Original Research Article

Seasonal Variation in Thermoregulation of Wild Free-Ranging Nile Crocodiles: Recovery of a 36-Year Old Data Set

Charles H. Hocutt *

P.O. Box 6096, Vineta, Namibia

*Corresponding author

A B S T R A C T

Thermoregulation data for four 'problem' Nile crocodiles (*Crocodylus niloticus*) introduced to Lake Ngezi, Zimbabwe were collected from winter through early summer 1986-87 using abdominally implanted radio-transmitters with calibrated thermistors. These remain after 36 years the largest (1.94-3.48 m) wild free-ranging Nile crocodiles thus far evaluated re: body temperatures and thermoregulation. Both cooling and heating rates were highest in the smallest subjects, progressively lower in larger individuals. Body temperatures (T_b's) cooled at night, but remained above or equal to water temperatures (T_w). All T_{bmax}'s exceeded maximum air temperatures (T_a) by 10^oC during daytime with the highest recorded T_b being 36.4^oC. Daily T_b amplitude's of $\geq 10^o$C were routinely exhibited in all specimens, regardless of size or sex. Both T_{bmax} and T_{bmin} generally lagged T_{amax}'s and T_{amin}'s by about two hours, respectively. The mean T_b's increased ~2^oC monthly from June through October 1986 for each individual regardless of size or sex with supplemental data inferring T_b 's' increased through January-February 1987.

Introduction

Hocutt (1989a, b), based at Lake Ngezi, Zimbabwe in 1986-1987, was the first researcher to publish on the use of radiotelemetry to monitor freshwater fish behaviour on the African continent (Burnett *et al.,* 2021). An opportunity was presented during that time to also study the movement behaviour of four 'problem' Nile crocodiles (*Crocodylus niloticus*) transplanted into the study area (Hocutt *et al.,* 1992); however, thermoregulation data collected simultaneously were only recently recovered and are presented here.

Lake Ngezi is a 580-ha impoundment located at *20.108 S x 29.803 E* in Ngezi Recreational Park at an elevation of ~1,255 m. The area typically experiences a cool dry season from April to August and a hot dry season from September to commencement of the rainy season, which normally occurs November to March. Night-time air temperatures during June and July can decline to

2°C with water temperatures ~15°C. A natural population of Nile crocodile occurs in the lake.

Prior to this 1986 study, only Loveridge (1984) had published on body temperatures (T_b) and thermoregulation in Nile crocodile. The only other known data base on body temperatures and thermoregulation for Nile crocodile is that of Downs *et al.,* (2008). Published data on daily and seasonal thermoregulation in large crocodilians is limited (Grigg *et al.,* 1998; Downs *et al.,* 2008), but includes studies on *Alligator mississippiensis* (Spotila, 1973; Johnson *et al.,* 1978), *Crocodylus johnstoni* (Johnson *et al.,* 1976; Seebacher and Grigg, 1997), *C. novaeguineae* (Johnson, 1974), *C. palustris* (Whitaker and Srinivasan, 2018), *C. porosus* (Grigg *et al.,* 1998); *Caiman crocodilus* (Diefenbach, 1975); and *Paleosuchus palpebrosus* (Campos and Magnusson, 2013).

The 36-year old data set is unique in that (1) it is the only study thus far to measure body temperatures of wild free-ranging Nile crocodiles using (2) abdominally-implanted transmitters; (3) the sizes of the study animals (25-260 kg) were considerably larger than the only other two studies thus far published on thermoregulation in Nile crocodile: 0.5-1.5 kg body weight (Loveridge, 1984) and 1.94-3.48 m total length here vs. 1.14-1.87 m (no weights given) of Downs *et al.,* (2008); (4) seasonal profiles of body temperatures were collected from winter through early summer; and (5) data, although sparse, are available for a female (2.97 m, 149 kg) that was fortuitously gravid and eventually nested.

Materials and Methods

Anaesthesia, surgical implantation of transmitters and biotelemetry procedures were published in Hocutt *et al.,* (1992), who enlisted a veterinarian for surgery and noted that ventral insertion of transmitters was preferable to ventro-lateral (due to the presence of a lateral abdominal vein). Animals were immobilised with gallamine triethiodide (Loveridge and Blake, 1982) and procaine hydrochloride served as the local anaesthetic

(Loveridge and Blake, 1987). Neostigmine was applied as the antagonist, injected into the tail of each individual at the time and site of their release (WARNING: the response is immediate and a tail whip may ensue!). All procedures were in accordance with acceptable ethical guidelines at that time with the full cooperation of the Zimbabwe Ministry of Natural Resources and Tourism.

Advanced Telemetry Systems, Inc. equipment was employed, notably Model TL2300 oval-shaped transmitters powered by a 1.5-v lithium D-cell battery weighing 220 g. Each transmitter operated in the 48-49 MHz band and had a built-in thermistor and internal coiled antennae. Thermistors were individually calibrated over a range of 10-40 ^{o}C in a Grant heated circulating bath (within the laboratory of Prof. J.P. Loveridge).

Four crocodiles were radio-tagged and released on 21-27 June 1986: (1) a sub-adult female (1.94 m, 25 kg); (2) a young male (2.56 m, 81 kg); (3) a mature female that nested (2.97 m, 149 kg); and a mature male with severed tail tip (3.48 m, 260 kg), hereafter referred to in the text as crocodiles 1, 2, 3 and 4. Data collection commenced on 28 June 1986 within 1-7 days of tagging and release of the animals.

Air (T_a), surface water (T_w) and body (T_b) temperature readings were taken hourly over a 24-36 hour cycle once per month June-October 1986, where possible, with supplemental data collected through February 1987. The range of the transmitters was typically 0.5–1.0+ km depending upon terrain, eliminating the need to be precisely at the subject's location.

There were constraints on the study preventing reaching its full potential: (a) the author worked alone to conduct 24-36 h surveys each month in addition to fish biotelemetry tracking; and (b) the crash of Mozambique President Samora Machel's plane in October 1986 caused rioting in Harare in an already tension-filled Zimbabwe, resulting in the evacuation of the researcher's wife to South Africa for the birth of their son on 5 December. Thus, no

data were collected in November and December as originally conceived, while only limited information was collected in January and February 1987 upon return to Zimbabwe, after which the author's Senior Research Fulbright Fellowship was fulfilled.

There were occasional gaps in the temperature data base for each crocodile (T_b) as well as ambient conditions (T_a and T_w). Intermediate values were extrapolated between valid measurements to develop contiguous curves which otherwise would appear as a scatter diagram. Examination of such data sets verified only minor influence on mean T_b's. By example, (a) the five-point September T_b data set for the 25-kg female averaged 28.3°C, whereas insertion of six intermediate values to form a curve also resulted in a mean of 28.3°C; and (b) the seven-point October data set for the 81-kg male averaged 29.7°C over a 24-h period, but 30.07°C with the insertion of 20 intermediate values to form a time sequenced curve.

