THE ROLE OF THE CARDIOVASCULAR SYSTEM IN THERMOREGULATION OF CROCODYLUS JOHNSTONI

GORDON C. GRIGG AND JENNIFER ALCHIN
School of Biological Sciences, University of Sydney, N.S.W. 2006, Australia
(Accepted 11/20/75)

The Australian freshwater crocodile, *Crocodylus johnstoni*, heats significantly faster than it cools. Under the experimental conditions, cooling rate was found to be approximately 80% of heating rate in both air and water. Heart rate during heating is more rapid than during cooling. Convective transfer of heat within the body is effected by the circulatory system, and this far exceeds rates of heat transfer by conduction alone. Localized heating of the body surface results in a cutaneous vasodilation which promotes uptake of heat. Localized cooling of the body surface results in cutaneous vasoconstriction, promoting heat conservation. Increase or decrease in heart rate accompanies cutaneous vasodilation or vasoconstriction. The dilation or constriction of cutaneous blood vessels and the acceleration or deceleration of heart rate are seen as separate responses to surface heating or cooling. Together they promote heat gain or retard heat loss and provide physiological mechanisms contributing to thermoregulation in *C. johnstoni*.

Thermally significant behavior patterns in reptiles were noted by Cowles and Bogert (1944). These authors showed that, by behavioral means, many reptiles maintain a high and relatively stable body temperature during times of activity even though environmental temperatures may fluctuate markedly. As a result of much work by many authors, behavioral control of body temperature appears to be typical of all reptiles. Emergence or retreat, selection of a favorable microclimate, basking, orientation, postural changes, and even social aggregation are all patterns of behavior which can modify the heat budget of an individual reptile (Bogert 1959; Brattstrom 1965; Bradshaw and Main 1968). Behavioral thermoregulation enables reptiles to extend periods of activity into times when external temperatures would otherwise prohibit activity.

More recently it has been shown that many reptiles augment behavioral thermoregulation by physiological mechanisms which further extend the abilities of reptiles to maintain a favorable body temperature. Experiments on many species have shown that heating rate may far exceed cooling rate in live reptiles, whereas in dead (control) animals under the same conditions, heating rate equals cooling rate. Such results have been interpreted as indications of physiological mechanisms facilitating heat gain and/or retarding heat loss (Bartholomew and Tucker 1963, 1964; Spray and May 1972; see also review by Schmidt-Nielsen and Dawson 1964). Metabolic heat production and peripheral cardiovascular adjustments are thought to be the major factors influencing the observed rates of heat gain and loss, and the relative importance of these factors may differ in different species. In *Amphibolurus barbatus* (Bartholomew and Tucker 1963), *Amblyrhynchus cristatus* (Bartholomew and Lasiewski 1965), *Dipsosaurus dorsalis* (Weathers 1970), and some turtles (Spray and May 1972), circulatory adjustments

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1 The authors wish to acknowledge financial assistance from a University of Sydney research grant and from the Science Foundation for Physics within the University of Sydney.
were the major factor. In the Australian varanids (Bartholomew and Tucker 1964) and Tiliqua scincoides (Bartholomew, Tucker, and Lee 1965), endogenous heat production had a greater effect in control of heating and cooling.

In the above studies, implication of cardiovascular involvements was derived only from observations on heart rate. That is, at any body temperature, heart rate was higher during heating than during cooling. This alone may be insufficient evidence to implicate the cardiovascular system in a thermoregulatory role because heart rate is responsive to other physiological demands as well. Indeed, Weathers and White (1971) showed that heart rate in some turtles depended more upon respiration than on heating and cooling rates.

More direct evidence for the role of circulatory adjustments in effecting control over heat loss or gain has been presented. In the lizard Amblyrhynchus cristatus (Morgareidge and White 1969) and some turtles (Weathers and White 1971) localized heating of the body surface results in localized cutaneous vasodilation. Furthermore, during heating of Iguana iguana, more blood is circulated than is necessary for oxygen transport, for cardiac output increases while the arterio-venous oxygen difference is reduced (Baker and White 1970). The importance of the circulatory system as a vehicle for convective heat transfer within reptiles has been amply demonstrated (Heath 1964, 1966; Webb and Heatwole 1971).

