

BLOOD FLOW TO APPENDAGES AND THE CONTROL OF HEAT EXCHANGE IN AMERICAN ALLIGATORS

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Small American alligators (200–400 g) were heated and cooled from 20 to 35 to 20 C in a temperature-controlled wind tunnel. Blood flow to the limbs and tail was periodically occluded, using remotely controlled occlusion cuffs. When blood flow in all appendages was occluded, the rate of heating was significantly reduced from that when blood flow was unrestricted. The rate of cooling was not significantly affected by occlusion of blood flow in all appendages, however. Blood flow to appendages, rather than a generalized perfusion of the skin, appears to be primarily responsible for the differences in the rates of heating and cooling in alligators.

INTRODUCTION

The control of energy exchange in reptiles has been the object of considerable interest for biologists since the prescient work of Cowles (1958). In a series of ingenious experiments, Cowles noted that the lizard *Dipsosaurus dorsalis* warmed substantially faster than it cooled and also showed that blood flow to the skin increased simultaneously during warming. He postulated that this adjustment in the circulation was responsible for the difference in heating and cooling rates. Since then, differences in rates of heating and cooling and concomitant cardiovascular adjustments have been described for a number of species spanning three orders of the class Reptilia (see White [1976] and Smith [1979] for reviews).

It has often been tacitly assumed that a simple redistribution of cardiac output to the surface of the body is sufficient to explain the differences between heating and cooling rates in reptiles. However, there is growing evidence that physiological control of heat exchange by blood flow is not so simple.

For example, the distributions of temperature within the bodies of lizard-shaped reptiles (those reptiles with limbs, a long tail, and a fusiform torso) during changes in body temperature are complex. The temperatures of the appendages behave differently during temperature transients from the temperature of the torso (Brattstrom 1968, 1973; Drane, Webb, and Heuer 1977; Turner, Ham-

mond, and Tracy 1980; Turner and Tracy 1980). Also, the thermal interactions between the appendages and the environment are sufficiently different from those of the torso to suggest that appendages may be much more effective sites for control of heat exchange, particularly in small animals (Turner et al. 1980; Mitchell et al., in preparation). These observations suggest that control of heat exchange by blood flow may arise from a complex interaction among body size, body shape, and the regional flow of blood. We report here results of experiments which demonstrate the importance of blood flow to appendages in the control of heating and cooling rates in young American alligators (*Alligator mississippiensis*).

MATERIAL AND METHODS

MEASUREMENTS OF APPENDAGE BLOOD FLOW

Blood flow in the forelimb, as measured in the brachial artery, was measured using a 20-MHz Pulsed Ultrasound Doppler Velocity Meter (PUDVM, Hartley Mfg., Houston, Texas). In the alligator, almost all of the forelimb vasculature is perfused by the brachial artery (Reese 1915). Therefore, changes in brachial artery blood flow should reflect changes in total perfusion of the appendages.

Measurements of forelimb blood flow were done in a refrigerated cold room in which air temperature was maintained at 10–15 C. The animal was heated using a 250-W incandescent flood lamp suspended 60 cm above the back of the animal. Cooling of the animal was initiated by switching off the lamp and switching on the fan of the room's refrigeration unit.

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Colonic temperature was sensed with a 20-gauge copper-constantan thermocouple inserted 1–2 cm into the colon. Temperature of the thermocouple was measured with a TH-60 thermocouple thermometer (Wescor, Logan, Utah).

Output from the PUDVM was amplified, using a DC differential amplifier, and recorded on a two-channel Brush oscillographic recorder. Calibrations of the instrument and chart recorder were accomplished electronically.

The probe of the PUDVM (a 0.3-mm² piezoelectric crystal) must be accurately positioned with respect to the artery in which blood flow is being measured. The probe was held by a stereotaxic instrument that afforded linear movement in three dimensions and radial movement through one plane. A cast of plastic surgical webbing was placed about the shoulders and left forelimb and around the pelvis. The animal was then clamped into a frame made from aluminum bar stock. Three buret clamps were used to immobilize the animal, one each at the shoulders, pelvis, and distal left forelimb. This was sufficient to maintain rigid alignment of the probe and artery.