A quadratic equation was fitted to data collected on 14-15 July using least squares in the form temp = a time + b time^2 + c for all four Nile crocodiles as though they were a single individual. The residuals were determined by subtracting the observed temperature from the predicted temperature for each time and each crocodile. Data were analysed separately for times between 0800 and 1700 on 14 July (times when body temperatures were rising) and 1700-0800 on 14-15 July (during cooling).

Time was made a continuous variable by adding twenty-four (24) hours to times after midnight on 15 July, thus 01h00 = 25h00, 02h00 = 26h00, etc. An ANOVA was then employed in conjunction with a Duncan's Multiple Range Test to determine if there were differences of heating and cooling rates between the four crocodiles based on size. Quadratic equations were also fitted to monthly data to evaluate heating and cooling trends. Amplitude was defined as the difference between the highest (T_{bmax}) and lowest (T_{bmin}) body temperatures recorded in a 24-h cycle each month.

Results and Discussion

Basking Behaviour

The basking behaviour of all four crocodiles was near identical, i.e., they all pulled out onto the shoreline by approximately 10h00 every day and remained basking until late afternoon unless startled. Exemplary data are those obtained on 14-15 July 1986 (Fig. 1). As expected, air temperatures (T_a) increased from dawn to a daily peak, then decreased from dusk through the night, while there was less variability in water temperature (T_w). A bimodal pattern was exhibited by the smallest crocodile (25 kg); this was an artefact of it being startled and re-entering the water for a brief time. Otherwise, all crocodiles continuously basked for 1-2 hours beyond peak T_a before re-entering the water. Excluding one exception (discussed below), T_b's remained above T_w at night and all T_{bmax}'s exceeded maximum T_a during daytime, but generally lagged T_{amax}'s by 1-2 hours. The lowest T_b's also lagged T_{amin}'s by approximately two hours.

Seasonal Mean (μ) and Highest T_b's

The range of environmental data (T_a and T_w) collected from winter through early summer months at Lake Ngezi in 1986 are presented in Table 1. Mean (μ) T_a and T_w increased during this time and were compared with the mean (μ) body temperatures (T_b) of each crocodile. The ranges of T_a and T_w effectively were T_{amin}/T_{amax} and T_{wmin}/T_{wmax}, respectively, while T_b ranges represent T_{bmin} and T_{bmax}.

Sub-adult female (25 kg, 1.94m)

Mean (μ) core body temperatures of the young female (1) increased from June (17.9°C) through September (28.3°C) (Fig. 2). The mean T_b for October was slightly less (28°C) than September, but was most likely influenced by the individual's behaviour or cloudy conditions given that the T_b at 06h00 in October (23°C) was 4.5 °C higher than at 06h00 in September (18.5°C). A maximum T_b of

35°C was recorded on 11 September at an air temperature of 28°C and water temperature of 21.5 ^{o}C (Table 1).

Young male (2.56 m, 81 kg)

Mean T_b's of the young male crocodile (2) steadily increased from 22.8^{o}C in June to 30.6^{o}C on 12 October. Its highest T_b, 36.4^{o}C, was recorded on 12 October with T_a 29°C and T_w 27°C. The 36.4^{o}C measurement was taken at 18h00 after the individual had returned to the water at 15h20, then resumed basking (Fig. 3), and represents the highest T_b recorded for all the research individuals during this study.

Mature female (2.97 m, 149 kg)

Mean (μ) T_b's increased monthly for the large female crocodile (3) from June through September, 18.2, 23.8, 25.9 and 28.2^{o}C, respectively (Fig. 4). Corresponding monthly environmental data are presented in Table 1.

Nesting began in September, after which the female seldom entered the water until 21 January when the eggs began to hatch. She moved the hatchlings into a crèche across the river that she attended until 11 February 1987, when the study was terminated. This female's highest recorded T_b (35.5^{o}C) occurred on two days, 11-12 October, when T_{amax} was 29°C and T_{wmax} 27°C. These dates coincided with those for the young male when a T_{bmax} of 36.4^{o}C was recorded.

Mature male (3.48 m, 260 kg)

The mature male (4) is the largest free-ranging Nile crocodile to date for which thermoregulation data exists. The time sequence (Fig. 5; Table 1) clearly demonstrated a steady increase in mean T_b from June through October 1986 (note: September data are missing), ranging by month from 20.3 to 22.9, 25 and 27.5^{o}C, respectively, gaining almost 2°C monthly. Mean T_b was ~31°C in January 1987 based on available data. A maximum T_b of 33.2^{o}C was recorded on 23 August at 1445-1600 h when T_a was

25°C and T_w 19°C. The mean T_b was 25°C the previous day when a 24-h time sequence was conducted (Table 1).

Amplitude Changes in T_b

The T_b amplitudes ranged from 6.3 to 17.2^{o}C with all crocodiles exhibiting shifts over 10°C with no apparent seasonal effect. Virtually all T_{bmin}'s were within 1-4 ^{o}C of T_{wmin} (Table 1) for all crocodiles. Inexplicably, the T_{bmin} of the small female was lower than T_{wmin} on 22 August. This may have been because of (a) T_{wmin} was lower than 17°C before the start time of observations at 06h00, (b) the crocodile was exposed to the air before 06h00, (c) it may have been active at depths cooler than surface T_w, or (d) an incorrect reading was possibly taken.

Heating and Cooling Rates

The relationship between time and rising T_b for all four Nile crocodiles on 14 July 1986 is presented in Fig. 6. When temperature was regressed against time while the air temperature was increasing throughout the day, the resulting quadratic equation was Temp $= (6.24*\text{time}) + (-0.17*\text{time}^2) - 24.7$, with an $R^2 = 0.80$. For the most part, the T_b's of the smallest two crocodiles were above the predicted line and the largest two below the predicted line.

The residuals for the four crocodiles were significantly different ($p < 0.05$, df = 3) for rising air temperatures (Fig. 7). The Duncan's Multiple Range test showed that residuals for the smallest two crocodiles were significantly different ($p < 0.05$) from (a) each other and (b) from the largest individual. The residuals for crocodiles 2 and 3 were not significantly ($p < 0.05$) from each other but differed from crocodile 4's rate, which was significantly different from all others. These data (Figs. 6 and 7) demonstrated a faster heating rate trend in smaller individuals.

The relationships between time and declining T_b's for all four crocodiles were taken after T_b's peaked on 14 July through 08h00 15 July (Fig. 8). The

quadratic equation Temp = (-3.46*time) + (-0.56*time^2) + 73.2, with an R^2 = 0.69 was derived when T$_b$'s were regressed against time while T$_a$ decreased throughout the night. For the most part, T$_b$'s of the smallest two crocodiles were below the predicted line and the largest two above.