Very few studies of physiological thermoregulation in crocodiles have been reported. In view of the high specific heat of water, aquatic reptiles face greater difficulties than a terrestrial reptile in retarding heat loss, and one might suppose that the physiological mechanisms may be better developed. In some aquatic turtles (Weathers and White 1971) and the partly aquatic Galapagos marine iguana (Bartholomew and Lasiewski 1965; Morgareidge and White 1969) this appears to be the case. Larger differences between heating and cooling rates were found in the aquatic species than have been reported for terrestrial reptiles. These differences were attributed to changes in peripheral circulation leading to a change in the effective peripheral insulation.

The primary aim of the present series of experiments was to establish whether physiological mechanisms facilitate heat gain and/or retard heat loss in the Australian freshwater crocodile, Crocodylus johnstoni, and to assess the role of the circulatory system in thermoregulation.

MATERIAL AND METHODS

ANIMALS

Crocodylus johnstoni (Krefft) inhabits inland waters of northern Australia. The six specimens used in this study were captured in the Northern Territory in December 1971 and shipped by air to Taronga Zoological Park, Sydney. At the zoo they were maintained in a large wire mesh enclosure with radiant heaters in one corner and a heated pool. They were fed twice weekly on fish and remained in good health. At the time of the study their weights ranged from 2.4 to 17.5 kg (see table 1).

<table>
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<th>TABLE 1</th>
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<tr>
<td>THE EXPERIMENTAL ANIMALS</td>
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<tr>
<td>Crocodile</td>
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<tr>
<td>A</td>
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<tr>
<td>B</td>
</tr>
<tr>
<td>C</td>
</tr>
<tr>
<td>D</td>
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<td>E</td>
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TEMPERATURE

Temperatures were measured using a single channel telethermometer (Yellow Springs Instrument Company, Model 43TD) equipped with an 11-channel selector switch. Calibrated thermistor probes were used as follows: (a) Core temperature; a vinyl bead thermistor inserted rectally. (b) Head temperature; a bead thermistor mounted in the tip of a 19G hypodermic needle inserted beside the brain. (c) Subdermal temperature; a bead thermistor mounted in a 19G hypodermic needle inserted under the skin. (d) Air and/or water temperature; vinyl bead thermistors.

DETERMINATION OF HEART-RATE

Heart rate was determined by recording the electrocardiogram. Electrodes (made from 22G hypodermic needles) were inserted subdermally in the ventral midline anterior and posterior to the heart. A third electrode in the tail region served as an earth. The signal was amplified by a Tektronix Type 122 low-level preamplifier before being applied to FKG and Driver modules of a Grass Polygraph (Model 5). In experiments where crocodiles were heated and cooled in water, the electrocardiogram was recorded telemetrically using a circuit modified from that described by Fryer (1970). The transmitter was a flat rectangular package (6.0 × 1.5 × 0.5 cm) easily slid under the skin of the ventral surface. Electrodes, made from surgical stainless steel, protruded from one end of the package. Sterile procedure was used for the surgical implantation, and the skin incision healed well. Signals were monitored on a Lafayette Guardian 600 radio in the “air” band (108–136 mHz). Each depolarization of the heart produced an audible modulation in the carrier frequency so that heart rate could be counted.

EXPERIMENTS

1. Heating and cooling in air.—These experiments were based on techniques developed by Bartholomew and Tucker (1963, 1964) and Bartholomew et al. (1965). In each experiment, a crocodile at 20–22 C, with temperature and heart-rate leads attached and enclosed in a chicken-wire cage, was placed into a temperature-controlled room at 33–35 C. The experimenter then left the room but could observe the crocodile through a small hole in the door. In this way the animal was undisturbed throughout the experiment. All recording devices were located outside the temperature-controlled room. Heart rate and temperatures were recorded every 10–15 min as the body temperature rose to room temperature. The room was then cooled very quickly (about 5 min) and the same observations continued. Crocodiles B and E were used in these experiments, with animal A (dead) as a control. Note that this same combination of animals was used for the experiments on heating and cooling in water.

