniles to all sizes of crocodylians. This study attempts to extend the knowledge of crocodylian thermoregulation to another species, *C. niloticus*, and to include all sizes of animals from hatchlings to mature adults.

## MATERIAL AND METHODS

Field observations of basking behaviour of crocodiles were made on the Zambezi river at Mana Pools, at Sinamwenda on Lake Kariba (wild populations) and at Kyle National Park and Kariba crocodile farm (captive populations). Environmental temperatures were recorded using a Grant 8-channel miniature temperature recorder while the

crocodiles were being observed from a hide. Body temperatures of crocodiles captured in the wild were measured using a Yellow Springs Instrument telethermometer with a blunted type 418 soil thermistor probe inserted into the cloaca. Water and air temperatures were measured with type 418 and 405 thermistors respectively.

For telemetric studies of body temperatures, crocodiles were forced a calibrated temperature-sensitive transmitter (Mini-Mitter Co. type V). The signals were received up to 2 m away using an AM radio and timed using a stopwatch. Environmental temperatures were measured using a Yellow Springs telethermometer with appropriate probes and extension cables.

In laboratory experiments temperatures were recorded by a Grant 8-channel recorder. Cloacal probes were inserted to a depth of 2.5–13 cm depending on the size of the crocodile. Body surface temperatures were measured with a disc-shaped thermistor taped to the skin, tongue temperatures were measured with a needle probe inserted beneath the tongue epithelium and black bulb temperatures with a thermistor covered by a spherical steel bulb, 1.5 cm diameter, painted matt black. Crocodiles used in experiments came from a wide variety of sources, but most were maintained in the laboratory for a period of years. The larger animals were captured in the wild and the experiments were done before they were relocated on crocodile farms. All crocodiles above the weight of 30 kg used in laboratory experiments were immobilized using gallamine (Loveridge & Blake, 1972).

Crocodiles were cooled in a walk-in cold room with an air temperature ( $T_a$ ) of 2°C until their cloacal temperature ( $T_b$ ) was below 15°C. They were then rapidly transferred to a hot room ( $T_a = 30^\circ\text{C}$ ) and tied to a metal frame on a dry sand substrate. In one series of experiments substrates of pebbles, wet sand, dry and wet *Salvinia molesta* were also used. Air in the hot room was stirred by a ceiling fan rotating slowly (89 rpm). In experiments on the effect of wind speed on heating rate a wind tunnel was used to blow air over the crocodile, from head to tail, at speeds of 1.0, 2.5 or 4.5 m s<sup>-1</sup>. In experiments requiring the use of a radiant heat source, two 1000 W lamps were suspended with their filaments 93 cm above the substrate and 30 cm apart. For all heating and cooling experiments,  $\tau$  – the time take for  $T_b$  to change by 63% of the difference between  $T_b$  and  $T_a$  – was calculated (Smith, 1976a). The advantage of the use of  $\tau$  (the thermal time constant) is that it is independent of the magnitude of the difference between  $T_b$  and  $T_a$  and remains constant with time during the exponential approach of  $T_b$  towards  $T_a$  (Grigg, Drane & Courtice, 1979).

Respiratory rates were observed and timed with a stopwatch. Heart rates were recorded by picking up the ECG with needle electrodes

inspired subcutaneously into a forelimb and hind-limb. The signal was amplified and fed into a chart recorder. Rates of evaporative water loss from the tongue and roof of mouth were measured using a tight-fitting double capsule ventilated at either 150 or 270 ml min<sup>-1</sup>. Uprstream and downstream humidity was measured and water loss calculated as described by Lovelidge & Crayé (1979).

## RESULTS

### Thermoregulatory Behaviour

The precise patterns of basking behaviour are dependent on the season of the year and the prevailing weather conditions. Generally speaking, crocodiles emerge from the water for basking once the sun is shining on the basking site, or the air temperature exceeds the water temperature. They may remain ashore, basking for the best part of the morning, retreating to the water for short periods of time when they may wholly or partly submerge (Fig. 1). This shuttling between sun and water is more pronounced in small crocodiles and in hot weather. During the hottest part of the day few crocodiles are out basking; rather they emerge from the water again around 15.00 hours and onwards. During the late afternoon, when black bulb and substrate temperatures are falling, crocodiles spend longer periods ashore and may remain in there after sunset. The two main periods of basking, in early morning and middle to late afternoon, are reflected in a typically bimodal relationship between time and numbers of crocodiles basking in a captive population (Fig. 2). This bimodal pattern is evident in crocodiles of all ages. Observations of adult crocodiles at Sinamwenda indicated that they frequently came ashore festooned with the floating aquatic weed, *Salvinia molesta* (Fig. 3). Basking crocodiles made no attempt to rid themselves of the weed, and the supposition that this insulating material influences the rate of heating gave rise to some of the experiments described later (p. 457).

A record was made of the incidence of mouth gaping during observations of young crocodiles on the Zambezi, gaping frequently occurred on first emergence from the water as well as immediately before re-entry to the water (Fig. 1). In adults particularly, mouth gaping was used on crowded sandbanks and appeared to reflect a social interaction. Other observations suggest that mouth gaping may serve more than a thermoregulatory role. At Sinamwenda at 20.19 hours on 13 October 1971 during a night-capture exercise, a 1.6 m crocodile was seen gaping while

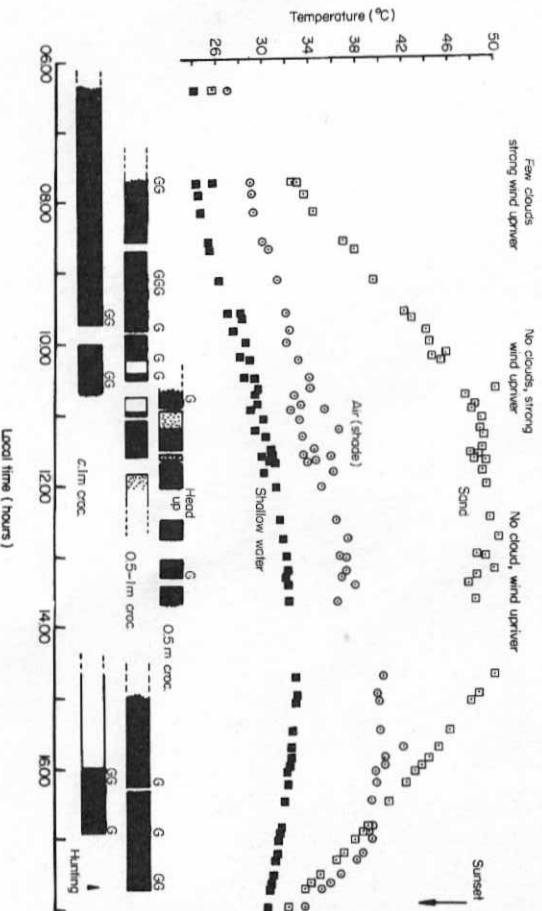


FIG. 1. Basking behaviour of young crocodiles and environmental temperatures, Zambezi River, 22-23 October 1968. Solid bars - crocodiles out of water; stippled - partly in water; G - gaping.

