Energetic cost of running and heat balance in a large bird, the rhea

C. Richard Taylor, Razi Dmi’el, Michael Fedak, and Knut Schmidt-Nielsen
Department of Zoology, Duke University, Durham, North Carolina 27706

The energetic cost of locomotion in mammals and birds has lately received increasing attention (4, 6, 8, 9). The cost of running for quadrupedal mammals was found to be a function of body weight by Taylor, Schmidt-Nielsen, and Raah (8), who also observed that available data for running man place him at about twice the value that could be predicted for a quadrupedal mammal of his size. The reason for this deviation is not obvious, but it seems possible that running on one pair of appendages and freeing the other pair from locomotion has been achieved at the expense of a higher energetic cost of locomotion. It is therefore of interest to compare man with other large bipedal homeotherms. The rhea, an ostrichlike bird of South America, is a large bipedal runner in which we could measure the energetic cost of running.

The heat balance of the running rhea is also of interest. Much of our knowledge about temperature regulation during exercise comes from studies of humans and dogs (2, 5). There is no a priori reason to expect that the rhea uses similar strategies of temperature regulation. Different animals can, in fact, be expected to display differences in their temperature regulation. For example, we have recently shown that the African hunting dog (Lycaon pictus) has a very high body temperature while it runs and thereby conserves water which would otherwise be required for evaporative cooling (7). The rhea, unlike man, dog, and hunting dog, probably is not a long-distance runner, and we believe that this may be important to the means it has adopted for temperature regulation. We therefore wanted to investigate in the rhea both the energetic cost of locomotion and temperature regulation during running.

MATERIALS AND METHODS

Animals. Four newly hatched rheas (Rhea americana) were purchased and hand reared. Two were successfully trained to run on a treadmill while wearing a ventilated hood. Experiments were not begun, however, until they were nearly fully grown. During the experiments the birds weighed between 18 and 25 kg.

Experimental design. Oxygen consumption, carbon dioxide production, water loss through respiratory evaporation, and cloacal temperature were measured while animals rested quietly and while they ran at various speeds. Measurements were recorded continuously for a resting period prior to running, during 20 min of running, and again after the run until the oxygen consumption had returned to the initial level. Our reason for using a 20-min run was that at the highest running speeds (12.5 km hr⁻¹ at 25 C, 10 and 12.5 km hr⁻¹ at 35 C, and 10 km hr⁻¹ at 43 C) the birds incurred an oxygen debt, and the amount of oxygen used in repayment of this oxygen debt was measured during the following rest period and was included in the calculation of the total heat production of running. Experiments were made at three controlled air temperatures and humidities: 25 C, 22 % rh; 35 C, 14 % rh; and 43 C, 8 % rh. In order to simulate the normal air flow over the animal as it runs, a centrifugal fan was placed in front of the treadmill and the wind velocity was matched to the treadmill speed. The maximum difference between tread speed and wind velocity in the area where the bird ran was about 2 km hr⁻¹.

Another set of experiments evaluated the increased evaporation after running, the role of cutaneous evaporation, and the interaction of environmental heat load and the heat generated by exercise. In these experiments the rheas ran for 20 min at 5 km hr⁻¹ and then rested for 40 min. Their oxygen consumption for the 1-hr period was about 3 times the resting level. From the oxygen consumption, carbon dioxide production, respiratory evaporation, total evaporation, and rectal temperature during the 1-hr period, we calculated each term of the heat balance for the hour: heat production - evaporative heat loss ± non-evaporative heat loss ± storage of heat.
ments were made while the animals rested quietly for an hour. By subtracting the values obtained during the resting hour from values obtained during the 1-hr period of 20 min running plus 40 min rest, we obtained the effect of running plus recovery on heat loss. These experiments were also carried out at air temperatures from 25 to 43 C and relative humidities from 25 to 6%.

