Cutaneous heat flow during heating and cooling in *Alligator mississippiensis*

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The purpose of this study was to measure the effects of heating and cooling on the rate of heat flow through the integument of the intact alligator. In addition, various drugs were used in an effort to determine the nature of neural control of cutaneous blood flow.

**METHODS**

Four alligators ranging in weight from 2.1 to 4.4 kg were obtained from the Rockefeller Wildlife Refuge, Grand Chenier, La. They were maintained in 1.5 x 1.5 m fiberglass tanks at 25°C ± 5°C and fed chopped rabbit. A dry basking site was available and 250-W lamps provided controlled photoperiod (12 h L:12 h D). Experimental animals were fasted and maintained at 30°C ± 1°C 2 wk prior to each experiment.

Yellow Springs Instrument Co. thermistor thermometer (model 43TD) and thermistor probes (400 series) were used to monitor stomach, subcutaneous, deep tail, surface tail, and ambient temperatures. Heart rate was determined by a strip-chart recorder (Nareo Bio Systems physiograph 4B). Heat flow was measured by tellurium-silver/copper heat flow disk (7) available from Ernest Turner Electrical Instruments, Ltd., Chiltern Works Totteridge, High Wycombe, Bucks, England. The microvolt output from the heat flow disks was measured on a model 95A Boonton sensitive DC meter.

Hypothermia ($T_h = 10°C$) was used for anesthesia. Two heat flow disks were implanted subcutaneously near the base of the tail (Fig. 1). Prior to implantation each heat flow disk was covered with a thin coat of dental acrylic to insulate it from the body fluid. The air/skin disk additionally had a stainless steel wire (no. 26 gauge) attached to its circumference to provide loops for attachment. One disk was approximately 5 cm posterior to the other. A third disk was sutured in place directly over the anterior one. Heat-conductive paste was applied between the skin and outer disk. In the Xylocaine experiment a fourth heat flow disk was positioned over the posterior subcutaneous disk. A thermistor was placed subcutaneously near the anterior heat flow disk. A second thermistor was positioned deep in the tail near the caudal vertebrae. A third thermistor was placed through the mouth into the stomach region posterior to the pectoral girdle. A fourth thermistor was placed laterally on the surface of the tail near the skin/air heat flow disk. The alligators were maintained at 30°C for 3-5 days after surgical implantation of the subdermal disks to allow recovery from hypothermia and surgery.

**RESULTS**

**Cutaneous Vasomotor Response**

Many reptiles can alter their rate of heat exchange with the environment. An increased rate of warming and reduction in heat loss during cooling enables reptiles to remain active at or near their preferred temperatures longer and thus better exploit their environment (13, p. 204).

Under controlled conditions of heating and cooling in air and water, the American alligator (*Alligator mississippiensis*) was found to heat more rapidly than it cooled (11). Indirect evidence (from telemetric measurements of free-ranging alligators) suggested that cardiovascular adjustments were responsible for the changes observed (10). Measurements of blood flow by $^{133}Xe$ clearance (9) demonstrated adaptive alterations in cutaneous blood flow in response to heating and cooling in the green iguana (1), the marine iguana (9), the spiny-tailed iguana (15), and in turtles (16).

The rate of heat exchange between an animal and its environment can be altered by changing the amount of peripheral perfusion. Measurements of the alteration of cutaneous blood flow in response to temperature describe a mechanism by which reptiles alter their rate of heat exchange, but do not provide indications of the magnitude of changes in thermal conductance. In physiological thermoregulation it is the concurrent alteration in thermal conductance of the integument that is adaptively significant. Measurements of cutaneous heat flow during heating and cooling of reptiles have not previously been made.
Individual alligators, with thermistors and electrocardiogram (ECG) electrodes attached, were restrained in the prone position in an environmental chamber at 15°C for 24 h prior to the measurements. The animals were positioned approximately 1 m from a fan that provided airflow of approximately 300 cm/s. Measurements were made while the animals were warmed to a body temperature of 35°C. The alligators were returned to the 15°C chamber and cooling responses observed. Relative humidity in both chambers was maintained at 70% ± 5% throughout the 24-h acclimation and experiment.

After one or more control experiments, atropine (0.5 mg/kg) was injected intraperitoneally and the experiment repeated. The intended effect of atropine was to remove vagal control of the heart, resulting in increased heart rate and possibly increased peripheral perfusion during cooling and thereby minimizing differences in heat exchange during heating and cooling (see discussion). After atropine treatment the animals were maintained at 30°C for 7 days to allow for the degradation and elimination of atropine. Phenoxylbenzamine (12 mg/kg) was injected intraperitoneally and the experiment repeated. It was hoped this drug would increase peripheral perfusion and the heat flow during cooling. Injections were given 1 h before the warming and cooling experiments. After the phenoxylbenzamine experiment the heat flow disks were removed. Animals used for autonomic blocking experiments were not used again for heat flow measurements. All animals recovered from the surgery and drug treatment with no apparent ill effects.