OCCLUSION OF APPENDAGE BLOOD FLOW

Six small (200–400 g) American alligators (*Alligator mississippiensis*), hatched from eggs and reared in our laboratory, were used as the subjects of the experiments described below. Animals were warmed and cooled in a temperature-controlled wind tunnel. Temperatures of the body (measured 1–2 cm into the colon) and air were measured with 20-gauge copper-constantan thermocouples and transduced with a digital thermocouple thermometer (Wescor TH-60). Blood flow in the appendages was occluded during the experiments by remotely controlled occlusion cuffs. This allowed occlusion periods of relatively short duration while eliminating the need for opening the wind tunnel or otherwise manipulating the animal during the course of an experiment.

We performed two different experiments, using different occlusion protocols in each. In the first experiment (simul-

taneous occlusion), the alligator was outfitted with a colonic thermocouple and occlusion cuffs at the bases of all four limbs and the tail. The animal was then taped to a small Plexiglas platform that was designed to hold it in the center of the wind tunnel, where the airflow was laminar. The alligator was placed into the wind tunnel, and internal air temperature lowered to 20 C. Wind speed was maintained at a constant 2 m/s. The alligator was allowed to equilibrate to air temperature for at least 1 h. Then, air temperature was raised to 35 C, and the animal was allowed to warm for 45 min (sufficient time for the animal to thermally equilibrate). At that time, air temperature was lowered again to 20 C, and the animal was allowed to cool for 45 min.

After an initial 5-min period of temperature change, blood flow in all appendages was repeatedly occluded for 5-min intervals, followed by 5 min of unrestricted blood flow. There were four such cycles of occlusion and unrestricted flow for the periods of heating and cooling. Air and colonic temperatures were monitored at 1-min intervals. Heating and cooling rates for each 5-min interval of occlusion or unrestricted flow were expressed as the equilibration rate, E , defined as

$$E = d\{-\ln [(T_t - T_\infty)/(T_0 - T_\infty)]/dt\}, (1)$$

where E = equilibration rate, T_t = temperature at any time, t , during the transient, T_0 = temperature at the beginning of the transient, and T_∞ = temperature at equilibrium.

Occlusion of blood flow in the first experiment might have been stressful or might otherwise have frightened the alligator, causing a general peripheral vasoconstriction. Thus, we conducted a second experiment (intermittent occlusion) to control for such a complication. The alligator was prepared as in the first experiment; however, occlusion cuffs were fitted only at the base of the left forelimb, right hind limb, and tail. Heating and cooling in this experiment were identical with the first, but the occlusion protocol was slightly different. After an initial 5-min period of temperature change, blood flow in the left forelimb only was

occluded for 2 min. Then, blood flow was restored in the forelimb and occluded in the right hind limb only for 2 min. Then blood flow was restored to the hind limb and occluded in the tail only for 2 min. The cycle was repeated six times during the course of the temperature transient. Equilibration rates were calculated for the entire 45-min period of temperature change, using equation (1).

Mean equilibration rates were calculated for six treatment groups: heating—no occlusion; heating—intermittent occlusion; heating—simultaneous occlusion; cooling—no occlusion; cooling—intermittent occlusion; cooling—simultaneous occlusion. Differences between treatment groups were assessed using a one-way analysis of variance. The Honestly Significant Difference (HSD) among treatments was calculated for $P = .05$, using Tukey's Multiple Range Comparison procedure (Sokal and Rohlf 1969).

RESULTS

APPENDAGE BLOOD FLOW

Representative results for brachial artery blood flow in one individual are shown in figure 1. During warming (upward-pointing arrows), blood flow in the brachial artery increases. During

cooling, however (downward-pointing arrows), blood flow in the brachial artery declines (fig. 1).

OCCUSION OF APPENDAGE BLOOD FLOW

Simultaneous occlusion of blood flow in all appendages depresses the equilibration rate during heating from that when flow in all appendages is unrestricted. During cooling, simultaneous occlusion of blood flow in all appendages has no effect on equilibration rate (fig. 2). Intermittent occlusion of only a single appendage at a time during both heating and cooling has no effect on rates of temperature change, each being equivalent to its respective equilibration rate when flow is unrestricted (fig. 2).