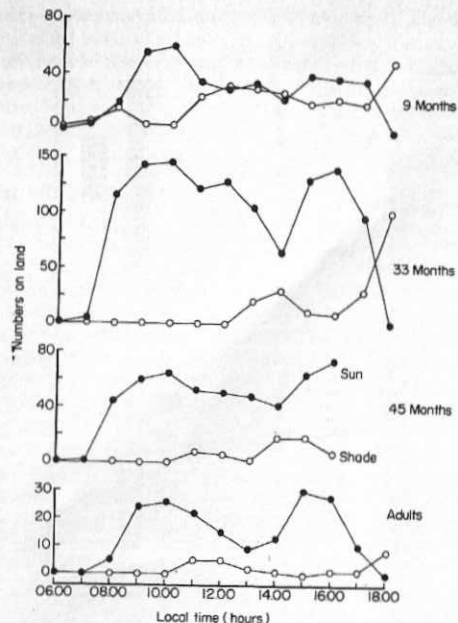


FIG. 2. Numbers of crocodiles of different ages basking in the sun (●) and in the shade (○) at Kariba crocodile farm, 24 August 1976.

out of water, on a rock. The substrate, dried *Salvinia*, was 23.9°C,  $T_a$  was 23.8°C and the water temperature was 25.2°C. At Kyle National Park at 08.25 hours on 3 June 1971 when  $T_a$  was 10.4°C and the water temperature was 13.4°C, a 2.8 m female crocodile lay gaping for 4 min in the water with the water wetting the tongue. This individual only emerged to start basking at 10.11 hours on that day.

#### Body Temperatures

Measurements of body temperatures of both captive crocodiles and wild juvenile crocodiles were made during mark and release studies.



FIG. 3. Adult crocodile partially covered with the aquatic weed, *Salvinia molesta*, basking on a sandbank, Mwenda River, 31 August 1968. The vertical wire to the left is the lead crossing the river to measure the substrate temperature.

#### Body temperatures during daytime, when on land

Most of the data available in this category are from captive crocodiles, and are summarized in Table I. The highest mean  $T_b$  of 33.4°C was recorded from a sample of 15 juvenile crocodiles on a very hot January day. The highest individual  $T_b$  in this group (and in the whole study) was 39.0°C. Smaller crocodiles, of body weight less than about 19 kg, appeared to have higher body temperatures than larger ones (Table I). In the two groups of crocodiles with mean body weights of 91 and 97 kg the highest  $T_b$  was 33.0°C and 29.5°C respectively.

There are some data on the body temperatures of wild juvenile crocodiles caught in a handnet while on land, at Ngezi National Park (J. Hutton, pers. comm.). The information is limited to the cold dry season, at the beginning of Hutton's study, when water temperatures were low ( $17.1 \pm 0.7^\circ\text{C}$ , range 16–18°C). After 09.30 hours the body temperature of the captured crocodiles started exceeding the water temperature by  $3.1^\circ\text{C h}^{-1}$  (Fig. 4) so that by 12.15 hours crocodiles had  $T_b$ s in the range 23–31°C.

#### Body temperatures during night-time, when on land

During studies at Sinamwenda, Lake Kariba, a proportion (14.7% in a sample of 197) of juvenile crocodiles was captured on land or in the

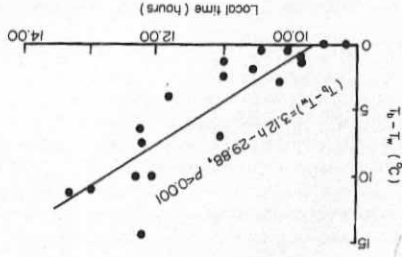
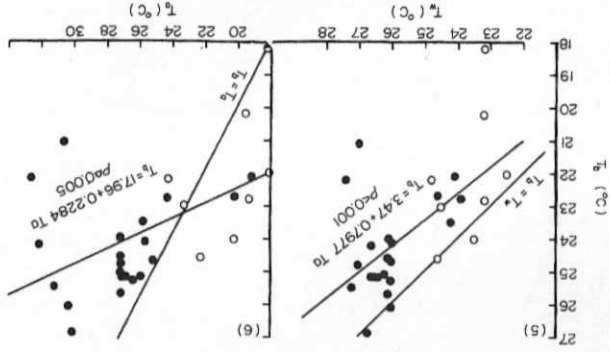


FIG. 4. The increase in body temperature ( $T_b$ ) above water temperature ( $T_w$ ) with time of juvenile crocodiles caught on land, Ngazi National Park during the cold season. (Data from J. Hutton.)

water after being on land. Nearly all these animals had a  $T_b$  below the water temperature,  $T_w$  (Fig. 5), both during the cold season (May–June) and the hot season (September–October). By contrast most of the crocodiles captured on land at night during the hot season had a  $T_b$  lower than  $T_w$  but during the cold season most had a  $T_b$  higher than  $T_w$  (Fig. 6). This no doubt arises from the fact that during the cold season  $T_w > T_a$ , which is reversed during the hot season.



FIGS 5 & 6. (5) The relationship between water temperature and body temperature of juvenile crocodiles caught ashore at night, Shammenda, solid symbols, September–October; open symbols, May–June. (6) The relationship between air temperature and body temperature of juvenile crocodiles caught ashore at night, Shammenda, solid symbols, September–October; open symbols, May–June.