2. Heating and cooling in water.—In these experiments, a crocodile at room temperature (20–22 C), with an electrocardiogram transmitter implanted and temperature leads attached, was placed in water at 36–37 C in a rectangular metal tank (120 × 40 × 25 cm). The crocodiles lay in the water with only the upper part of the head out of water. They were not restrained. As heating of the crocodile proceeded, temperatures and heart rate were recorded every few minutes. The animals became quite active as warming proceeded. When deep-body temperature was close to or the same as that of the water, cool (20–22 C) water was flushed into the tank and the same observations made as the crocodile cooled. As in heating and cooling in air, crocodiles B and E were used in these
experiments, with A (dead) as a control.

3. Radiant heating in air.—In each of these experiments, a crocodile was restrained in a V-shaped wooden rack and heated by a row of infrared lamps (250 w). Temperatures and heart rate were monitored during heating. Three different heating patterns were used: (a) Heating the whole animal with seven lamps 80–85 cm above the dorsal surface; (b) Heating the body only, from the same heat source, but with the head shielded in an insulated box covered by aluminum foil. This insured that no heat was applied directly to the head region; and (c) Heating the head only with two infrared lamps 50–55 cm above the head. In this case the body was shielded by an insulated box covered by aluminum foil, insuring that no heat was applied directly to the body.

In each experiment, temperatures and heart rate were recorded every 5–10 min during heating until cloacal temperature reached 35–36 C, or until head temperature reached 37 C, or until the animal began struggling. Crocodiles A, B, C, and D were then killed by injecting 3 ml Sagatal (containing 60 mg pento-barbitone sodium ml−1) intraperitoneally and the radiant heating experiment repeated.

4. Cutaneous blood flow.—Changes in cutaneous blood flow were recorded using a Xe133 clearance technique (Kjellmer et al. 1967, Morgareidge and White 1969). In this technique, changes in the slope of a washout curve for Xe133 injected under the skin indicated changes in cutaneous blood flow.

In an experiment, a crocodile was restrained on a wooden rack. A deep-body temperature probe was emplaced, as well as a subdermal temperature probe in each of two "injection sites." Both injection sites were mid-dorsal, one anteriorly near the front legs and one posteriorly but in front of the hind legs. Heat could be applied to either site independently with a 250-w infrared lamp 35 cm from the surface. Radioactivity at each site was monitored with suitable probes collimated to cover a 2 × 2-cm area of the surface. Each probe was connected to a Selo three-channel scintillation counter (Model DC3) and a three-channel analog recorder so that a recording of the washout curve was obtained. In an experiment, 50 µl of a solution of Xe133 in saline (approximately 0.025 mCi) was injected subdermally at each injection site. The position of the scintillation probes over the surface was adjusted for maximum count rate, and the time course of removal of radioactivity from the two areas was followed. After about 20 min, when a baseline had been established, heat was applied to the anterior (or posterior) site for 20 min. The heat was then turned off, and after a further 20 min the posterior (or anterior) site was heated for 20 min. Heating was then discontinued and observations continued for a further 20 min or so. Two crocodiles (A and B) were used, with a control experiment on a dead crocodile to establish the nature of the washout curve in the absence of any blood flow.