Nitroglycerin, a vascular relaxant, was administered by infusion into the external nares of one alligator and later intraperitoneally at rates of 0.004–0.2 mg/kg per min throughout the experiment. After a recovery period of 7 days at 30°C a fourth heat flow disk was attached directly over the posterior subcutaneous disk. Xylocaine (10 mg), a local anesthetic, was administered in multiple subcutaneous injections around the anterior subcutaneous heat flow disk 30 min prior to each experiment and at 30-min intervals during warming and cooling.

![Diagram showing placement of thermistor and heat flow disk in alligator.](http://ajplegacy.physiology.org/)

**RESULTS**

Under all experimental conditions the alligators heated more rapidly than they cooled confirming previous results (10, 11). Typical heating and cooling results are shown in Fig. 2. Similar results were obtained with the other animals. Drug treatment had no significant effect on rates of heating and cooling.

**Heat flow.** Cutaneous heat flow during warming exceeded heat flow during cooling and was proportional to the temperature across the skin. Figure 3 shows the relationship of heat flow and temperature across the skin. Alteration of heating and cooling values clearly indicates changes in the thermal properties of the skin.

Typical heat flow results are shown in Fig. 3. Heat flow between skin and air during heating exceeded subdermal heat flow ($P < 0.001$), but was not significantly different during cooling. Heat flow across the lone subcutaneous heat flow disk during cooling exceeded heat flow during warming ($P < 0.01$). Similar results were obtained with each of the alligators tested (See Table 1). None of the drugs used altered heat exchange rates.

**Autonomic blocking agents.** In two of the animals atropine did not alter heart rate significantly during the warming period compared with the same animal’s response during the control test. However, when the atropine-treated animal's heart rate was compared during warming and cooling it was found not to be significantly different in two of the three animals.
**Table 1. Comparison of heat flow during heating and cooling in air**

<table>
<thead>
<tr>
<th>Measurements</th>
<th>Body wt, g</th>
<th>Heat flow, cal/cm² per h</th>
<th>Skin/air (warm) – skin/air (cool)</th>
<th>Skin/air (warm) – muscle/skin (warm)</th>
<th>Skin/air (cool) – muscle/skin (cool)</th>
<th>Muscle/skin (heat) – muscle/skin (cool)</th>
<th>Muscle/skin (heat) – muscle/skin (cool)</th>
</tr>
</thead>
<tbody>
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<td></td>
<td>2,140</td>
<td>3.92</td>
<td>2.74</td>
<td>0.15*</td>
<td>-1.11</td>
<td>0.34*</td>
<td>-0.18*</td>
</tr>
<tr>
<td></td>
<td>3,320</td>
<td>2.60</td>
<td>2.14</td>
<td>-1.11</td>
<td>0.34*</td>
<td>-0.09*</td>
<td>-1.02*</td>
</tr>
<tr>
<td></td>
<td>4,360</td>
<td>2.33</td>
<td>2.76</td>
<td>0.34*</td>
<td>-0.09*</td>
<td>-0.09*</td>
<td>-0.09*</td>
</tr>
</tbody>
</table>

Drug treatment did not significantly alter heat flow comparisons. Mean heat flow differences are presented. * Not significant at 0.05 level. † With no skin/air disk over muscle/skin disk.

The same animals were restudied after treatment with phenoxybenzamine. One of the three animals had a significantly higher heart rate during the warmer period compared with control values. There was no consistent change in heart rate in any of the animals during cooling compared with control values. With phenoxybenzamine treatment each of the animals had a significantly (P < 0.001) higher heart rate during warming than during cooling.

**Nitroglycerin and Xylocaine.** A procedure similar to that described above was followed with an animal treated with nitroglycerin and Xylocaine. There were no significant changes in heart rate or heat exchange rate in either the heating or cooling period compared with control values.

**Discussion**

Biologists have been aware of the importance of thermal conductance to reptilian thermoregulation for some time. Thermal conduction was calculated from indirect measurements (2–4, 8) and used in modeling (5, 12).