TABLE 1  
Body temperature of basking captive crocodiles of different size (error estimates are  $\pm 1$  SD)

| Locality              | Month          | Mean $T_w$ ( $^{\circ}\text{C}$ ) |                              |                              | N  | Mean body weight (kg) |
|-----------------------|----------------|-----------------------------------|------------------------------|------------------------------|----|-----------------------|
|                       |                | $T_b$ ( $^{\circ}\text{C}$ )      | $T_w$ ( $^{\circ}\text{C}$ ) | $T_a$ ( $^{\circ}\text{C}$ ) |    |                       |
| Kariba Crocodile Farm | September      | 31.2 $\pm$ 1.9                    | 28.6 $\pm$ 0.4               | 24.9 $\pm$ 0.8               | 18 | 0.5 <sup>a</sup>      |
| Binga Crocodile Farm  | January        | 33.4 $\pm$ 3.5                    | 32.1 $\pm$ 1.9               | —                            | 15 | 0.69 $\pm$ 0.51       |
| University, Harare    | Various        | 29.7 $\pm$ 2.6                    | 26.5 $\pm$ 2.9               | 23.3 $\pm$ 2.5               | 26 | 1.51 $\pm$ 2.39       |
| Victoria Falls        | March          | 26.7 $\pm$ 3.6                    | 23.3 $\pm$ 3.0               | 25.3 $\pm$ 1.7               | 45 | 19.54 $\pm$ 2.87      |
| Victoria Falls        | March, October | 28.4 $\pm$ 2.5                    | 28.6 $\pm$ 2.8               | 24.3 $\pm$ 1.2               | 17 | 91.4 $\pm$ 26.1       |
| Various               | Various        | 25.1 $\pm$ 3.8                    | 23.4 $\pm$ 3.9               | 21.6 $\pm$ 3.1               | 19 | 97 <sup>a</sup>       |

<sup>a</sup> Mean body weight estimated from mean body length of sample.



### Body temperatures during night-time, when in water

Most crocodiles were caught in the water at night, and their  $T_b$  did not depart markedly from  $T_w$ , with the regression equation being  $T_b = 0.1458 + 0.9851 T_w$  ( $r = 0.915$ ,  $N = 168$ ). The relationship between  $T_b$  and  $T_a$  for crocodiles caught in the water is given in Fig. 7 which shows that below  $T_a = 25.2^\circ\text{C}$ ,  $T_b > T_a$  and above  $T_a = 25.2^\circ\text{C}$ ,  $T_b < T_a$ .

### Body Temperature and Thermoregulatory Behaviour

An attempt was made to unify the observations given in the preceding sections using telemetric techniques to monitor the body temperatures of captive crocodiles thermoregulating naturally in an outdoor enclosure. Sample results from different sized crocodiles and at different

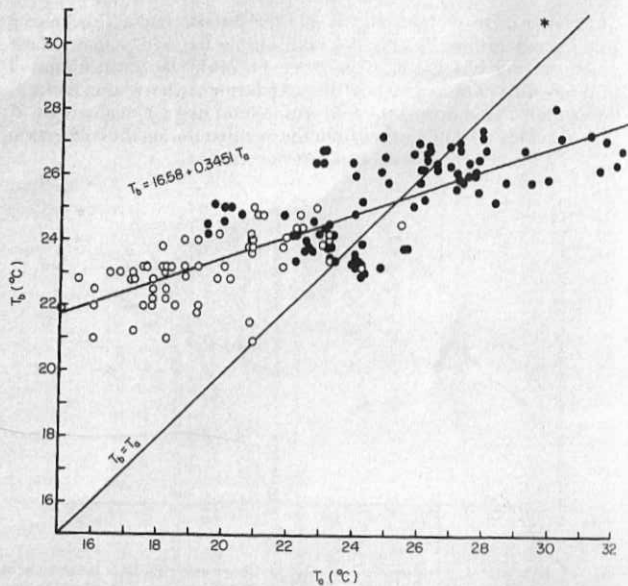


FIG. 7. The relationship between air temperature and body temperature of juvenile crocodiles caught in the water at night, Sinamwenda. Solid symbols, September–March; open symbols, May–June, asterisk, an individual caught during the day.

times of the year are given in Figs 8–10. On a cool, overcast day with intermittent drizzle [Fig. 8(A)], crocodiles came onto land for basking; but the  $T_b$  of the smaller (5.9 kg) only reached  $28^\circ\text{C}$  at 13.15 hours and the larger (38.2 kg) which started basking at 11.30 hours, reached a  $T_b$  of  $26^\circ\text{C}$  by 14.45 hours. Two days later when the weather was warm and partly overcast [Fig. 8(B)], the larger crocodile started basking earlier than the smaller and attained a  $T_b > 34^\circ\text{C}$  during late afternoon. The smaller crocodile was the victim of aggression by other crocodiles in the enclosure and, despite numerous attempts, spent only two periods

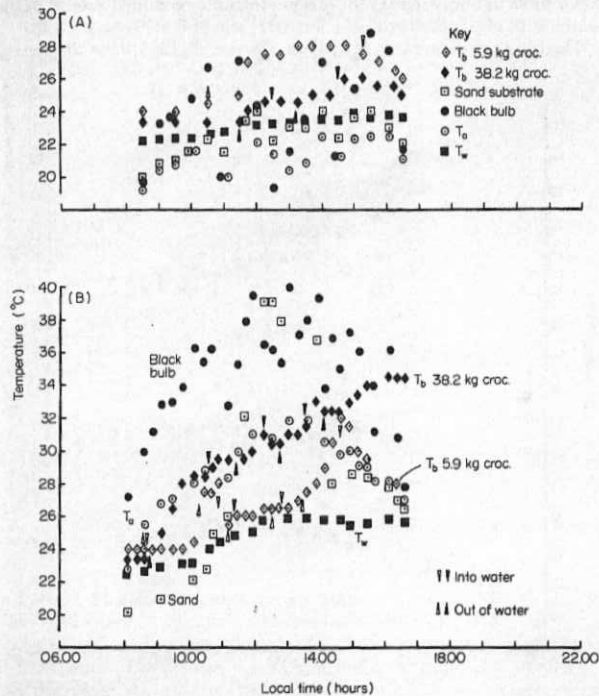


FIG. 8. Environmental temperatures and crocodile body temperatures measured by telemetry during February 1977, (A) on an overcast, intermittently drizzly day and (B) on a warm, partly overcast day.

basking, one in mid-morning, the other in early afternoon. In the latter period a  $T_b$  of 32°C was reached for a brief period.

On a day when there was much less cloud, but the weather was still warm, the body temperatures of both a large (37 kg) and small (5.6 kg) crocodile showed a distinctly bimodal pattern (Fig. 9). The  $T_b$  of both crocodiles rose rapidly to reach 32°C by mid-day, peaking at 34°C shortly thereafter in the case of the smaller animal. Both crocodiles spent about an hour in the water before emerging to bask again. The small crocodile after reaching a  $T_b$  of 34.7°C at 15.15 hours, entered the water once again, whereas the larger crocodile remained ashore in the shade until after 18.00 hours, when its  $T_b$  was still in excess of 31°C.