The Duncan's Multiple Range test showed that the residuals for cooling temperatures were significantly different ($p < 0.05$, df = 3) between each of the four different-sized crocodiles (Fig. 9). As expected, the smaller crocodiles cooled faster than the larger ones.

The present study results discussed with that Crocodilians are an important component of any general picture of reptilian thermal relations because of their great ontogenetic size range and their evolutionary status as living archosaurs (Grigg *et al.,* 1998). Only Loveridge (1984) had published on body temperatures (T$_b$) and thermoregulation in Nile crocodile prior to this research in 1986. His pioneer work considered wild hand-collected juveniles (0.5-1.5 kg body weight) from the Zambezi River/Lake Kariba, Zimbabwe. T$_b$'s were recorded by cloaca-inserted thermistors and by thermistors that were force-fed into the subjects. Mean T$_b$'s ranged 29.7-33.4^{o}C although basking temperatures 32-34°C were maintained by crocodiles up to 38 kg body weight. A proxy for other crocodilians, Raske *et al.,* (2012) found no evidence of endothermy in the American alligator, i.e., alligators could not sustain T$_b$'s above that of their surroundings in the absence of an external heat source. Mugger crocodile avoided temperatures exceeding 32°C (Whitaker and Srinivasan, 2018), while American alligator reached 35°C (Lang, 1979). Only two of 12 Cuvier's dwarf caiman studied by Campos and Magnusson (2013) had T$_b$'s exceeding 30°C.

While no conclusive data exist for Nile crocodile re: T$_b$'s and location of measurement, the work of Johnson *et al.,* (1978) is instructive for crocodilians: data collected by thermocouples implanted in small American alligators (37-91 cm) under controlled conditions of heating demonstrated that head temperatures were > subcutaneous temperatures > body temperatures > cloaca temperatures. Heart temperature closely followed subcutaneous temperature, also being higher than cloaca temperature. Subcutaneous readings will be dependent upon a number of variables, especially the location of thermistors. McMaster and Downs (2013) reviewed T$_b$ measurement methodologies in chelonians and concluded that thermal gradients existed in the bodies of large leopard tortoise (*Stigmochelys pardalis*) with cloaca temperatures being significantly lower than core T$_b$'s. However, they recognized that core T$_b$'s of small reptile individuals might not be different than cloacal measurements.

The only known data base other than Loveridge (1984) on body temperatures and thermoregulation for Nile crocodile was reported 24 years later by Downs *et al.,* (2008) that resembles this study, but with significant differences. Thermochron iButtons were implanted subcutaneously into four crocodiles held at the St. Lucia Crocodile Centre, Lake St. Lucia, KwaZulu-Natal, South Africa; internal implantation was considered too invasive. The specimens ranged from 1.14-1.87 m in length, the largest estimated weighing ~23 kg based upon the smallest sized radio-tagged specimen here. Data were collected over an 8-week winter period (July-September 2004), then averaged for interpretations. It was found that (a) crocodile T$_b$'s increased during the day, usually after 10h00 irrespective of body size; (b) heating rates were more rapid than the cooling rates; (c) mean T$_b$'s varied little (22.0–23.2^{o}C) over the 8-week period with (d) no daily plateaus in T$_b$'s that continuously oscillated within a range between T$_{bmin}$ and T$_{bmax}$, similar to *C. porosus* (Grigg *et al.,* 1998); and (e) mean minimum T$_b$'s ranged 18.8–19.6^{o}C and mean maximum T$_b$'s 26.9–29.2^{o}C.

Results here were similar to the general observations for Nile crocodile by Downs *et al.,* (2008) in that (a) basking behaviour was used to elevate T$_b$; (b) T$_b$'s did not reach a plateau *per se*, but oscillated daily dependent upon ambient conditions; (c) T$_b$'s commenced to rise after 10h00, peaking late afternoon if the animal was not disturbed; and (d) heating rates were more rapid than cooling rates.

However, these data also portray (a) a distinct seasonal shift in mean T_b's, ranging from 18.2, 24.1, 24.7, 27.5 and 29°C, June to October, respectively, with hence (b) a wider range (variability) in the mean minimum and maximum T_b's, being 15.8^{o}C for June and 32.8^{o}C for October, respectively, although the latter was slightly higher in September 33.3^{o}C.

Specifically, the averaged 8-week winter T_b database reported by Downs *et al.,* (2008) varied <3°C. Contrasting significantly, Ngezi data extending from winter (June) through early summer (October) depicted a seasonal trend with mean T_b's increasing each month ~2°C from June to October for each individual regardless of size or sex (Table 1), no doubt influenced by increased day length and seasonal ambient warming. For instance, the mean T_b's (Table 1) increased from 17.9 to 28°C in the 25-kg female; 23.8 to 30.6^{o}C in the 81-kg male; 18.2 to 28.2^{o}C in the 149-kg female; and 20.2 to 27.5^{o}C in the 260-kg male, that reached ~31°C by January 1987. Data for June, the coldest month, was somewhat an exception; however, June measurements were taken within hours/days of the individuals release when they most likely remained under the after effects of handling and relocation. Campos and Magnusson (2013) also recognized seasonal shifts in T_b of Cuvier's dwarf caiman, although not as dramatic as here due to their burrowing behaviour and ambient conditions.

Supplemental data for the mature female and male suggests their mean T_b 's increased into January and February. The male's mean T_b appeared to increase from 27.5 in October to ~31°C on 7 January 1987, the last date thermal information was obtained for the animal. Data for the large male in this study are especially important given that sex determination in wild Nile crocodile is temperature-dependent with cooler egg incubation temperatures favouring female hatchlings and 31°C being a threshold for maleness (Hutton, 1987). The mature female commenced to nest in September; her mean T_b was 28.2^{o}C on 11 September. She seldom entered the water until 21 January 1987 when the eggs commenced to hatch; her daytime T_b's were about 26-29°C. A single T_b reading of 30.6^{o}C taken on 10 February 1987 at 15h30 when T_a was 36 ^{o}C infers a seasonal increase in mean T_b. Although sparse, these are the only thermoregulation data known for a nesting Nile crocodile. Whitaker and Srinivasan (2018) noted the lack of data for post-nesting female mugger crocodiles which experience significant weight loss.

Daily amplitude differences of each Ngezi crocodile were routinely ≥10°C and as high as 17.2^{o}C, the latter being 9 ^{o}C above the daily T_{amax}. Except for June when the animals were introduced into Lake Ngezi, amplitudes generally decreased with increasing mass (Grigg *et al.,* 1998) each month. This is attributed to the thermal inertia of larger individuals, which also influenced heating and cooling rates. These Ngezi crocodiles often continued heating up to 17-18h00 and cooled overnight to ~09h00. Both heating and cooling lagged maximum and minimum air temperatures, respectively, by about two hours. Bimodal patterns of basking were not observed in this study unless the individual was startled; however, such patterns are expected during hot summer months.