Methods. The animals wore ventilated clear plastic masks, and room air was pulled past their face at flow rates between $5 \times 10^3$ and $20 \times 10^3$ l hr$^{-1}$. These flow rates exceeded the respiratory minute volume of the birds by one to two orders of magnitude, ensuring that no loss of exhaled air could take place. Flowmeters were calibrated to better than $\pm 1\%$ accuracy under the same pressure gradients as those existing in the experimental system. The difference in oxygen concentration between inflow and outflow air was measured with a Beckman model 215A infrared analyzer. The oxygen analyzer was calibrated by varying the gas pressure within its cell and was checked regularly with gases of known concentration. The accuracy of the analyzer permitted the measurement of oxygen consumption to better than $\pm 2\%$. The difference in carbon dioxide between air flowing into and out of the mask was measured with a Beckman model 215A infrared analyzer. An individual calibration curve was run each day by metering carbon dioxide into the mask. The accuracy of the measurements of CO$_2$ production was better than $\pm 2\%$.

Respiratory evaporation was measured by pulling a metered fraction of air leaving the mask through drying tubes immersed in an alcohol bath at $-60$ C. For cooling we employed a refrigeration system (Neslab Instruments, CC60F CryoCool freezing trap cooler) rather than the often used Dry Icc which would compromise the CO$_2$ determinations in nearby air. A blank value was obtained from a stream of room air drawn simultaneously through drying tubes at identical rates of flow. The amount of water frozen out in the drying tubes was determined by weighing. To determine the accuracy, water was evaporated into the mask at known rates similar to those encountered experimentally. Recovery was between 98.2 and 102.2%.

Total evaporation was estimated from the weight change of the animals during the experiments. The animals were weighed with a precision of better than $\pm 2.5$ g. The weight loss due to vaporization was calculated after correction for weights of oxygen uptake and carbon dioxide loss.

Cloacal temperature was measured with calibrated thermocouples inserted to a depth of about 10-12 cm and connected to a Leeds and Northrup recording potentiometer (accuracy $\pm 0.1$ C).

RESULTS

Cost of running. The oxygen consumption of rheas increased linearly with increasing running speed (Fig. 1). Oxygen consumption ($M$, ml O$_2$ g$^{-1}$ hr$^{-1}$) relative to running velocity ($v$, km hr$^{-1}$) could be expressed by the linear equation (using the data for 25 C and method of least squares): $M = 0.34 v + 0.39$. Within the limits of accuracy, this relationship was identical in experiments at air temperatures of 25, 35, and 43 C: The y intercept (extrapolated zero running velocity) was 0.39 ml O$_2$ g$^{-1}$ hr$^{-1}$, which is very close to our observed resting oxygen consumption at 25 C (0.38 ml O$_2$ g$^{-1}$ hr$^{-1}$). Our resting values are higher than those observed by Crawford and Lasiewski (1) for a 22-kg rhea from the equation established by Lasiewski and Dawson (3) for nonpasserine birds (0.29 ml O$_2$ g$^{-1}$ hr$^{-1}$) and higher than the values observed by Crawford and Lasiewski (1) for a 22-kg rhea (0.32 ml O$_2$ g$^{-1}$ hr$^{-1}$). A possible explanation for our higher values is that we made no selection for low values. (Sometimes our resting birds stood and other times they lay down.)

Heat balance during running. Heat production (calculated from oxygen consumption and RQ), heat lost by respiratory evaporation (assuming heat of vaporization = 580 cal per g H$_2$O), heat storage (assuming that changes in cloacal temperature reflect changes in mean body temperature and a specific heat of 0.83 cal per °C), and nonevaporative heat loss (see following for assumptions) are presented in Fig. 2 as functions of running speed at three air temperatures (25, 33, and 43 C). At higher running speeds the rheas stored, rather than dissipated, large amounts of heat, and the body temperature exceeded 45 C; the rheas became very reluctant to run, and the experiments were discontinued. The highest cloacal temperature which we recorded at the end of a run was 46.4 C, which caused no apparent ill effects to the bird.