The bimodal pattern in  $T_b$  was not observed in the animal illustrated

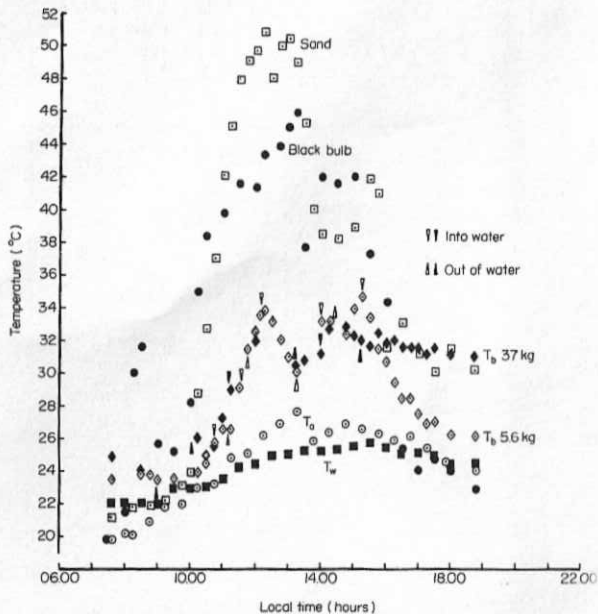


FIG. 9. Environmental temperatures and the body temperature of two crocodiles measured by telemetry during April 1973, on a warm, partly cloudy day. Note the bimodal pattern of  $T_b$  with time in both animals.

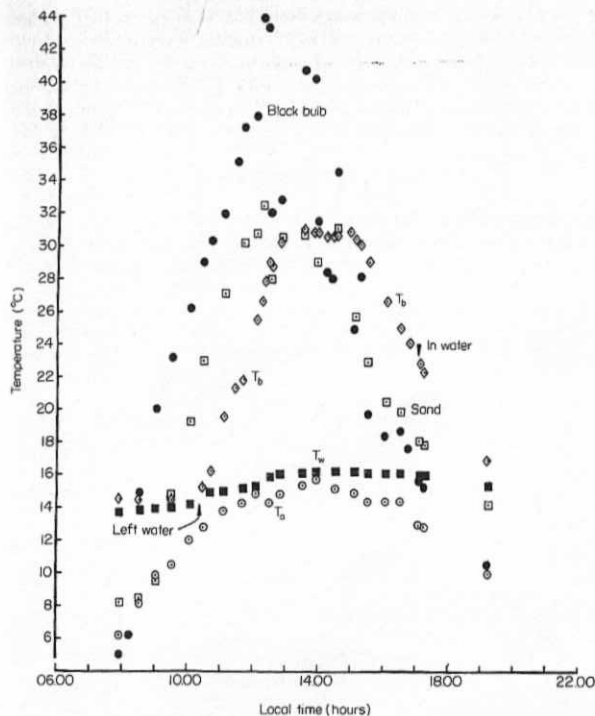


FIG. 10. Environmental temperature and the body temperatures of a 5.4 kg crocodile measured by telemetry on 29 June 1972, a warm day with intermittent cloud.

in Fig. 10. Basking commenced much later (10.00 hours), a  $T_b$  of 30°C was reached at 12.45 hours and remained above this level until 15.15 hours when it started dropping rapidly. The crocodile entered the water at 17.00 hours. On this day it is notable that at no time did  $T_a$  exceed  $T_w$ , but the clear sky allowed very high black bulb temperatures to be reached in early morning, contributing to the rapid heating once basking commenced.

All observations using telemetry indicated that crocodiles in water

during the morning had  $T_{\delta}$ s which were 1–2°C in excess of  $T_w$ . This contradiction with the results from night-capture of crocodiles in water (p. 452) where  $T_b$  was the same as  $T_w$ , may perhaps be explained by the fact that these crocodiles were much smaller. The biotelemetry studies also show that crocodiles with a body weight of 37–38.2 kg may have body temperatures in excess of 32°C when basking [Figs 8(B) & 9].

### Heating and Cooling Rates

#### Heating and cooling without radiation

For any particular size of crocodile in the range of body weight 75 g–4 kg, the time constant for heating was slightly greater than that for cooling (Fig. 11). The slopes and intercepts of the two regression lines are, however, not significantly different ( $P > 0.5$ ).

#### Influence of radiation and windspeed on heating

In nature, crocodiles almost invariably heat up during basking under the influence of the sun's radiant energy. The effect of body size on the thermal time constant ( $\tau$ ) for heating was measured with two 1000 W lamps providing a radiant heat source. Wind was also introduced as a variable, "no wind" being slow stirring of air by the overhead fan and windspeeds of 1.0, 2.5 and 4.5 m s<sup>-1</sup> being provided by a wind tunnel.

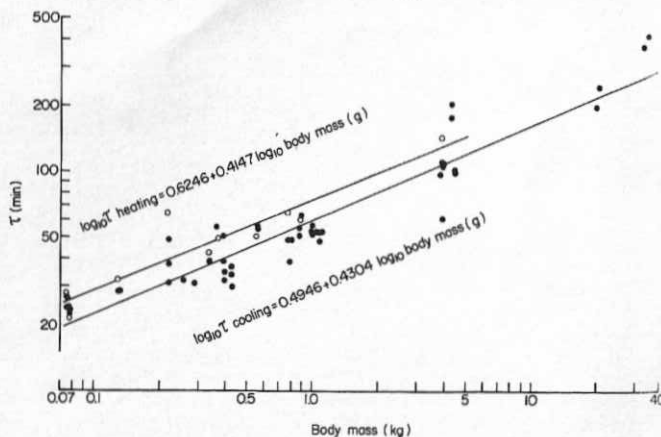


FIG. 11. The effect of body weight on the time constants for heating in the absence of a radiant source (open symbols) and cooling (solid symbols) of *C. niloticus*.

Results are given in the form of regression equations relating  $\tau$  and body weight (Table II). The data were compared by analysis of covariance using an SPSS statistical package. The slopes of the regressions for windspeeds 1.0, 2.5 and 4.5 m s<sup>-1</sup> were tested for homogeneity, and  $F_{2,8}$  was 0.543 ( $P > 0.25$ ). The intercepts for the three windspeeds were similarly tested, and  $F_{2,8}$  was 0.948 ( $P > 0.25$ ). Accordingly the data for all windspeeds between 1.0 and 4.5 m s<sup>-1</sup> were combined to give the fifth regression equation in Table II. This was compared with the first regression equation; in a test for homogeneity of the slopes,  $F_{1,19}$  was 0.071 ( $P > 0.25$ ), but the intercepts were significantly different ( $F_{1,19} = 34.647$ ,  $P > 0.005$ ). Thus, windspeeds between 1.0 and 4.5 m s<sup>-1</sup> have no significant influence on the rate of heating of crocodiles under 4.0 kg body weight exposed to a radiant source. Crocodiles exposed to winds in the range 1.0–4.5 m s<sup>-1</sup> have significantly lower time constants than those exposed to no wind; and wind or no wind does not significantly affect the slope of the relationship between the time constant and body weight.