**Cutaneous water loss.** It has been established that the integument of reptiles, including alligators, is not impervious to water. In this study relative humidity was maintained at 70% in both the warming and cooling experiments to approximate natural conditions. This presents the alligator with dissimilar conditions with respect to water vapor pressure during the two experiments. During the cooling experiment a warm (35°C) alligator is thrust into a cool (15°C), relatively dry environment. Cutaneous evaporative cooling would be expected, especially during the initial portion of the experiment, when the water vapor pressure deficit is greatest. Since the heat flow disk was impervious to water and was in contact with the skin, the effect of evaporative cooling was not observed in the measurement of heat flow. One might suspect this then represents an altered measure of heat flow because alligator skin normally does experience water loss and cooling by evaporation.

It should be noted, however, that the effects of evaporation would be most pronounced during the early portions of an experiment, when the water vapor pressure deficit is greatest, and one would expect an initial rate of cooling greater than the rate observed near the end of an experiment if evaporation was a problem. No such effect was observed (see Figs. 2 and 4). Heat flow due to cutaneous water loss at 25°C and with a water vapor pressure deficit of 14.8 mmHg (corresponding to experimental conditions) can be estimated (12) at 0.72 cal/cm² per h in still air. It is unlikely that this rate could be as much as doubled by the flowing air but even if this was the case the evaporative losses would still be considerably below the mean measured value of 13.6 cal/cm² per h.

During the warming experiment a cool (15°C) alligator is thrust into a warm (35°C), moist environment with a dew point of 28.7°C. During a large portion of the experiment (15–28°C) the alligator was covered with a very thin film of condensed water. Under these conditions evaporation was obviously not occurring and the heat flow measurements were again correct and representative of heat flow in adjacent alligator skin. That the effect of the water layer was negligible in altering the thermal time constant of the alligator is again clearly indicated by the temperature changes during warming shown in Fig. 2. If the effect of the water were a large fraction of the convection heat transport the alligator would show an altered rate of body temperature change above and below the dew point and also an altered heat flow rate (see Fig. 4).

Heat exchange values between the skin and air during warming exceeded those during cooling (Figs. 3 and 4, Table 1). Figure 3, showing heat flow plotted as a function of the temperature drop across the skin, eliminates any effects of evaporation or condensed water and shows clearly that skin thermal conduction is greater during warming. This is necessary if the rate of heating is to exceed the rate of cooling. The mean of the skin/air heat flow measurements for the three alligators during cooling (13.6 cal/cm² per h) was approximately 76% of the mean of the three central skin/air measurements during warming (17.9 cal/cm² per h).

![Figure 4. Relationship of heat flow to temperature difference between animal (Tₐ) and ambient (Tₐ). Solid lines indicate heat flow between air and skin. Broken lines indicate heat flow between skin and muscle directly under skin/air heat flow disk. Dotted lines indicate heat flow between skin and muscle without skin/air heat flow disk.](http://ajplegacy.physiology.org/Downloadedfromhttp://ajplegacy.physiology.org/10.1152/jn.01315.2014.on April 1, 2017)
This is in agreement with the observation that the three alligators heated in 77% of the time required for cooling (Table 2). Thus changes in cutaneous heat flow were sufficient to account for changes in rates of heat exchange of the alligator. It is likely that metabolic heat production becomes important in large animals with their lower surface-to-volume ratio.

The rate of heat flow from the air to skin exceeded the rate of heat flow between skin and underlying tissue during warming (see insert in Fig. 1). Heat passed through the outer disk first, then through the subcutaneous disk. Without cutaneous perfusion, the two disks would show similar values of heat flow. During warming, however, the outer disk indicated a significantly greater heat flow than did the inner disk. This observation indicates an alternate path for heat flow that bypassed the inner disk, suggesting blood flow between the disks. Blood of approximately the same temperature flowed on both sides of the inner disk, effectively shunting a portion of the heat around it. Alternately, blood between the disks carried heat away from the outer disk, increasing the quantity of heat flow during warming.

The two heat flow disks in series did not show a significant difference during cooling, indicating there was no longer an alternate path for heat flow. Furthermore, this observation suggested a reduction in cutaneous blood flow and provides an explanation for the greater time required to cool. Reduction in the rate of warming during disturbance bradycardia provided evidence for the importance of blood flow in heat exchange (11).

The lone subdermal disk (Fig. 1) generally indicated lower values than the subdermal disk with the outside disk (Fig. 4). This may have been the result of increased thermal exchange of the skin/air disk due to its greater surface area and the air turbulence over its surface. The thermal characteristics of the surface disk were different from living alligator skin both in texture and color.

The isolated subdermal disk indicated greater heat flow during cooling than during warming. This was to be expected. During cooling, heat is lost largely by thermal conduction through the skin. Cutaneous perfusion was low and increased in response to heat. The subdermal heat flow disk was bathed on both sides with blood of similar temperature during warming and heat flow through the disk decreased.