The effects of latitude and altitude on basking behaviour of Nile crocodiles have never been examined. Downs *et al.,* (2008) research was conducted at St. Lucia Crocodile Centre, South Africa, located at *-28.357 S x 32.418 E* just meters above sea level. Lake Ngezi is located *-20.108 S x 29.803 E* at a rather high altitude of ~1,255 m, thus it is expected that more extreme seasonal ambient conditions occur to influence heating and cooling, especially during winter months. The four Ngezi crocodiles (Table 1) each had T_{bmin}'s 3-4°C below the average T_{bmin} (19.1^{o}C) reported by Downs *et al.,* (2008), while T_{bmax}'s were 5-8°C above their average T_{bmax} (28°C). However, these differences are envisaged to be due to contrasting size (range) and seasonal environmental effects rather than physiological differences between the populations. This is supported by the fact that the highest recorded T_b for Lake Ngezi crocodiles was 36.4^{o}C, virtually identical to the maximum T_b of 36.5^{o}C recorded by Downs *et al.,* (2008) at St. Lucia.

Table.1 Range and mean (μ) of air, water and body temperatures (T_b's) of four Nile crocodiles from 06h00 to 17h00 on the same day. Amplitudes (°C) in daily T_b's, i.e., the difference between T_{bmin} and T_{bmax}, are given (*did not fully emerge; +data only for 10h00-17h00; NA = not available).

	28 June	14 July	22 Aug	11 Sept	15 Oct	Highest Tb (°C)/ Date
T_a Range (°C) μ	7.5-26 16.4	8-26 19.1	11-24 16.9	14.5-27 20.1	16-31 25.5	
T_w Range (°C) μ	15-19 15.9	15-19 17.2	17-21 18.65	18.5-22.8 20.25	22.7-25.5 24.2	
T_b (°C) 25 kg ♀ μ Amplitude	15-21.3 17.9 6.3	16.7-33.8 25.3 17.1	15.8-33 23.2 17.2	18.6-35 28.3 16.4	23-33.8 28 10.8	35 11 Sept
T_b (°C) 81 kg ♂ μ Amplitude	15.6-31.8 23.8 16.2	16.9-32.8 24.4 15.9	*NA	19.4-33 26.1 13.6	23.5-36.4 31.4 12.9	36.4 11 Oct
T_b (°C) 149 kg ♀ μ Amplitude	15.6-22 18.2 6.4	18.1-33 23.8 14.9	20-32.7 25.9 12.7	22.5-31.9 28.2 9.4	NA	35.5 11&12 Oct
T_b (°C) 260 kg ♂ μ Amplitude	16.9-27.5 20.3 10.6	18.3-29.6 22.9 11.3	20-30.7 25 10.7	NA	+25.5-28.3 +27.5 +2.8	33.2 23 Aug

Fig.1 Air, water and internal abdominal (T_b) temperatures (°C) of four Nile crocodiles at Lake Ngezi, Zimbabwe vs. time (24-h clock), 14-15 July 1986. (Crocodile 1 = 25-kg female; 2 = 81-kg male; 3 = 149-kg female; and 4 = 260-kg male.).
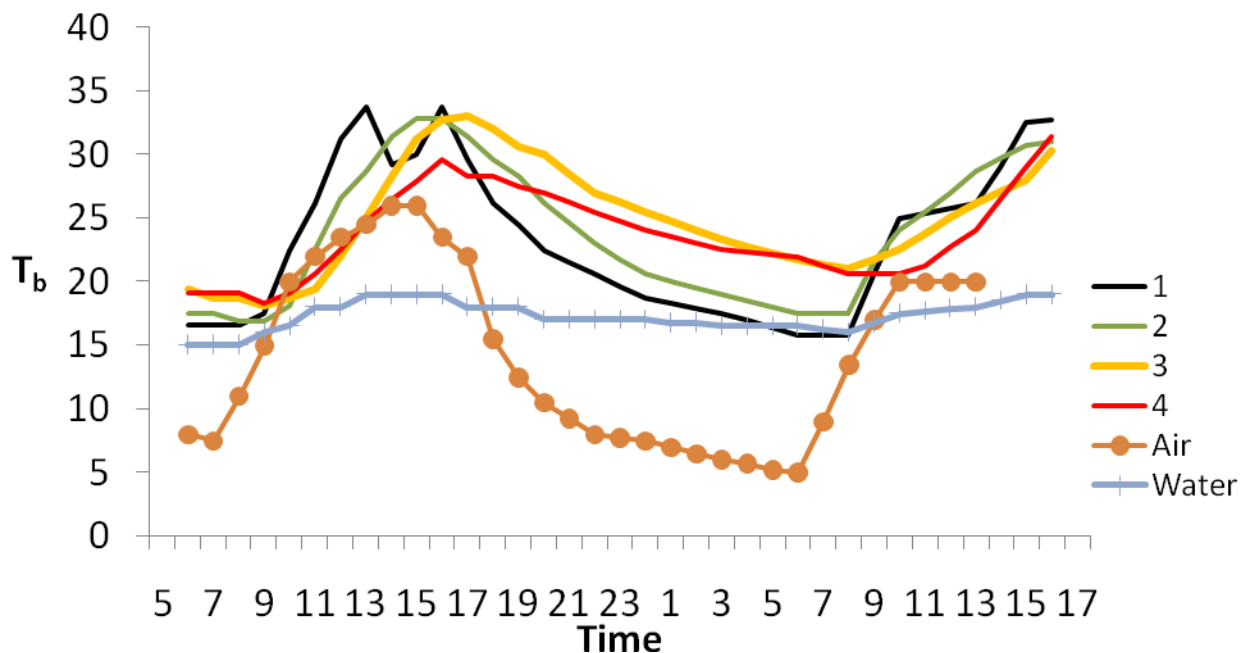
Fig.2 Body temperatures (°C) on 28 June, 14 July, 22 August, 10 September and 15 October 1986 of a 25-kg, 1.94-m immature female Nile crocodile at Lake Ngezi, Zimbabwe.
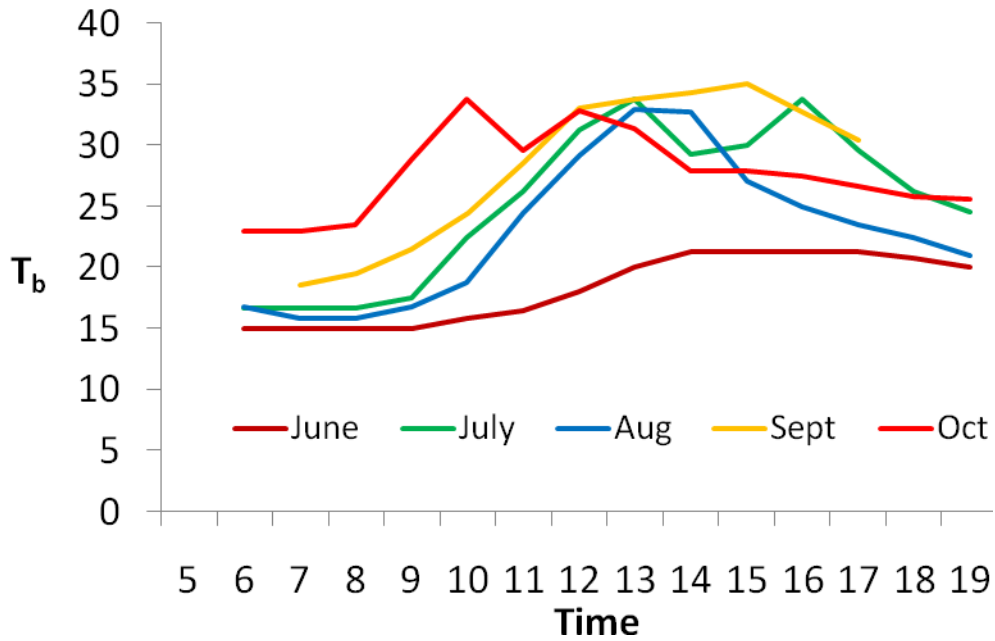