TABLE II

The effect of body size and windspeed on the rate of heating of crocodiles < 4.0 kg body weight under two 1000 W lamps

| Windspeed (m s <sup>-1</sup> ) | N  | Regression equation   |
|--------------------------------|----|---|
| "No wind"                      | 9  | $\log_{10} \tau$ (min) = 0.5796 + 0.3583 $\log_{10}$ weight (g) |
| 1.0                            | 5  | $\log_{10} \tau$ (min) = 0.3897 + 0.3873 $\log_{10}$ weight (g) |
| 2.5                            | 4  | $\log_{10} \tau$ (min) = 0.5153 + 0.3265 $\log_{10}$ weight (g) |
| 4.5                            | 5  | $\log_{10} \tau$ (min) = 0.3096 + 0.4067 $\log_{10}$ weight (g) |
| 1.0–4.5                        | 14 | $\log_{10} \tau$ (min) = 0.4061 + 0.3734 $\log_{10}$ weight (g) |

#### The influence of substrate and insulation on heating

In these experiments a single crocodile was used over a short space of time, so keeping the body weight fairly constant. The thermal time constant for heating was similar when the substrates were dry sand or large pebbles, but  $\tau$  increased by some 6 min when the sand was wet and by nearly 10 min when the substrate was wet *Salvinia* (Table III). Dry *Salvinia* substrate gave a similar thermal time constant to wet *Salvinia*. The most marked influence on  $\tau$  was evident when wet *Salvinia* was piled on the back of the crocodiles, as is often seen in the wild (Fig. 3). In this case  $\tau$  increased by 62–68% over the corresponding values for the same substrates without an insulation of *Salvinia*.

#### Heart and respiratory rates during heating

No consistent pattern of respiratory rate emerged during heating experiments. In most individuals the respiratory rate was high initially,



TABLE III  
The effect of substrate type and insulation on the thermal time constants for a 1 kg crocodile exposed to two 1000 W bulbs and "no wind"

| Body mass (kg) | $\tau$ (min) | Substrate           | Insulation              |
|----------------|--------------|---------------------|-------------------------|
| 1.038          | 44.8         | Dry sand            | -                       |
| 1.091          | 43.0         | Pebbles             | -                       |
| 0.990          | 51.0         | Wet sand            | -                       |
| 0.987          | 54.7         | Wet <i>Salvinia</i> | -                       |
| 1.063          | 56.5         | Dry <i>Salvinia</i> | -                       |
| 1.091          | 72.5         | Dry sand            | <i>Salvinia</i> on back |
| 0.993          | 86.0         | Wet sand            | <i>Salvinia</i> on back |

becoming lower as  $T_b$  increased (Fig. 12). This pattern is attributed to handling stress at the start of the experiment. In other crocodiles the respiratory rate remained fairly constant or increased during heating (Fig. 13). In all the heating experiments in which heart rate was measured there was a steady increase in heart rate with the increase in  $T_b$  (Fig. 13).

#### Effect of body size on heating

Crocodiles of body weight in the range 220 g–314 kg were heated in air under two 1000 W lamps. On the graph (Fig. 14), crocodiles that were immobilized using gallamine are indicated. There does not seem to be any difference between immobilized and non-immobilized crocodiles in the thermal time constant,  $\tau$ . One 4.25 kg animal had a  $\tau$  of 75 min when immobilized and 81.5 min when not immobilized. The results of Grigg & Alchin (1976) for *Crocodylus johnstoni* heating in air are indicated on Fig. 14 (although not included in the regression analysis) as well as the regression line of Grigg *et al.* (1979) for lizard-shaped reptiles heating in air. Although the *C. niloticus* and *C. johnstoni* thermal time constants are similar, there is a large discrepancy between thermal time constants for crocodiles and those for other lizard-shaped reptiles (including *Alligator*), with the lizard-shaped reptiles heating much more rapidly than a crocodile of the same body weight.

#### The Significance of Gaping

It was found to be impossible to induce spontaneous gaping during laboratory experiments with crocodiles. Measurements were, however, made of the temperature below the tongue epithelium and of the rate of evaporative water loss from the epithelium of tongue and roof of mouth when the mouth was propped open. In three cases where the tongue

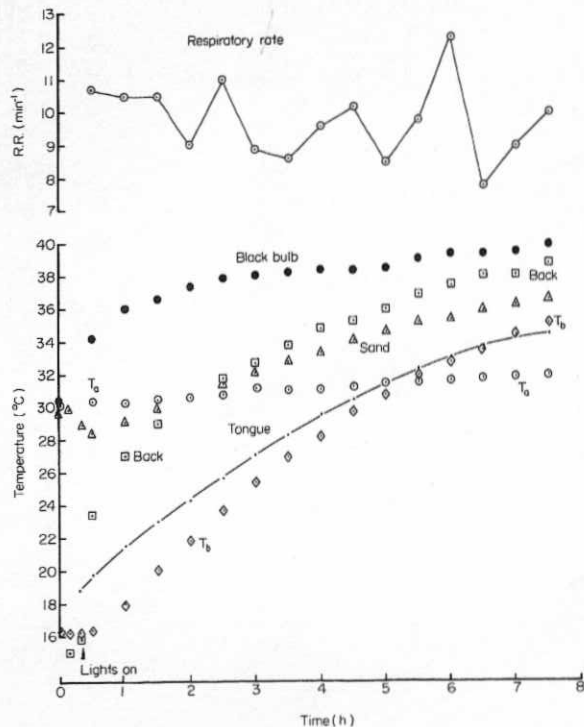


FIG. 12. The heating curve of a 19.9 kg crocodile under two 1000 W lamps. Tongue and back temperatures and the respiratory rate (R.R.) are also indicated.

temperature was measured during heating it was higher than  $T_b$  during the initial phase of heating (Fig. 12). As  $T_b$  increased, the difference between tongue temperature and  $T_b$  decreased until at a  $T_b$  of 34.3°C the two temperatures were equal and tongue temperature was lower than  $T_b$  thereafter (Fig. 12). In the other two experiments, where the crocodile was exposed to the sun's radiant heat, the points at which  $T_b$  was equal to tongue temperature were 35.8°C and 36.1°C. These data imply that when  $T_b$  increases to a certain level, evaporation of water