Heat flow (cal/cm² per h) presented here may be compared with previously published thermal conductance values (cal/cm² per h per °C) by dividing by the (Tₐ - Tₓ) temperature drop. At the body midtemperature (25°C) in this study 10°C was dropped.

Previously published calculated values of thermal conductance (12) were considerably lower than measured values. Thermal conductance between the ground and an alligator with a fat thickness of 0.7 cm was calculated to be 0.0097 cal/cm² per min per °C. This is equivalent to 0.58 cal/cm² per h per °C. Mean measured values in this study (AT of 10°C, airspeed of 300 cm/s) were 17.9 and 13.6 cal/cm² per h during warming and cooling, respectively (see Table 2). This is equivalent to 1.79 and 1.36 cal/cm² per h per °C during warming and cooling, respectively. One would expect even higher values for conduction from a solid substrate. Spotila et al. (12) ignored the influence of cutaneous blood flow and assumed heating and cooling rates were similar. Their calculated values were 32 and 49% of the measured warming and cooling values, respectively, and are probably below the values for a dead alligator. Dead alligators were found to heat and cool more slowly than living animals. One 730-g alligator heated and cooled when alive in 60 and 78% of the time required for heating and cooling when dead (11). In modeling reptilian thermoregulation the influence of cutaneous blood flow and the alteration of blood flow in response to recent thermal history should not be ignored.

Thermal conductance from the present study of 1.79 and 1.36 cal/cm² per h per °C during warming and cooling, respectively, may be compared to previously published values in units of ml O₂/g per h per °C by conversion. The caloric equivalent of 4.7 cal/ml O₂ and specific heat of 0.82 is assumed. The relation of surface area to volume of A = 10 W²/³ (A is surface area in cm² and W is weight in g) was used to convert weight-specific values of conductance to surface-area-specific values.

Table 3 shows a comparison of calculated conductance from various sources and measured values from this study. Caution needs to be observed in applying the above conversion to birds and mammals, with their
reduced surface area. Also the last three entries were obtained in still air and should be approximately doubled for comparison with the results obtained in moving air (2, 3).

As Table 3 illustrates, the ratio of cooling-to-heating thermal conductance for the alligator is smaller than that of other animals studied. This indicates that the alligator has relatively greater control over its thermal conductance and thus possesses a higher degree of physiological thermoregulation than other reptiles studied. As had been stated before (2-4, 8) ectotherms tend to have a relatively higher thermal conductance and lower metabolism than endotherms. The present study clearly supports that thesis.

Radiotelemetric studies (10) showed a significantly greater temperature drop across the skin during pre-basking compared with the postbasking period. This was interpreted to be a result of reduced peripheral blood flow during suboptimal temperatures. Heating and cooling experiments under laboratory conditions (11) added validity to the field study (10) by again showing a greater temperature drop across the skin during cooling. In this study there was a consistently greater temperature difference between the deep tail and subcutaneous thermistors during cooling compared with warming values. Again this is evidence of reduced blood flow during cooling. These results demonstrated the utility of multiple temperature measurements as an indirect measure of thermal conductance and blood flow.

Drug treatment. In mammals atropine blocks the action of acetylcholine at the cholinergic receptor sites in smooth and cardiac muscles. If the action in alligators were similar, one might expect heart rate, cardiac output, and perhaps peripheral perfusion to increase, resulting in increased cooling rates and thus a minimized difference in heating and cooling rates. These postulated responses of heat exchange were not observed. However, in two of the three animals tested, the heart rates during cooling were as high as those during warming. This suggests that vagal influences were active during cooling and normally contributed to the cooling-evoked bradycardia. As might be expected heart rate during warming was unaffected. Atropine was ineffective in altering heat exchange rates in the alligator, suggesting that parasympathetic control of heart rate alone was not sufficient to alter cutaneous blood flow and heat exchange. Similar results were reported by Weathers and White (16) for the turtle *Chelydra serpentina*.

Phenoxybenzamine is a sympathetic blocking agent affecting alpha receptors in mammals. Based on evidence obtained in mammals, this drug would not be expected to directly affect heart rate but it should modify peripheral vasoconstriction and might result in a reflex increase in heart rate. However, the present study showed no consistent changes in heart rate. Importantly, phenoxybenzamine did not alter rates of heat exchange. This is in contrast to results obtained by Weathers (14) in a lizard, *Dipsosaurus dorsalis*, for he obtained significant alteration of both heart rate and heat exchange with the peripheral sympathetic blocking agent bretylium tosylate.