Fig.3 Time series (24-h clock) on 28-29 June, 14-15 July, 11 September and 12-13 October 1986 of abdominal temperatures of a 81-kg male Nile crocodile at Lake Ngezi, Zimbabwe.
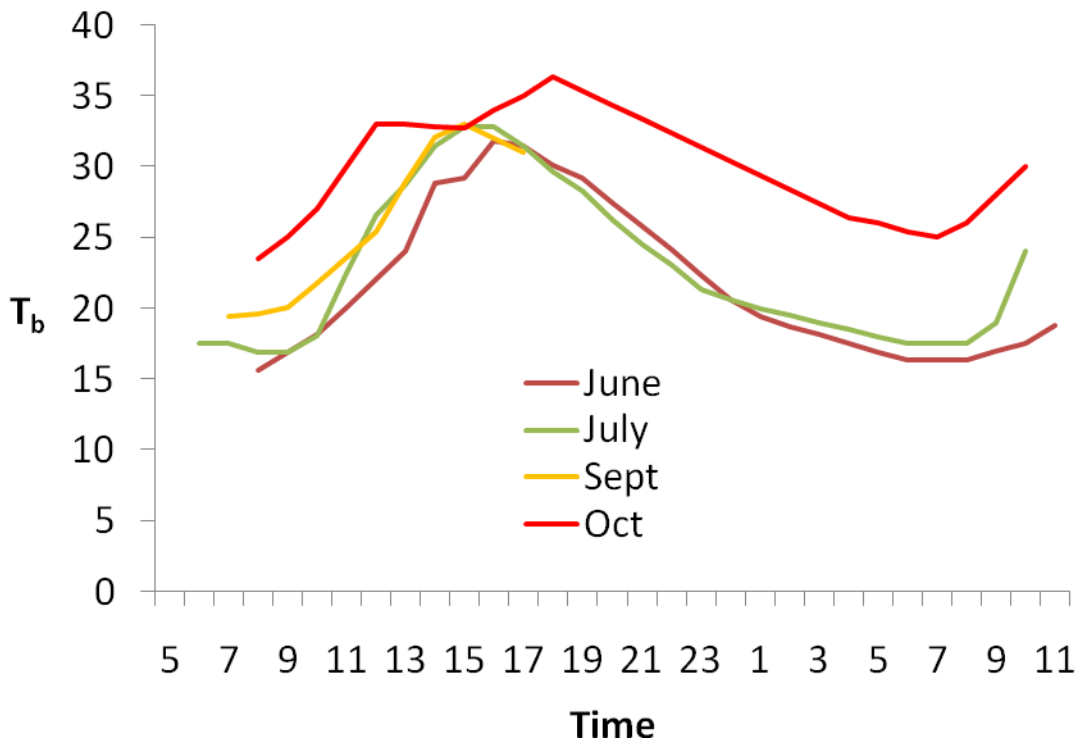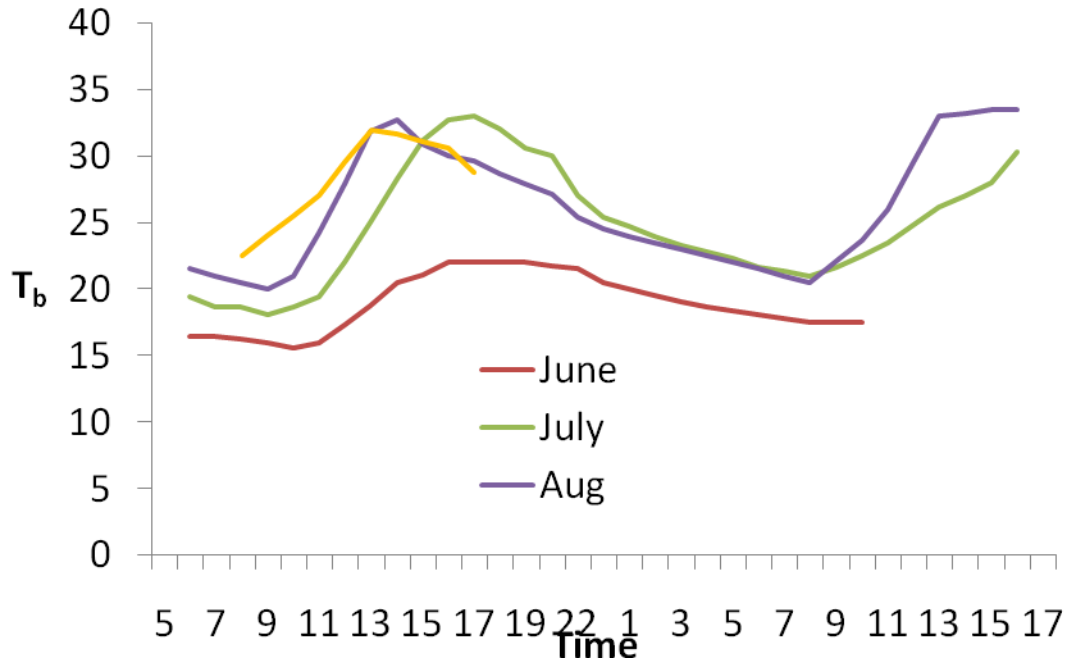
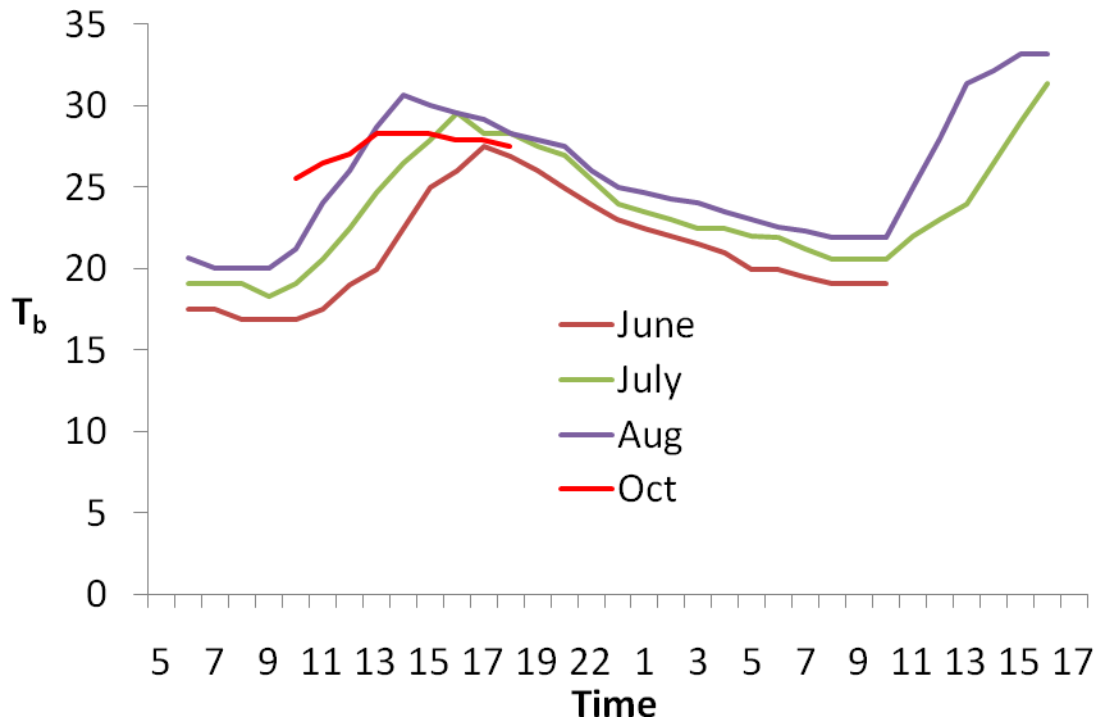**Fig.4** Time series (24-h clock) on 28-29 June, 14-15 July, 22-23 August and 11 September 1986 of abdominal temperatures of a 149-kg female Nile crocodile at Lake Ngezi, Zimbabwe.