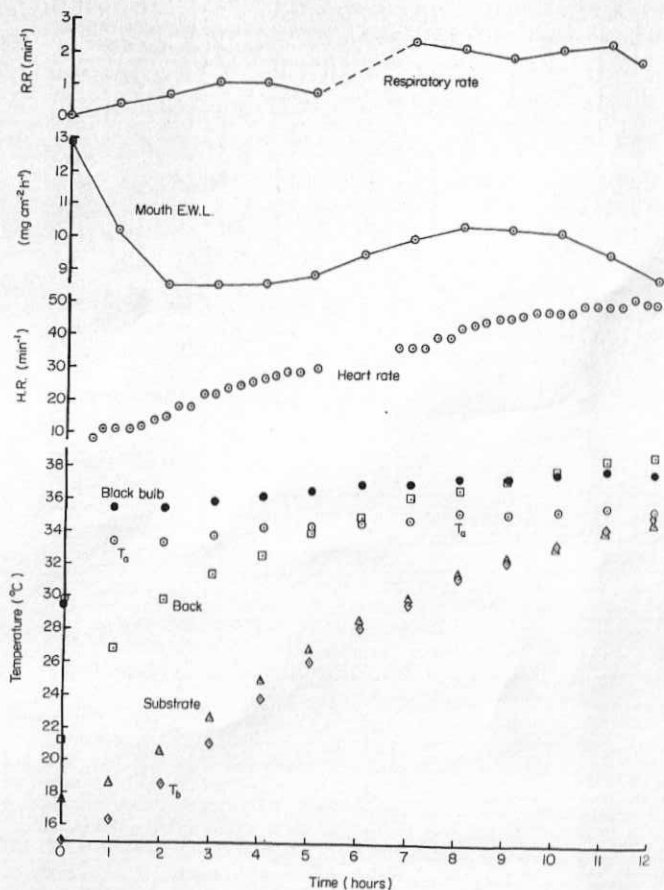


FIG. 13. The heating curve of a 60 kg crocodile under two 1000 W lamps. Respiratory rate (R.R.), evaporative water loss (E.W.L.) from the mouth and heart rate (H.R.) are also plotted as well as changes in environmental temperature variables.

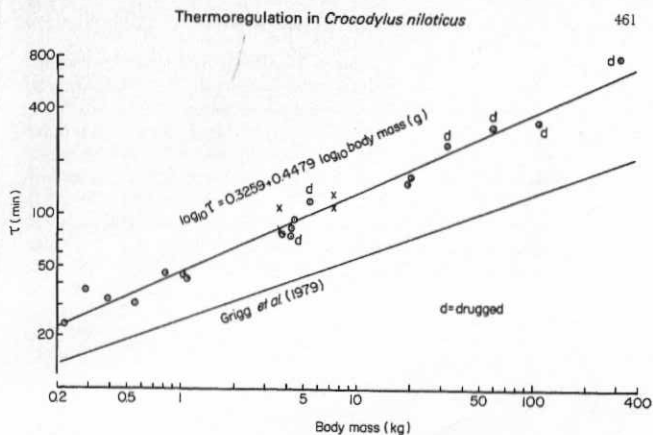


FIG. 14. The effect of crocodile bodyweight in the range 220 g to 314 kg on the time constant for heating under two 1000 W lamps. Time constants for heating *C. johnstoni* in air (Grigg & Alchin, 1976) are plotted (x) as well as the line for lizard-shaped reptiles (from Grigg et al., 1979).

from the tongue is also increased, so cooling the lingual epithelium to a temperature below that of the body.

This hypothesis was not confirmed by data on the evaporative water losses from the oral epithelia. There was no trend for the water loss to increase as  $T_b$  rose during heating experiments (Fig. 13). Although water loss was usually fairly constant during an experiment, there was substantial variation between experiments. Water losses measured from tongue alone varied between 2.8 and 21.2  $\text{mg cm}^{-2}\text{h}^{-1}$  whilst from tongue and roof of mouth variation was lower, in the range 1.4–9.6  $\text{mg cm}^{-2}\text{h}^{-1}$  (Table IV). Tongue water loss certainly was much higher than tongue and roof of mouth combined in the 60 kg crocodile, the one case where comparable flow conditions were used.

## DISCUSSION

### Thermoregulatory Behaviour

Patterns of thermoregulatory behaviour described on pp. 446 and 452 serve to confirm the main conclusions of Cott (1961) in his study of adult *C. niloticus*. Cott (1961) did not, however, follow the behaviour of individual animals which is, for some purposes, more informative than

the behaviour of large groups. On hot, clear days crocodiles emerge to bask once  $T_a > T_m$  or the sunlight is on the basking site. By mid-day or early afternoon crocodiles frequently retreat to the water (Figs 2, 9) or bask in early to mid-afternoon (Fig. 9). This is the typical pattern of diurnal activity shown by Cott (1961) from counts of crocodiles on land, in the water or partly ashore. Basking behaviour is, however, modified by prevailing weather conditions so that on rainy days or during the coldest part of the year [Figs 8(A) & 10] emergence for basking may be delayed, with no return to the water in the middle of the day. Retreat to the water does not always occur by sunset (e.g. the larger crocodile in Fig. 9), and by no means all of the juveniles captured at Sinamwenda were found in the water, although nearly all adults were seen in the water during night capture exercises.

### Body Temperatures

During the day, crocodiles emerge from the water to bask, thus behaving as typical heliotherms. This behaviour is anomalous in one respect, however, as crocodiles are not active during the day, but show peak activity during the early evening (Cloudsley-Thompson, 1964; Brown & Lovridge, 1981). Thus the preferred body temperature (PBT) as defined by Cowles (1962) would be that maintained during the active period of early evening, when the crocodiles are moving about and hunting. Body temperatures of basking crocodiles seem to show some relationship to body weight (Table 1), with juveniles of 0.5–1.5 kg having mean body temperatures in the range 29.7–33.4°C, and larger crocodiles (above 19 kg) having lower body temperatures. The data for the larger crocodiles probably suffer from the fact that fewer individuals had achieved preferred (basking) body temperatures because of their slow heating rates. Bioclimetric studies [Figs 8(B) & 9] strongly suggest that crocodiles of 37–38.5 kg may achieve  $T_b$ s in the range 32–34°C during basking. Studies such as these should be undertaken on really large crocodiles to discover their body temperatures during basking. Cott (1961) gives some  $T_b$  data for adult *C. niloticus* shot in Uganda and Zambia. The mean  $T_b$  for those shot in the water was 24.7°C ( $N = 4$ ) and on land was 26.8°C ( $N = 3$ ). Studies on juvenile *Gaiman crocodilus* (Dietenbach, 1975) indicated that the PBT in a thermal gradient was 29.9°C for 150–350 g animals, 32.8°C for 700–1050 g animals and 34.8°C for 2–6 kg animals. Lang (1981) showed similar ontogenetic changes in PBT in *Crocodylus novaeguineae* maintained in outdoor thermal gradients. Hatchlings up to two weeks old had  $T_b$ s of 33.4–33.9°C while those two to five weeks old had  $T_b$ s of