RESULTS

1. Heating and cooling in air

a) Core temperature.—Whereas a dead crocodile (A) heated and cooled at the same rate, animal B heated significantly faster than it cooled (P < .01) (fig. 1). The ratio of cooling rate to heating rate was 0.83. In animal E however, heating and cooling rates were equal. This was attributed to the fact that, whereas animal B remained quiescent during both heating and cooling, animal E was markedly active during the cooling phase. One year later these experiments were
repeated with the same pair of crocodiles. The data for all four experiments with live B and E are summarized in table 2. Heating and cooling rates are compared at 28°C, where the difference between core and air was 7°C during both heating and cooling. In the second series of experiments animal E heated faster than it cooled (cooling/heating = 0.83), but animal B cooled twice as fast as it heated.

b) Heart rates (table 2).—Heart rate was consistently higher during heating than during cooling in animal B (fig. 2).

TABLE 2
HEART RATE AND RATE OF CHANGE IN TEMPERATURE OF "CROCODYLUS JOHNSTONI" DURING HEATING AND COOLING IN AIR AND WATER, AT A BODY TEMPERATURE OF 28°C (AIR) AND 29°C (WATER)

<table>
<thead>
<tr>
<th>Crocodile</th>
<th>Rate of Change (°C Min⁻¹)</th>
<th>Heart Rate (Beats Min⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>During Heating</td>
<td>During Cooling</td>
</tr>
<tr>
<td>Air:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>E*</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>A (dead)</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>E</td>
<td>0.06</td>
<td>0.05</td>
</tr>
<tr>
<td>B</td>
<td>0.08</td>
<td>0.16</td>
</tr>
<tr>
<td>Water:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>0.40</td>
<td>0.30</td>
</tr>
<tr>
<td>E</td>
<td>0.24</td>
<td>0.20</td>
</tr>
<tr>
<td>A (dead)</td>
<td>0.34</td>
<td>0.33</td>
</tr>
</tbody>
</table>

* Crocodile E active during cooling in this experiment.
In animal E, which was active during cooling and in which heating rate equaled cooling rate, heart rate at any one core temperature was equal during heating and cooling. No heart rates were recorded during the repeat experiments on these crocodiles.

c) Head temperature—core temperature.—Large differences between head and core temperatures were not seen. In both B and E, however, a consistent pattern emerged (fig. 3) in which head temperature rose faster than body temperature. Its rate of increase then declined relative to core temperature increase. At the end of heating, head temperature was lower than core temperature in all cases. This is in contrast to the control in which head temperature remained higher than body temperature throughout.

2. HEATING AND COOLING IN WATER

a) Core temperature.—As in heating and cooling in air, the dead crocodile (A) heated and cooled at the same rate (fig. 4). In both live crocodiles, B and E, heating rate exceeded cooling rate, the cooling/heating ratios being 0.75 and 0.83, respectively. Results for E are shown in figure 4. All results are given in table 2. Heating and cooling rates are compared at 29°C because at this temperature the difference between water and core temperatures was equal (8°C) during both heating and cooling.

b) Heart rates.—At all temperatures and in both animals, heart rate was

![Graph](image_url)
higher during heating than during cooling (table 2, fig. 5).

c) Head temperature—core temperature.
—Head temperature in the live crocodiles remained about 3°C below body temperature, whereas in the control (A) head temperature stabilized 6.5°C lower than core temperature (fig. 6). It can be seen that on three occasions during heating, head temperature fell by about 1°C while body temperature was still rising.

3. RADIANT HEATING IN AIR

Results typical of all three types of radiant heating experiments are shown in figure 7.

![Graph of heating and cooling temperatures](image)

**Fig. 3.**—Relation of $T_{\text{head}}$ and $T_{\text{core}}$ to time during heating of a live crocodile (E) and a dead crocodile (A) in air.

![Graph of temperature changes](image)

**Fig. 4.**—Relation of difference between $T_{\text{core}}$ and $T_{\text{water}}$ (°C) to time in a dead crocodile (A) and a live crocodile (E) in water. During heating, $T_{\text{water}} = 37$°C; during cooling $T_{\text{water}} = 20$°C.
a) **Heating the whole animal.**—Core temperature rose faster in the live animals than in the controls. Head temperatures remained lower in live animals than in the controls.

b) **Heating the body only.**—In live animals head temperature rose almost as fast as core temperature, whereas in the controls head temperature rose very little. Subdermal temperatures rose more slowly, and the core warmed more rapidly in live animals than in the controls.

c) **Heating the head only.**—In the controls head temperatures rose much more rapidly than in live animals. Core and subdermal temperatures in dead crocodiles showed no increase but increased slowly in live animals.