DISCUSSION

Appendages have long been recognized as important sites for the control of heat exchange in mammals and birds (Turner 1982). In addition, there are numerous examples of other parts of the body serving as "ancillary" sites for the control of heat exchange, such as the large pinnae of desert hares (Hill and Veghte 1976), the horns of goats (Taylor 1966), the bills of ducks (Hagan and Heath 1980a, 1980b)

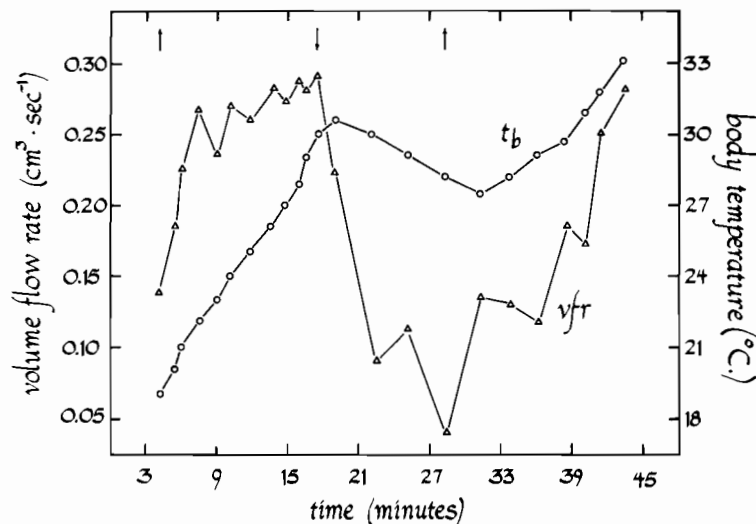


FIG. 1.—Volume flow rate in the brachial artery of a small American alligator during bouts of heating and cooling. Blood flow measurements were made transcutaneously using a 20-MHz Pulsed Ultrasound Doppler Velocity Meter. Open circles signify body temperature. Open triangles signify volume flow rate. Upward-pointing arrows signify the initiation of heating. The downward-pointing arrow signifies the initiation of cooling.

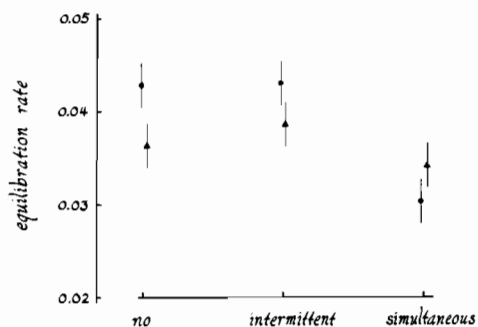


FIG. 2.—Equilibration rates for no appendage occlusion, intermittent appendage occlusion, and simultaneous appendage occlusion, during heating and cooling. Circles represent mean equilibration rates for heating; triangles represent mean equilibration rates for cooling. Vertical bars represent the Honestly Significant Difference for the test, calculated at $P = .05$. Results of one-way analysis of variance: all treatments, $F(5, 30) = 19.74$, $P < .05$. Hierarchical test for simultaneous vs. no occlusion only: levels, $F(3, 20) = 10.123$, $P = .0005$; samples, $F(20, 72) = 1.038$, $P = .4321$.

and the large dorsal projections that characterize some extinct reptiles, such as *Stegosaurus* (Farlow and Thompson 1976) or *Dimetrodon* (Bramwell and Fellgett 1973; Tracy, Turner, and Huey, in press). However, this subject has received relatively little attention in living reptiles, aside from reports of presumed augmentation of evaporative heat loss caused by urination or defecation on the legs during thermal crises (Riedesel, Cloudsley-Thompson, and Cloudsley-Thompson 1971; Cloudsley-Thompson 1974; Sturbaum and Riedesel 1974).

Yet there is no reason why blood flow to appendages should not be equally important to control of heat exchange for reptiles as it is for endothermic animals such as birds or mammals. The physical laws governing heat exchange will be the same regardless of whether an animal is ectothermic or endothermic. Consequently, the same factors which impel endotherms to use their appendages as sites for the control of heat exchange (such as large surface-volume ratio, small boundary layers for convection, etc.) should apply equally well to ectotherms. Indeed, reptiles may control heat exchange at their appendages as an adjunct to behavioral thermoregulation. A familiar example is the contortions of the hind limb of certain

turtles during basking, so that the webbing of the foot is exposed to the environment (Boyer 1965). Some authors argue persuasively that this behavior serves purposes other than thermoregulation, such as destruction of ectoparasites (Cagle 1950) or epizoitic algae (Neil and Allen 1954). However, there is no obvious reason why it could not serve for thermoregulation at the same time. Interestingly, similar contortions of the hind limbs during basking are seen in certain Australian skinks of the genus *Egernia* (Sharon Fraser, personal communication). In addition, many lizards, including Galapagos marine iguanas (*Amblyrhynchus*) and Galapagos land iguanas (*Conolophus*) often adopt postures during basking in which the limbs are prominently sprawled away from the body and are fully exposed to the sun (Howard Snell and Heidi Snell, personal communication). Also, warming the bodies of lizards (*Iguana iguana*, 2–3 kg, and *Tupinambis nigropunctatus*, 1–2 kg; Baker, Weathers, and White 1972) and alligators (fig. 1) is accompanied by marked increases of limb perfusion, above that when body temperature is constant or declining.