Fig.5 Time series (24-h clock) on 28-29 June, 14-15 July, 22-23 August 1986 and 15 October 1986 of internal abdominal temperatures of a 260-kg male Nile crocodile at Lake Ngezi, Zimbabwe.

Fig.6 Observed and predicted (solid line) body temperatures of four Nile crocodiles from the smallest (1) to the largest (4), weighing 25, 81, 149 and 260 kg, respectively, during rising temperatures on 14 July 1986.
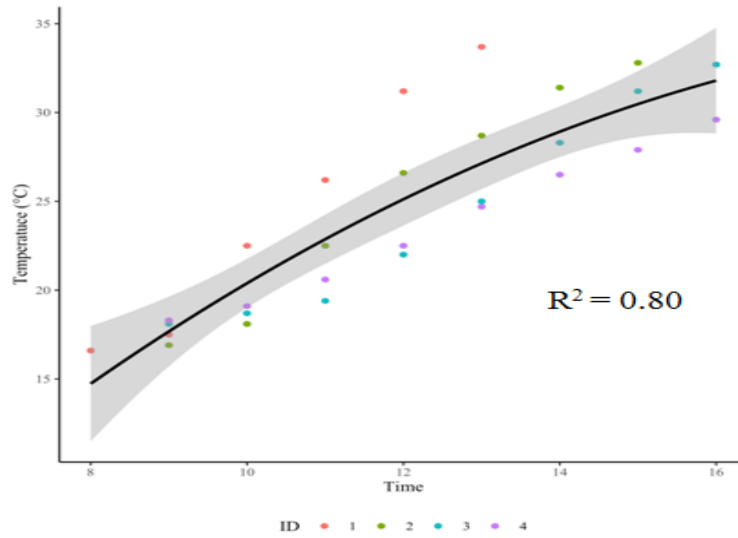
Fig.7 The residuals (observed – predicted) of the body temperatures for the smallest (crocid 1) to the largest (4) Nile crocodiles during rising temperatures.
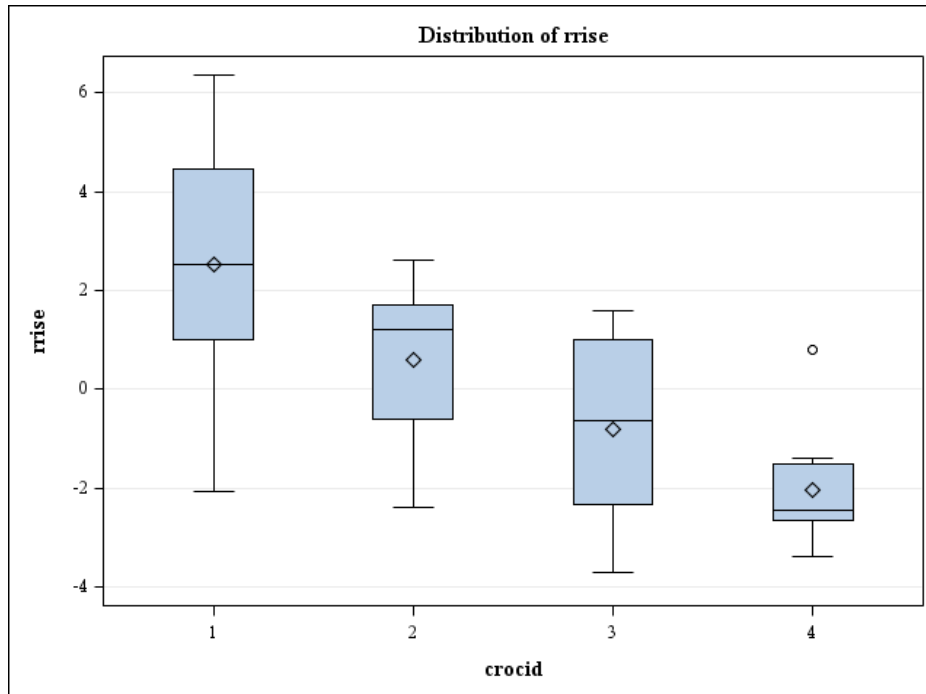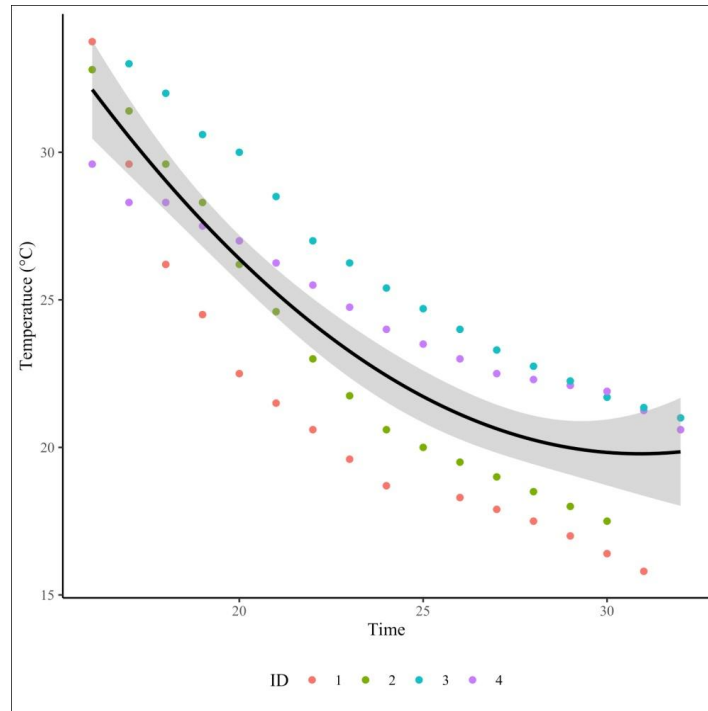
Fig.8 Observed and predicted (solid line) body temperatures of four Nile crocodiles from the smallest (1) to the largest (4), weighing 25, 81, 149 and 260 kg, respectively, during cooling air temperatures on 14-15 July 1986. (24 hours is added to time after midnight, e.g., 01h00 = 25 and 06h00 = 30 on graph).