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**Figure 5.** Heart rate as a function of core temperature during heating and cooling of crocodile B in water.

**Figure 6.** Relation of $T_{head}$ and $T_{core}$ to time during heating of a dead crocodile (A) and a live crocodile (E) in water; $T_{water} = 37$ °C.

4. **CUTANEOUS BLOOD FLOW**

A control experiment firmly established that, with no cutaneous perfusion, no appreciable decrease in radioactivity occurred during an experimental period, either with or without heating. Therefore, any observed washout of radioactivity in live crocodiles can be attributed to removal of Xe$^{133}$ by blood flow. Furthermore, the system itself was not temperature sensitive. Results typical of experiments with both crocodiles (A and B) are presented in figure 8. In all cases, before application of heat, the washout curve appeared exponential. At the onset of localized heating of either anterior or posterior injection site, the washout curve steepened, indicating increased removal of the Xe$^{133}$. Heating one region had no effect on the washout...
FIG. 7.—Rise in $T_{body}$, $T_{head}$, and $T_{subdermal}$ with time during radiant heating of crocodile in air when alive (top row) and dead (bottom row). In the left column, the whole animal was heated evenly. In the center column the head was shielded from the heat source. In the right column, only the head was exposed to the heat source.
curve from the unheated area. Heart rate increased almost immediately when heat was applied to either site and then decreased with removal of the heat source. Small increases in core temperature were observed a few minutes after heating began, suggesting heat transfer from periphery to core.

**DISCUSSION**

1. **THE CONVECTIVE ROLE OF THE CIRCULATORY SYSTEM**

The experiments on radiant heating of crocodiles in air (fig. 7) showed very clearly that heat transfer is much more rapid in live crocodiles than in dead ones. It seems safe to assume that this

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**Fig. 8.—Clearance of Xe$^{133}$ from anterior and posterior subdermal injection sites in crocodile A, as influenced by application of heat to the anterior and then the posterior site. Note the increase in heart rate which accompanies each application of heat, followed in each case by a slight rise in $T_{\text{core}}$.**
is due to the convective role of the circulatory system. In the dead animal, large gradients existed between core and periphery, whereas in live crocodiles these gradients were much reduced. Experiments in which either the head or the body of the dead animal was shielded from the heat source indicate the slow transfer of heat in nonperfused tissue. The same experiments on a live crocodile, however, indicate that the whole animal could be warmed by heating either the head or body only. Furthermore, perfusion of the heated area prevented the high surface temperatures reached in the control experiments.

2. RATES OF HEATING AND COOLING IN AIR AND WATER

The dead crocodile heated and cooled at the same rate in air, 0.05 C min\(^{-1}\) (fig. 1). In water it also heated and cooled at essentially the same rate, 0.33 — 0.34 C min\(^{-1}\) (fig. 4). The large difference between overall heat exchange in air and water, a seven-fold difference, results from the high specific heat of water. This emphasizes that aquatic reptiles would appear to have difficulty in maintaining body temperature higher than that of the water.

