Physiological responses of the lizard *Sauromalus obesus* to changes in ambient temperature

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CRAWFORD, EUGENE C., JR., AND GEOFFREY KAMPE. Physiological responses of the lizard *Sauromalus obesus* to changes in ambient temperature. Am. J. Physiol. 220(5): 1256-1260. 1971.—Animals were subjected to ambient temperatures from 26 to 43.5 °C. Body temperatures remained 0.2-0.7 °C above ambient. Cutaneous evaporation increased from 2.0 to 9.5 mg H$_2$O/cm$^2$-day, with a $Q_{es}$ of 2.43. Respiratory evaporation increased with a $Q_{es}$ of 3.96 to 40 °C (from 1.3 to 8.0 mg H$_2$O/g-day). Between 40 and 43.5 °C, respiratory evaporation increased abruptly to 38 mg H$_2$O/g-day. A change in respiratory pattern was associated with the increase in respiratory evaporation. The mouth opened, tidal volume decreased to one-third its initial value, respiratory rate increased 5 times, and pulmonary ventilation doubled. At 43.5 °C 45% of the metabolic heat production was dissipated by respiratory evaporation and 66% was dissipated by total evaporation. The thermal conductance of 1 cal/cm$^2$-hr-°C is about 3 times that of mammals of comparable size. The respiratory pattern is similar to that observed in panting homeotherms.

**MATERIALS AND METHODS**

We made simultaneous measurements of $O_2$ consumption, cutaneous evaporation, respiratory evaporation, ambient temperature, body temperatures, respiratory rate, and tidal volume. Figure 1 shows the experimental arrangement.

A chamber partitioning the animal's head from the rest of the body was housed in a temperature cabinet so that ambient temperature could be controlled (±0.5 °C). Ncopenre gaskets on both sides of plate (B) were attached to the lizard's neck with dental latex (Rubberjel), insuring an air tight seal between anterior ($C_1$) and posterior ($C_2$) chambers. An open-circuit airflow system was employed. Room air, dried by passing through drying columns ($D_1$ and $D_2$) and a Dry Ice-ethanol mixture, was pulled through the chambers. The excurrent air from $C_1$ was passed through a Dry Ice-ethanol mixture, freezing out water evaporated from the head of the animal. Evaporative water loss from the remainder of the body was similarly collected from the excurrent air of $C_2$ and weighted (±1.0 mg). To obtain respiratory evaporation, estimated surface of the head was subtracted from the total surface of the animal (cm$^2 = 10^{1.22}$) (3). Evaporation from the remainder of the body surface determined. This value was used to calculate evaporation from the skin of the head which was subtracted from evaporation in $C_1$ and added to evaporation in $C_2$. The area included within the neck seal was less than 3% of the total skin area and was neglected.

Air from $C_1$, after drying, was passed through an oxygen analyzer (Beckman G-2) and the $P_{O_2}$ in the excurrent air was continuously recorded. Mean oxygen consumption during the experimental period was computed by planimetric integration of the record. Auxiliary drying columns ($D_3$ and $D_4$) were present so that $P_{O_2}$ could be monitored without passing air through the freezing column. Deep-body
and chamber (C2) temperatures were recorded from copper-
constantan thermocouples.

Pressure fluctuations occurred in C2 as the animal breathed. These were sensed by a pressure transducer, the output of which was recorded by a Gilson polygraph. Solenoid valves (S1 and S2), activated by a timing switch, were closed for 2 of every 30 min, rendering C2 airtight so that pressure changes could be converted to volume.

To ensure linearity of response, the calibration of the oxygen analyzer was tested with standard gases (purchased and analyzed, ±0.05%) prior to each experiment. Temperature recordings from thermocouples were accurate to 0.2 C. Calibration with a standard thermometer revealed no differences between thermocouples, so that differences in temperature could be estimated to 0.1 C. The pressure transducer was calibrated with the lizard in situ by injecting known volumes of air into C2 with the solenoid valves closed. Calibration varied with the size of the lizard and the state of inflation of the lung; however, changes in volume of 0.1 ml could be detected. Water collection, tested by evaporating known amounts of water into the system, revealed a recovery of 106% (±5.0%). A second drying tube arranged in series collected no additional water, showing that recovery was complete in the first tube.

Animals (Sauromalus abesus), obtained through a commercial supplier, were maintained on a diet of lettuce and dog food and remained apparently healthy throughout the experiments. Their mean weight was 140 g, range 96-210 g. No effort was made to render the animals postabsorptive nor was an RQ correction applied in the calculation of oxygen consumption. Values for oxygen consumption, expressed at STPD, were converted to heat production using 4.85 Cal/ml O2. Cloacal thermocouples were inserted to a depth of 3 to 4 cm and the vent was sealed with Rubberjel to prevent urinary and fecal water loss. Experimental animals were placed in the darkened apparatus and, after attaining temperature equilibrium, a further equilibration period of 1 hr was allowed before the start of a 2-hr experimental period.