A mammalian vascular relaxant, nitroglycerin, had no effect on the heart rate of heat exchange in the alligator. This may indicate that the dosage was ineffective or that absorption from the site of introduction was inadequate to exert an effect. It may also indicate a species difference in the drug’s action (6). Little is known about neural control of muscle (vascular and cardiac) function in reptiles. Understandably, negative results with one drug and one species may lack general interspecific application. The observation that atropine did block a decrease in heart rate during cooling of the alligator strongly suggested some vagal control of the heart of these animals. Xylocaine had no significant effect on heat exchange in the alligator, nor did it affect the disappearance rate of $^{133}$Xe from the dewlap of *Iguana iguana* found by Baker et al. (1). They interpreted their data as indicating that central neural connections were nonessential in the local response to heating and cooling.

Two problems arise in using the $|T_a - T_b|$ temperature drop. First, no one value of $T_b$ adequately describes a living animal. Various parts of the body are at different temperatures and have unequal values of specific heat. This introduces an undefined error in whole-body conductance values.

Second, $|T_a - T_b|$ is not an accurate estimate of the temperature drop between an animal and the environment. In still air, and to a lesser extent in moving air, there exists a convection layer of air next to the skin across which is a considerable temperature drop. A much more useful measurement would be a measure of skin surface temperature.

In describing (and comparing) physiological alteration of cutaneous thermal conductance, the temperature drop across the skin, $|T_a - T_n|$ (subcutaneous – surface) would be more meaningful. Although the whole-body effect is adaptive to the animal it is the skin conductance that is being modulated physiologically.

In this study approximately 3.5°C was dropped across the skin at the midtemperature (Fig. 3). This provides skin conductance values of 5.11 and 3.89 cal/cm² per h per °C during warming and cooling, respectively. These values are obviously higher than those in the literature.

<table>
<thead>
<tr>
<th>Species</th>
<th>Weight, g</th>
<th>Air Speed, cm/s</th>
<th>$T_a$, °C</th>
<th>Conductance, cal/cm² per h per °C</th>
<th>Ratio</th>
<th>Ref</th>
<th>Present Study</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alligator mississippiensis</em></td>
<td>3,273</td>
<td>230</td>
<td>25</td>
<td>1.76</td>
<td>1.38</td>
<td>0.78</td>
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</tr>
<tr>
<td><em>Amblyrhynchus cristatus</em></td>
<td>373</td>
<td>240</td>
<td>25</td>
<td>2.55</td>
<td>2.14</td>
<td>0.84</td>
<td>2</td>
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<tr>
<td><em>Tiliqua scincoides</em></td>
<td>512</td>
<td>136</td>
<td>30</td>
<td>1.35</td>
<td>1.33</td>
<td>0.97</td>
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<tr>
<td><em>Veranus gouldii</em></td>
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<td>270</td>
<td>25</td>
<td>1.54</td>
<td>1.65</td>
<td>1.07</td>
<td>3</td>
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<tr>
<td>Theroretical varanid lizard</td>
<td>3,273</td>
<td>330-380</td>
<td>30</td>
<td>1.84</td>
<td>1.98</td>
<td>1.07</td>
<td>3</td>
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<tr>
<td>Theroretical mammal (24 species)</td>
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<td>0.12</td>
<td>0.92</td>
<td>0.92</td>
<td>1.00</td>
<td>3</td>
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<tr>
<td>Theroretical bird (31 species)</td>
<td>3,273</td>
<td>0</td>
<td>0.09</td>
<td>0.81</td>
<td>0.90</td>
<td>1.00</td>
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<tr>
<td>Theroretical bird (plucked)</td>
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<td>0.72</td>
<td>0.72</td>
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<td>Theroretical bird (skinned)</td>
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<td>0.90</td>
<td>0.90</td>
<td>1.00</td>
<td>6</td>
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</table>

* Assuming 1) specific heat of 0.82; 2) 4.7 cal/mg°C; and 3) area (cm²) = 10 W (g°C)*² (see text).
due to the use of $|T_a - T_s|$ instead of $|T_a - T_b|$, but more accurately describe the actual physiological alteration of cutaneous thermal conduction.

**Conclusion.** Direct measurement of heat flow across the skin of living alligators provided evidence that these animals are able to control the rate of heat exchange with the environment by altering the amount of cutaneous perfusion. This was reported in other reptiles and is probably widespread. It is adaptive in shortening the required basking time and lengthening the amount of time the animal is at a preferred temperature. Measured thermal conductance was similar to that reported by indirect measurement for varanid lizards and 10–20 times higher than values obtained indirectly in still air. minion perfusion. This was reported in other reptiles and

REFERENCES