$$R^2 = 0.69$$

Fig.9 The residuals (observed – predicted) of the body temperatures for the smallest (crocid 1) to the largest (4) Nile crocodiles during cooling temperatures.
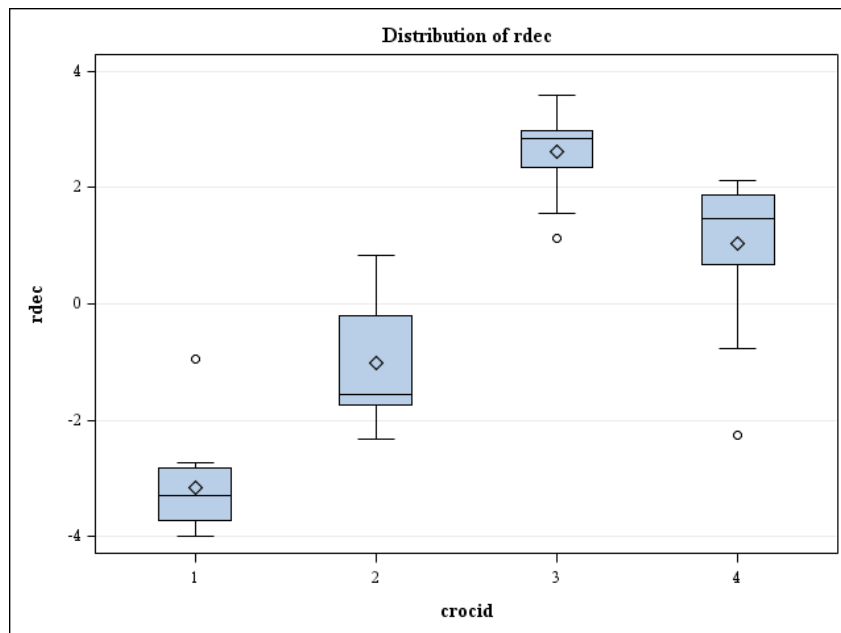
Seebacher *et al.,* (1999) stated "*Twenty years ago Grigg (1977) speculated that Crocodylus porosus would become warmer with increasing mass and show increased stability in body temperature (T_b). Recently, both these predictions have been confirmed empirically by Grigg et al., (1998).*" Data presented here are not robust nor were they collected to test these hypotheses, but seemingly do not support the former. For instance, an inverse relationship between mean T_b's and size was recorded in July. Alternately, Lake Ngezi data support the latter hypothesis. With respect to the two hypotheses, the same explanation is offered for Ngezi results, i.e., thermal inertia is dictated by mass with smaller individuals demonstrating greater variability in T_b as observed by Grigg *et al.,* (1998). Campos and Magnusson (2013) found no correlation between body size of Cuvier's dwarf caiman (2.5-20 kg) vs. daily amplitude fluctuations regardless of season; however, these high-altitude tropical caiman burrow during cooler months and otherwise have limited basking areas to elevate T_b.

Grigg *et al.,* (1998) put forward a proposal worth repeating here, i.e., thermoregulation (and bio-energetics) in crocodilians may well be unlike other reptiles, principally due to their large ontogenetic size range. Smaller crocodiles may mimic lizard patterns by shuttling back and forth from water to basking to thermoregulate. *However, as mass increases, as seen in C. porosus, time constants become too large to make short-term shuttling behaviour effective for thermoregulation, even with access to water. Behavioural patterns of larger individuals change over a much longer time-scale, between day and night, and between seasons, and T_b forms a continuous cycle rather than a daily plateau. We speculate that this shift in the pattern of T_b occurs somewhere between a mass of 20 and 30 kg*. This inference seems valid.

With respect to future investigations on thermoregulation behaviour of crocodilians, two points regarding methodology are made: (1) These Ngezi data for wild free-ranging specimens, although collected some 20 years prior to the study of Downs *et al.,* (2008) at the St. Lucia Crocodile Centre, add veracity to such thermoregulation experimentation in confined or controlled environs (Grigg *et al.,* 1998; Whitaker and Srinivasan, 2018). (2) Secondly, it is acknowledged that the use of surgically implanted transmitters into vertebrates is highly contentious. However, these data strongly support the ethical application of this procedure:

Retention

Two of six (33%) iButtons implanted by Downs *et al.,* (2008) were ejected within four months, while Loveridge (1984) reported regurgitation of force-fed transmitters. This compares to 100% retention of the internally implanted transmitters after nine months, with two of four transmitters functioning after two years and the status of the other two unknown (J. Loveridge, *pers. comm.*), thus possibly still operating. This compares favourably to externally-attached transmitters prone to failure, damage or loss up to 40% (Strauss *et al.,* 2008) and that cannot provide the same diversity of data. Whitaker and Srinivasan (2018) implanted HOBO ™ Tid-Bit V1 temperature loggers in the peritoneal cavities of 10 mugger crocodiles, but only three were recovered for downloading data; a fourth logger found in faeces (with no retrievable data) suggests intestinal encapsulation and expulsion, although not verified (N. Whitaker, *pers. comm.*).

Ventral insertion of transmitters into the abdomen is recommended vs. ventro-lateral due to the presence of a major vein running laterally on either side of the abdomen. Also, contrary to subjective thinking of slithering, crocodilian movement typically is either quadrupedal or a swimming motion without undue abdominal abrasion (of sutures).