RESULTS AND DISCUSSION

Figure 2 shows the relationship between body temperature and cutaneous evaporation. Since reptiles have no sweat glands, cutaneous evaporation is a function of vapor pressure deficit across the skin and is limited by cutaneous permeability. Vapor pressure increases with increasing temperature and cutaneous evaporation rises with a Q10 of 2.43 from 2 mg H2O/cm2·day at 26 C to 9.5 mg H2O/cm2·day at 43.5 C. The values reported here are about twice those obtained by Bentley and Schmidt-Nielsen (4), who determined cutaneous evaporation from Sauromalus in still air at 23 and 40 C. The values plotted in Fig. 2 were obtained from a continuous-flow system in which the relative humidity of the excurrent air of both front and rear chambers was maintained below 10%. The increase in airflow reduces the boundary layer of air surrounding the animal, thus providing greater opportunity for evaporation at higher temperatures.

As body temperature increased from 26 to 40 C, respiratory evaporation increased from 1.3 to 8 mg H2O/g·day (Fig. 3). The Q10 for respiratory evaporation (3.96) is greater than that for cutaneous evaporation (2.43). This increase in evaporation can be attributed to two factors: a) the increase in vapor pressure which is essentially the same in both chambers, and b) the increase in ventilation necessary to meet increasing metabolic demands. At 43.5 C there is an abrupt increase in respiratory evaporation to 38 mg H2O/g·day. This might be due to an increase in ventilation because of a dramatic rise in metabolism at 43.5 C. However, Fig. 4 shows that as body temperature was elevated oxygen consumption increased predictably with a Q10 of 2.23. There is no unexpected increase in metabolism between 40 and 43.5 C. Values at 26, 30, and 40 C were used to determine the Q10. At 35 C the animals showed signs of
increased activity, a condition that was not apparent at other temperatures. When obvious struggle occurred, data were discarded. It is noteworthy that 35°C is the body temperature at which *Sauromalus* is most active in its natural habitat (15).

The values for cutaneous and respiratory water loss reported here are similar to those obtained by Bentley and Schmidt-Nielsen (4) from *Sauromalus* at 23 and 40°C. Cutaneous evaporation exceeded respiratory evaporation at all temperatures except 43.5°C, amounting to about 67% of total evaporation at 26°C and about 50% of the total at 40°C. The decrease in the cutaneous contribution at higher temperatures is due to the larger $Q_{10}$ for respiratory evaporation.

These data agree with recent measurements which show that cutaneous evaporation is a large avenue for evaporative water loss in reptiles (4, 6, 7, 12, 16, 18).

The greater increase in respiratory evaporation is due, in part, to the increased capacity of air for water vapor at 43.5°C. However, if one assumes zero% humidity of inspired air and complete saturation of expired air at body temperature, evaporation from the respiratory tract is approximately 50% greater than can be accounted for from ventilation alone. Our most imprecise procedure was the estimation of ventilation, particularly at 43.5°C where panting was often interrupted by periods of normal breathing. Evaporation of secretions from the nasal salt gland would also have been collected; however, when obvious secretion occurred experiments were discarded. Additional evaporation could arise from the tongue and mucosa of the open mouth and may occur during both inspiration and expiration. At lower temperatures respiratory evaporation is about 20% less than predicted from saturation at body temperature and the respective ventilation rates. This may be due to incomplete saturation of expired air; however, Schmidt-Nielsen et al. (19) have suggested another possibility. During inspiration, evaporation due to the flow of dry air over the nasal mucosa causes cooling of the surfaces. On expiration, warm saturated air passes over the cooled nasal passages and moisture condenses onto the surfaces. The result of this "temporal counter-current flow" is a reduction in respiratory water loss. This situation would not pertain if expiration occurred through the mouth.

During normal respiration, the amount of water evaporated from the respiratory tract relative to oxygen consumption is about 1 mg H$_2$O/ml O$_2$ consumed (20). The values between 26 and 40°C in Table 1 are about one or less, indicating that the increase in ventilation which occurs over this temperature range is a response to the elevation of metabolism. The increase from 0.61 mg H$_2$O/ml O$_2$ at 26°C to 1.24 mg H$_2$O/ml O$_2$ at 40°C is apparently due to the nature of the change in pulmonary ventilation which would...
It appears, then, that the additional respiratory evaporation at 43.5 °C is due to an increase in ventilation which is greater than that required for metabolic demands. Alterations of ventilation can be accomplished by changes in tidal volume and respiratory rate. Augmentation of ventilation results in an increase in anatomical dead space ventilation at higher temperatures.

The respiratory pattern described here for Sauromalus is similar to that observed in panting homeotherms. The additional ventilation seems to be obtained economically since there is no dramatic increase in metabolism at 43.5 °C. Whether these animals pant at the resonant frequency of the respiratory system, as has been shown for dogs (9), is not known.