The heating and cooling curves obtained in air (table 2, fig. 1) are of particular interest because the typical reptilian pattern of slower cooling relative to heating was not observed in every case. In the first series of experiments, animal B heated faster than it cooled (fig. 1), and its heart rate was higher during heating than during cooling (fig. 2). It is interesting to note that animal E, which was active during the cooling phase of that experiment, heated and cooled at the same rate and also had the same heart rate during heating and cooling (table 2). In the second series, animal E behaved according to the typical reptilian pattern, whereas animal B cooled twice as fast as it heated. Rapid cooling has also been observed by Spray and May (1972) in two species of terrestrial turtle. They suggest that rapid cooling may be an ecological advantage in times of heat stress. We are unaware of any report in the literature where both accelerated and retarded cooling has been observed in the same species. Such flexibility of behavior is not unreasonable and warrants further investigation. Fresh-water crocodiles are probably subjected to heat stress in the surface waters of the billabongs where they live. In the summer, the surface water temperature may be very high (personal observation), and it is likely that a crocodile could benefit from being able to descend to deeper, cooler water and rapidly discharge its heat load. These speculations may find a firmer base when field studies are undertaken.

The experiments on heating and cooling in water confirm the hypothesis, as outlined in the introduction, that mechanisms of retarding heat loss or augmenting heat gain may be more in evidence in the water because of the high specific heat of water. Rates of heat exchange, expressed as the change in temperature per unit time, were approximately seven to eight times higher in water than in air. In both animals B and E, cooling was accompanied by a precipitous drop in heart rate (table 2, fig. 5). The lowest ratio of heating to cooling (0.75) was seen in an experiment carried out in water. This is not as low as the ratio seen in the marine iguana which was approximately 0.5 in both water and in air (Bartholomew and Lasiewski 1965). Weathers and White (1971), working on turtles, found lower heating: cooling ratios in water than in air.
3. HEAD TEMPERATURE

Some limited comments can be made on regulation of head temperature. Recent papers (Heath 1964; Webb and Heatwole 1971) have suggested that the regulation of head temperature may be an important aspect of reptilian thermoregulatory mechanisms. During heating in air, we observed that, at the end of heating, head temperature was always slightly lower than core temperature (fig. 3). In the controls the reverse was true. During heating in water, however, animal E showed three sharp drops in head temperature (fig. 6). In this experiment the animal was floating with the head at the water surface with the upper part in cooler air. Thus one would expect that head temperature would stabilize lower than core temperature, though closer to it than observed in the control. The three sudden drops in head temperature suggest an active cooling which could result from transient increase in respiratory rate leading to evaporative cooling in the nasal passages, or the release of cooled blood from the lungs in a manner postulated by Webb and Heatwole (1971). This question awaits further investigation.

4. CUTANEOUS BLOOD FLOW

The experimental results (fig. 8) clearly demonstrate local increase in cutaneous blood flow in response to heat applied at that site. Morgareidge and White (1969) and Weathers and White (1971) showed similar vascular responses in Amblyrynchus cristatus and Dipsosaurus dorsalis. Decreased blood flow on removal of heat is also apparent from the Xe133 washout curves. It seems likely that in Crocodylus johnstoni, as in other reptiles studied so far, rapid localized cutaneous vascular changes alter the peripheral thermal conductance and facilitate heat uptake or retard heat loss.

The cutaneous vasomotor responses occurred before any change in core temperature was observed. Thus, the vasodilation seems to depend on local thermal sensors rather than on the temperature of the central nervous system.

Morgareidge and White (1969) found heart rate to be independent of the cutaneous vasomotor response in the marine iguana. Accordingly, they suggested that higher heart rates observed during heating are secondary to the peripheral vascular changes. That is, overall heating induces generalized cutaneous vasodilation to which tachycardia is a compensatory reflex. In C. johnstoni, however, heart rate increased almost immediately with the local application of heat to either site. This suggests that tachycardia is a primary, not a secondary, response to cutaneous heating in the crocodile.

It seems then that there are two physiological responses to cutaneous heating: peripheral vasodilation and tachycardia. Both result in increased blood flow and a higher rate of heat transfer between core and periphery. Conversely, peripheral vasoconstriction and brachycardia during cooling would decrease heat flow from the animal.

In relation to these rapid local peripheral responses, one must consider the one experiment where heat loss occurred at twice the rate of heat gain. This would appear to be in direct conflict with the observations on peripheral blood flow, and this question must await further investigation.
LITERATURE CITED