Non-invasive

The presumable mating (Hocutt *et al.,* 1992) and subsequent nesting of the large female in this study also implies that internal insertion of transmitters can be reasonably non-invasive and provide valuable behavioural and physiological data for crocodilians not otherwise obtainable. The HOBO loggers used by Whitaker and Srinivasan (2018)

required surgical implantation, then animal recapture and surgical removal of the loggers for data retrieval. Conceptually, modern radio-transmitters are a far more powerful tool than loggers and do not necessitate recapture for data retrieval or, alternately, facilitate recapture if so required.

Sensitivity

The bimodal pattern of heating of the small female crocodile in July (Fig. 1) demonstrated the sensitivity of the abdominal-implanted transmitters: T_b reached 33.7 ^{o}C by 13h00 before the individual was startled and re-entered the water with T_b decreasing to 29.2 ^{o}C by 14h00. It commenced to bask once more and T_b reached 30°C by 15h00, peaking again at 16h00 with T_b being 33.75^{o}C.

Lastly, and in retrospect, one glaring fact was realised in the preparation of this manuscript. In spite of the uniqueness of the Crocodylia and their separation from the Squamata for 180-200 million years, there is a paucity of thermoregulation studies for the 24 extant species. There was a 24-year hiatus between the publications of Loveridge (1984) and Downs *et al.,* (2008) for the Nile crocodile and another 14 years before this data base surfaced, each adding a dimension of understanding to this important phenomenon.

Acknowledgements

Competing Financial Interest

References

Burnett, M. J., G. C. O'Brien, F. J. Jacobs, G. Jewitt and C.T. Downs. 2021. Fish telemetry in African inland waters and its use in management: A review. Rev. Fish. Biol. Fisheries 31: 337-357.

Campos, Z. and W. E. Magnusson. 2013. Thermal relations of dwarf caiman, *Paleosuchus palpebrosus*, in a hillside stream: Evidence for an unusual thermal niche among crocodilians. J. Therm. Biol. 38: 20-23.

Diefenbach, C. O. D. C. 1975. Thermal preferences and thermoregulation in *Caiman crocodilus*. Copeia: 530-540.

Downs, C. T., C. Greaverb and R. Taylor. 2008. Body temperature and basking behaviour of Nile crocodiles (*Crocodylus niloticus*) during winter. J. Ther. Biol. 33 (2008): 185–192.

Grigg, G. C. 1977. Body temperature of crocodiles and dinosaurs. In: H. Messel and H. Butler (Eds.). Australian animals and their environment. Shakespeare Head Press, Sydney, pp. 355–367.

Grigg, G. C., F. Seebacher, L. A. Beard and D. Morris. 1998. Thermal relations of large crocodiles, *Crocodylus porosus*, free-ranging in a naturalistic situation. Proc. R. Soc. Lond. B 265: 1793-1799.

Hocutt, C. H. 1989a. Seasonal and diel behaviour of radio-tagged *Clarias gariepinus* (Burchell) in Lake Ngezi, Zimbabwe. J. Zool., Lond. 219: 181-199.

Hocutt, C. H. 1989b. Behaviour of a radio-tagged *Tilapia rendalli* Boulenger in Lake Ngezi, Zimbabwe. J. Limnol. Soc. south. Afr. 14(2): 124-126.

Hocutt, C. H., J. P. Loveridge and J. M. Hutton. 1992. Biotelemetry monitoring of translocated *Crocodylus niloticus* in Lake Ngezi, Zimbabwe. J. Zool., Lond. 226: 231–242.

Hutton J M. 1987. Incubation temperatures, sex ratios and sex determination in a population of Nile crocodiles. J. Zool., Lond. 211: 143-155.

Johnson, C. R. 1974. Thermoregulation in crocodilians - I. Head-body temperature control in the Papuan-New Guinean crocodiles, *Crocodylus novaeguineae* and *Crocodylus porosus*. Comp. Biochem. Phys. 49A: 3-28.

Johnson, C. R., G. J. W. Webb and C. Tanner. 1976. Thermoregulation in crocodilians - II. A telemetric study of body temperature in the Australian crocodiles, *Crocodylus johnstoni* and *Crocodylus porosus*. Comp. Biochem. Phys. S3A: 143-146.

Johnson, C. R., W. G. Voight and E. N. Smith. 1978. Thermoregulation in crocodilians - III. Thermal preferenda, voluntary maxima, and heating and cooling rates in the American alligator, *Alligator mississippiensis*. Zool. J. Linn. Soc. 62: 179-188.

Lang, J. W. 1979. Thermophilic response of the American alligator and the American crocodile to feeding. Copeia 1979: 48 – 59.

Loveridge, J. P. 1984. Thermoregulation of the Nile crocodile *Crocodylus niloticus*. Symp. Zool. Soc. Lond. 52: 443–467.

Loveridge, J. P. and D. K. Blake. 1982. Techniques in the immobilisation and handling of the Nile crocodile, *Crocodylus niloticus*. Arnoldia, Rhodesia 5: 1-14.

Loveridge, J. P. and D. K. Blake. 1987. Crocodile immobilization and anesthesia. In: G.J.W. Webb, S.C. Manolis and P.J. Whitehead (Eds.). Wildlife management: Crocodiles and alligators. Surrey Beatty & Sons, Chipping Norton, Australia, pp. 259-267.

McMaster, M. K. and C. T. Downs. 2013. Thermal variability in body temperature in an ectotherm: Are cloacal temperatures good indicators of tortoise body temperature? J. Therm. Biol. 38: 163-168.

Raske, M., *et al.,* 2012. Body temperatures of selected amphibian and reptile species. J. Zoo. Wildl. Med. 43: 517–521.

Seebacher, F. and G. C. Grigg. 1997. Patterns of body temperature in wild freshwater crocodiles, *Crocodylus johnstoni*: Thermoregulation versus thermoconformity, seasonal acclimatization, and the effect of social interactions. Copeia 3: 549-557.

Seebacher, F., G. C Grigg and L. A. Beard. 1999. Crocodiles as dinosaurs: Behavioural thermoregulation in very large ectotherms leads to high and stable body temperatures. J. Exp. Biol. 202: 77-86.

Spotila, J. R. 1973. Behavioral thermoregulation of the alligator - Body temperatures of free roaming individuals under natural conditions. In: J.W. Gibbons and R.R. Sharitz (Eds.), Thermal ecology. U.S. Tech. Inform. Serv., Springfield, Va., Oak Ridge National Laboratory, pp. 332-334.

Strauss, M., H. Botha and W. van Hoven. 2008. Nile crocodile *Crocodylus niloticus* telemetry: Observations on transmitter attachment and longevity. S. Afr. J. Wildl. Res. 38(2): 189-192.

Whitaker, N. and M. Srinivasan. 2018. Preliminary observations on deep body temperatures in female mugger crocodiles (*Crocodylus palustris* Lesson:1831) in a captive facility. Int. J. Curr. Microbiol. App. Sci. 7(12): 2835-2842.