The contribution of evaporation to the total heat balance of the animal can be evaluated by comparing the heat dissipated by evaporation to the metabolic heat production (Fig. 5). At temperatures of 40 °C or less, evaporation from the skin has the greater cooling effect, accounting for the dissipation of about 20% of the heat production. There is little change in cutaneous evaporative cooling over the entire temperature range studied. Respiratory evaporative cooling increases slightly up to 40 °C. At 43.5 °C, however, it increases abruptly, resulting in the dissipation of 45% of the metabolic heat production. Total evaporation, at this temperature, eliminates 66% of the heat load.

Under the conditions of these experiments the animals did not dissipate the entire metabolic heat production. As a consequence, body temperature remained above ambient temperature (Table 2). That portion of the heat production which was not transferred to the environment by evaporation must be stored or lost by conduction through the integument. The values for thermal conductance recorded in Table 2 were calculated from experiments in which the difference between ambient and body temperature did not detectably change during the experimental period. Thermal conductance between 26 and 40 °C remained essentially unchanged at about 0.0012 w/cm²°C. The apparent increase at 43.5 °C is due to a high calculated thermal conductance for one individual and the mean is not significantly different from the conductances at lower temperatures. The values reported here for Sauromalus are similar to those obtained by Bartholomew and Tucker (1, 2) for Varanid and Agamid lizards. The conductance of Sauromalus is about 3 times that of a mammal of comparable size (14, 21), sup-

![FIG. 5. Percent of metabolic heat production which is dissipated by respiratory, cutaneous, and total evaporation at various body temperatures.](http://ajplegacy.physiology.org/)

### TABLE 1. Effects of temperature on ventilation and respiratory evaporation/O₂ consumption

<table>
<thead>
<tr>
<th>Body Temp, °C</th>
<th>Resp Evap/O₂ Cons, mg H₂O/ml O₂</th>
<th>Tidal Volume, ml</th>
<th>Respiration Rate, breaths/min</th>
<th>Ventilatory Rate, ml/min</th>
</tr>
</thead>
<tbody>
<tr>
<td>26 (n = 10)</td>
<td>0.61±0.05</td>
<td>1.05±0.06</td>
<td>5.39±0.19</td>
<td>5.66±0.45</td>
</tr>
<tr>
<td>30 (n = 9)</td>
<td>0.68±0.14</td>
<td>1.45±0.09</td>
<td>8.32±0.57</td>
<td>11.79±0.64</td>
</tr>
<tr>
<td>35 (n = 10)</td>
<td>0.70±0.21</td>
<td>1.25±0.10</td>
<td>10.80±1.06</td>
<td>14.03±2.21</td>
</tr>
<tr>
<td>40 (n = 12)</td>
<td>1.24±0.17</td>
<td>1.46±0.10</td>
<td>13.34±1.50</td>
<td>18.40±1.56</td>
</tr>
<tr>
<td>43.5 (n = 13)</td>
<td>4.82±0.84</td>
<td>0.47±0.05</td>
<td>64.50±2.60</td>
<td>31.07±4.03</td>
</tr>
</tbody>
</table>

Values are means ±SE, with number of animals given in parentheses. Differences between 40 °C and 43.5 °C are significant (P < 0.001 for all values except ventilation where P < 0.01). * Values expressed at BTPS.

### TABLE 2. Thermal conductance of Sauromalus at various body temperatures

<table>
<thead>
<tr>
<th>Body Temp, °C</th>
<th>TB - TA °C</th>
<th>Thermal Conductance* w/cm²°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>26 (n = 10)</td>
<td>0.23±0.03</td>
<td>0.0011±0.0002</td>
</tr>
<tr>
<td>30 (n = 9)</td>
<td>0.30±0.02</td>
<td>0.0012±0.0003</td>
</tr>
<tr>
<td>35 (n = 10)</td>
<td>0.68±0.05</td>
<td>0.0008±0.0001</td>
</tr>
<tr>
<td>40 (n = 12)</td>
<td>0.44±0.04</td>
<td>0.0012±0.0001</td>
</tr>
<tr>
<td>43.5 (n = 13)</td>
<td>0.25±0.04</td>
<td>0.0023±0.0011</td>
</tr>
</tbody>
</table>

Values expressed as means ±SE, with number of animals given in parentheses. T_B: body temperature. T_A: ambient temperature. Cond = M - (E_m - E_a)/(T_B - T_A) where M is metabolic heat production, E_m and E_a are heat transferred to the environment by respiratory and cutaneous evaporation. † 1 cal/cm²·hr·°C = 0.00116 w/cm²·°C.
porting the general contention that lizards characteristically have high thermal conductances relative to homeotherms. However, the resulting evaporative cooling is of marginal importance in the overall heat balance of this species.

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REFERENCES