TABLE IV  
Evaporative water losses from the oral epithelium of crocodiles measured with a ventilated capsule  
(error estimates are  $\pm 1$  SD)

| Crocodile body weight (kg) | Evaporating surfaces     | $T_b$ (°C) | Flow rate (ml min <sup>-1</sup> ) | Inflowing relative humidity (%) | Water-loss (mg cm <sup>-2</sup> h <sup>-1</sup> ) |
|----------------------------|--------------------------|------------|-----------------------------------|---------------------------------|---|
| 5.4                        | Tongue only              | 30.0       | 147 $\pm$ 0.4                     | 5.8 $\pm$ 0.1                   | 2.8 $\pm$ 0.1                                     |
| 5.4                        | Tongue only              | 16.6–36.4  | 148 $\pm$ 0.3                     | 5.6 $\pm$ 0.1                   | 4.1 $\pm$ 1.0                                     |
| 60                         | Tongue and roof of mouth | 15.0–34.0  | 269 $\pm$ 1.1                     | 3.6 $\pm$ 0.1                   | 9.6 $\pm$ 1.2                                     |
| 60                         | Tongue only              | 30.0       | 269 $\pm$ 0.0                     | 3.5 $\pm$ 0.0                   | 21.2 $\pm$ 1.2                                    |
| 109                        | Tongue and roof of mouth | 18.0–31.1  | 147 $\pm$ 2.9                     | 7.0 $\pm$ 0.5                   | 7.2 $\pm$ 1.1                                     |
| 109                        | Tongue only              | 32.1–34.6  | 269 $\pm$ 4.0                     | 5.7 $\pm$ 0.3                   | 18.9 $\pm$ 4.4                                    |
| 314                        | Tongue and roof of mouth | 25.5–28.0  | 147 $\pm$ 0.8                     | 5.0 $\pm$ 0.5                   | 1.4 $\pm$ 0.1                                     |

31.8–32.2°C. These levels declined so that two-year-old juveniles and adults had a  $T_b$  of about 30°C. Johnson, Webb *et al.* (1976) showed that the PBT of juvenile *Crocodylus johnstoni* was 31.3–32.5°C and of juvenile *C. porosus* was 32.2–33.1°C. Lang (1979a) demonstrated that fasted juvenile *Alligator mississippiensis* selected a  $T_b$  of 28.7°C (daytime) and 26.9°C (night-time); and fasted juvenile *Crocodylus acutus* selected a  $T_b$  of 27.9°C (daytime) and 28.0°C (night-time) in a thermal gradient. In both species there was a significant elevation in both daytime and night-time  $T_b$  due to thermophilic behaviour when the animals were fed.

In contrast to the large number of studies on crocodilian body temperatures during basking, there have been few studies of the  $T_b$  of crocodiles during the night, which is their active period. In this study, data were obtained for juvenile crocodiles in a wild population. Those caught on land had a  $T_b$  below that of the water at all seasons of the year (Fig. 5) whereas  $T_b$  generally exceeded  $T_w$  during the cold months but was lower than  $T_w$  during the hot months (Fig. 6). Crocodiles caught in the water, however, had a  $T_b$  equal to  $T_w$  at all seasons of the year. It appears, therefore, that in order to forage on the land at night, juvenile crocodiles must tolerate a lowering of  $T_b$  by about 2°C from  $T_w$ .

Preliminary indications from the biotelemetry studies are that in larger crocodiles,  $T_b$  may not be entirely influenced by  $T_w$  when the animals are in the water at night (Figs 8, 9 & 10). Even before basking started in the morning,  $T_b > T_w$  by as much as 2°C. This may well be of great importance for larger crocodiles that are able, by physiological means, to prevent all the heat accumulated during the day from being lost to the water at night.

### Heating and Cooling Rates

Work on *Alligator mississippiensis* (Smith, 1976a; Johnson, Voigt *et al.*, 1978) has shown that juveniles heat very much more rapidly than they cool, but hatchlings (< 100 g) heat and cool at the same rate (Smith & Adams, 1978). Grigg & Alchin (1976) were unable to demonstrate a consistent difference in heating and cooling rates in juvenile *Crocodylus johnstoni*. In this study on *C. niloticus*, heating and cooling in air in the absence of radiant heat sources took place at the same rate (Fig. 11). Moreover, Nile crocodiles of 0.22–314 kg body weight took very much longer to heat than the equation of Grigg *et al.* (1979) predicts. The time constant for heating in a 300 kg *C. niloticus* is about 10 h (Fig. 14). This finding is supported by field observations, such as those of Cott (1961: 227) in which large crocodiles spend nearly all the daylight hours basking in one position without the need to return to the water.

The effect of different substrates and insulation on the time constant for heating can be significant (Table III). For example the time constant of 43 min for a 1 kg crocodile heating on pebbles is doubled when the crocodile is lying on wet sand with *Salvinia* on its back. Wind shortens the time constant for heating, although no difference is observed if the winds are increased from 1.0 to 4.5 m s<sup>-1</sup> (Table II). All these environmental factors should be considered in the design of heating and cooling experiments or the interpretation of field observations.

The question of whether crocodiles and alligators have different heating and cooling strategies needs to be answered, and may provide a corollary to differences in thermal behaviour between the two groups suggested by Lang (1979b).

### The Significance of Gaping

Cott (1961) was firmly of the opinion that gaping in *C. niloticus* exposed the moist oral mucosa to the air, so prompting evaporative cooling. He showed that as many as 60% of crocodiles ashore at 09.30 hours were gaping when the air temperature was as low as 26°C. Even at 06.30 hours when  $T_a = 20^\circ\text{C}$ , 25% of crocodiles ashore were gaping and it hardly seems possible that these animals were heat-stressed. Observations during the present study indicate that gaping may occur immediately after crocodiles come ashore (Fig. 1), at night and while in the water, as well as during the heat of the day. Diefenbach (1975) showed that gaping and gular fluttering were insignificant cooling mechanisms in heat-stressed *Caiman crocodilus*, while Johnson, Voigt *et al.* (1978) showed that gaping had little effect on head temperatures in *Alligator mississippiensis*. Spotila *et al.* (1977), however, showed in *Alligator* that gaping was important in reducing the rate of heat gain in the head region and that the thermal time constants for heating in alligators with mouths open were much higher than those in which mouths were closed.