Thus, the use by reptiles of appendages for physiological thermoregulation may be more widespread than the attention paid to it in the literature suggests. Unfortunately, no studies on reptiles have simultaneously considered both blood flow and distributions of heat within the appendages, so that the relative importance of circulation in different regions of the body for control of heat exchange can be evaluated. Rather, the published literature on rates of heating and cooling in reptiles often tacitly assumes that a simple increase of blood flow to the skin is always sufficient to increase rates of heating.

However, the importance of blood flow to the internal transfer of heat is affected by both body size and shape. Heat transfer by internal conduction is more important in animals with small torso diameter than in larger animals. Indeed, in animals as small as 1–2-cm torso diameter, conduction of heat within the torso might be so efficient that variations in blood flow will have little impact on exchange of heat within the torso (Mitchell et al., in prepara-

ration; Tracy et al., in press; and Turner and Tracy, in press). Likewise, conduction heat transfer between the core and appendages is always less efficient than that between the core and surface of the torso, because of the relatively small cross-sectional area through which heat is transferred to the appendages. Because conduction of heat along this route is usually inefficient, changes in the rate of blood flow to the appendages can have a substantial impact on the total heat transfer between the appendages and torso. In addition, the appendages will always be more efficient heat exchangers with the environment than the torso; we therefore would expect appendages always to be favored sites for control of heat exchange by blood flow.

The results reported here suggest that control of blood flow to the appendages is of paramount importance in the control of heat exchange by small alligators. Appendage perfusion during warming is very high, while during cooling, it drops to very low levels (fig. 1). If high rates of appendage perfusion during warming are the principal reason for a rapid rate of warming, occlusion of appendages during warming should bring about a large reduction in the rate of warming. This is precisely the result (fig. 2); elimination of appendage perfusion substantially lowers the animal's rate of warming to a level comparable to that at which it cools. Conversely, we would expect appendage occlusion to have little effect on rate of cooling, simply because appendage perfusion is already very low. Again, this is precisely the result; occlusion of appendage blood flow does not significantly reduce cooling rate from that when appendage blood flow is unrestricted.

To what extent could this interpretation of our results be confounded by the alligator's becoming frightened by the operation of the occlusion cuffs? Simultaneous application of pressure cuffs on all

the appendages may have been sufficiently stressful to elicit a general peripheral vasoconstriction similar to that occurring during "fright dives" (Anderson 1961; Gaunt and Gans 1969). However, it appears that the cardiovascular correlates of fright in reptiles subjected to stimuli like those in this experiment simply are not adequate to explain our results. For example, when the tails of restrained painted turtles (*Pseudemys scripta*) are pinched, there is an immediate drop in systemic blood flow and a simultaneous rise in pulmonary perfusion, arterial pressure, and peripheral resistance (White and Ross 1965). However, these animals begin to show signs of habituation to this stimulus after only 40 s of sustained tail pinch (fig. 5 in White and Ross [1965]). For this type of fright reaction to have affected the heating and cooling rates of the animals in this experiment, the cardiovascular changes would have had to have been sustained and substantial.

The experiment in which only one appendage was occluded at a time was almost certainly a sufficient control against a possible fright response. The position of occlusion was continuously changed and was changed more frequently than in the simultaneous occlusion experiment. Thus, the animal would have been less apt to become habituated to the stressful stimulus. If the reduction in heating rate during simultaneous occlusion of blood flow in all appendages were the result of peripheral vasoconstriction induced by fright, we would expect intermittent occlusion to also produce a substantial reduction in warming rate, comparable to that during simultaneous occlusion. This is clearly not the case, however (fig. 2). The only reasonable explanation for our results appears to be that blood flow to the appendages was entirely responsible for the difference in heating and cooling rates.

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