In experiments where tongue epithelium temperatures were measured during heating in crocodiles, tongue temperature exceeded  $T_b$  until  $T_b$ s of 34.3–36.1°C were reached. If, however, tongue temperature is compared with back temperature (Fig. 12), it is always about 5°C lower, indicating that substantial evaporative cooling of the tongue is occurring and that the rate of evaporation is roughly constant. This is supported by measurements of evaporative water losses from the oral epithelia which are in the range of 2.8–21.2 mg cm<sup>-2</sup>h<sup>-1</sup> and are much greater than the water loss from the general body surface of crocodiles of

mean body weight 3.87 kg which was  $0.114 \text{ mg cm}^{-2} \text{ h}^{-1}$  at  $23^\circ\text{C}$ , rising to  $0.202 \text{ mg cm}^{-2} \text{ h}^{-1}$  at  $35^\circ\text{C}$  (Brown & Loveridge, 1981).

It certainly seems that gaping allows evaporation of water from the oral mucosa. Whether this has any influence on head temperature or the rate of heating in *C. niloticus* is not known. It is possible that the site of the watery secretions from the tongue may be the salt glands recently described by Taplin & Grigg (1981) in *C. porosus* and known to occur in *C. niloticus* too. Gaping in crocodiles when there could be no advantage in evaporative cooling needs to be explained, perhaps in the social context.

## ACKNOWLEDGEMENTS

The help of D. K. Blake, P. R. Dewhurst, T. Harris, S. L. Childs and D. Parry in the experiments and L. Madziva in maintaining animals is gratefully acknowledged. I thank J. Hutton for permission to quote some of his unpublished results. Financial support came from the University of Zimbabwe Research Board.

## REFERENCES

- Brown, C. R. & Loveridge, J. P. (1981). The effect of temperature on oxygen consumption and evaporative water loss in *Crocodylus niloticus*. *Comp. Biochem. Physiol.* **69A**: 51–57.
- Cloudsley-Thompson, J. L. (1964). Diurnal rhythm of activity in the Nile crocodile. *Anim. Behav.* **12**: 98–100.
- Cloudsley-Thompson, J. L. (1969). Water relations of the young Nile crocodile. *Br. J. Herpet.* **4**: 107–112.
- Colbert, E. H., Cowles, R. B. & Bogert, C. M. (1946). Temperature tolerances of the American alligator and their bearing on the habits, evolution and extinction of the dinosaurs. *Bull. Am. Mus. nat. Hist.* **86**: 329–373.
- Cott, H. B. (1961). Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *Trans. zool. Soc. Lond.* **29**: 211–337.
- Cowles, R. B. (1962). Semantics in biothermal studies. *Science, N.Y.* **135**: 670.
- Diefenbach, C. O. da C. (1975). Thermal preferences and thermoregulation in *Caiman crocodylus*. *Copeia* **1975**: 530–540.
- Gans, C. (1976). Questions in crocodylian physiology. *Zoologica Afr.* **11**: 241–248.
- Grigg, G. C. & Alchin, J. (1976). The role of the cardiovascular system in thermoregulation of *Crocodylus johnstoni*. *Physiol. Zool.* **49**: 24–36.
- Grigg, G. C., Drane, C. R. & Courtice, G. P. (1979). Time constants of heating and cooling in the eastern water dragon, *Physignathus lesueurii* and some generalizations about heating and cooling in reptiles. *J. therm. Biol.* **4**: 95–103.
- Johnson, C. R. (1974). Thermoregulation in crocodylians – I. Head-body temperature control in the Papuan-New Guinean crocodiles, *Crocodylus novaeguineae* and *Crocodylus porosus*. *Comp. Biochem. Physiol.* **49A**: 3–28.
- Johnson, C. R., Voigt, W. G. & Smith, E. N. (1978). Thermoregulation in crocodylians – III. Thermal preferences, voluntary maxima, and heating and cooling rates in the American alligator, *Alligator mississippiensis*. *Zool. J. Linn. Soc.* **62**: 179–188.
- Johnson, C. R., Webb, G. J. W. & Tanner, C. (1976). Thermoregulation in crocodylians – II. A telemetric study of body temperature in the Australian crocodiles, *Crocodylus johnstoni* and *Crocodylus porosus*. *Comp. Biochem. Physiol.* **53A**: 143–146.
- Lang, J. W. (1979a). Thermophilic response of the American alligator and the American crocodile to feeding. *Copeia* **1979**: 48–59.
- Lang, J. W. (1979b). Crocodylian thermal behaviors: alligators vs. crocodiles. *Am. Zool.* **19**: 975.
- Lang, J. W. (1981). Thermal preferences of hatchling New Guinea crocodiles: effects of feeding and ontogeny. *J. therm. Biol.* **6**: 73–78.
- Loveridge, J. P. & Blake, D. K. (1972). Techniques in the immobilisation and handling of the Nile crocodile, *Crocodylus niloticus*. *Arnoldia (Rhodesia)* **5**(40): 1–14.
- Loveridge, J. P. & Crayé, G. (1979). Cocoon formation in two species of southern African frogs. *S. Afr. J. Sci.* **75**: 18–20.
- Smith, E. N. (1975). Thermoregulation of the American alligator, *Alligator mississippiensis*. *Physiol. Zool.* **48**: 177–194.
- Smith, E. N. (1976a). Heating and cooling rates of the American alligator, *Alligator mississippiensis*. *Physiol. Zool.* **49**: 37–48.
- Smith, E. N. (1976b). Cutaneous heat flow during heating and cooling in *Alligator mississippiensis*. *Am. J. Physiol.* **230**: 1205–1210.
- Smith, E. N. (1979). Behavioral and physiological thermoregulation of crocodylians. *Am. Zool.* **19**: 239–247.
- Smith, E. N. & Adams, S. R. (1978). Thermoregulation of small American alligators. *Herpetologica* **34**: 406–408.
- Spotila, J. R. (1974). Behavioural thermoregulation of the American alligator. In *Thermal ecology*: 322–334. Gibbons, J. W. & Sharitz, R. R. (Eds). Springfield, Virginia: U.S. Atomic Energy Commission.
- Spotila, J. R., Terpin, K. M. & Dodson, P. (1977). Mouth gaping as an effective thermoregulatory device in alligators. *Nature, Lond.* **265**: 235–236.
- Taplin, L. E. & Grigg, G. C. (1981). Salt glands in the tongue of the estuarine crocodile *Crocodylus porosus*. *Science, Wash.* **212**: 1045–1047.