Heat loss through respiratory evaporation increased with increasing running speed to an apparent maximum level of about 5 kcal kg$^{-1}$ hr$^{-1}$ (Fig. 2). At 25 C this level was not reached until running speed was about 10 km hr$^{-1}$.

Nonevaporative heat loss can be estimated from the heat production by subtracting heat storage and heat loss through respiratory evaporation (assuming that cutaneous evaporation during running is small enough to be disregarded, an assumption which later will be shown to be justified). Nonevaporative heat loss increased with increasing running speed at air temperatures of 25 and 35 C (Fig. 2); this increase was expected because the air flow over the bird was increased with the running speed. At 43 C there was a consistent small heat gain from the environment while the birds ran.

Heat balance during rest. Cloacal temperature remained
nearly constant at air temperatures from 25 to 43°C (Fig. 3A). The heat production of the rhea at rest did not seem to be influenced by air temperature (Fig. 4A). Evaporative heat loss increased, while nonevaporative heat loss decreased with increasing air temperature. At higher temperatures the rheas began to gain heat from the environment (Fig. 4A).

**Heat balance during a 1-hr period of running plus recovery.** Cloacal temperature increased on the average 2–3°C during a 20-min run at 5 km·hr⁻¹ (Fig. 3B). The increase was greater at higher air temperatures. Cloacal temperature returned to prerun level during the 40-min recovery period when air temperature was 25 or 35°C. When air temperature was 43°C, however, cloacal temperature was 0.2–0.5°C higher at the end of the 40 min recovery period than before the run.

Heat production during an hour which consisted of a 20 min run at 5 km·hr⁻¹ followed by a 40 min recovery period was the same at air temperatures from 25 to 43°C (Fig. 4B). During the hour both respiratory and cutaneous evaporation increased with increasing air temperature. Respiratory evaporation at 43°C remained close to its maximum level for the entire hour, helping to explain the return of cloacal temperature nearly to its prerun level at the end of 40-min recovery.

The additional heat generated by running for 20 min and the manner in which it was dissipated can be found by subtracting the values for 1 hr of rest from the values for 1 hr of running plus recovery (Fig. 5). The increment in heat production caused by running did not change significantly with temperature, in other words, cost of running was not affected by air temperature.
FIG. 5. Change in heat balance of rhea caused by a run, obtained by subtracting data collected during 1 hr rest (Fig. 4A) from data collected during 1 hr consisting of 20 min running at 5 km hr⁻¹ followed by 40 min recovery (Fig. 4B). Means ± 2 se.

FIG. 6. Fraction of heat production (in percent) stored during 20 min running at various speeds, determined at 25, 35, and 43 C.

There was no increase in cutaneous evaporation as a result of running; the increase in evaporation was entirely respiratory (Fig. 5). Nonevaporative heat dissipation is of particular interest, since even at an air temperature of 43 C, over one-fourth of the increment in heat production caused by running was dissipated without evaporation.

DISCUSSION

The rhea, like man, uses more energy in moving from one place to another than does a quadrupedal mammal. As discussed in a previous paper (8) the relationship between oxygen consumption and running speed in quadrupedal mammals is represented by straight lines, the slopes of which approximate the minimum cost of moving 1 g animal 1 km (Ṁ run). From the animal's weight Ṁ run can be predicted using the equation Ṁ run = 8.46 W⁻⁰.⁴⁰ where Ṁ run is in ml O₂ g⁻¹ km⁻¹ and W is the body weight in grams. According to this equation, the predicted Ṁ run for a 22-kg rhea would be about 0.15 ml O₂ g⁻¹ km⁻¹, which is less than one-half of the observed value of 0.34 ml O₂ g⁻¹ km⁻¹. The predicted Ṁ run for man using the same equation would also be one-half of the observed value (0.098 vs. 0.212 ml O₂ g⁻¹ km⁻¹ for a 70-kg man). Whether the higher-than-predicted cost of running in both man and rhea is coincidental or expresses that two-legged running is energetically about twice as expensive as four-legged running cannot be decided until additional species have been examined. If there is a simple relationship between body weight and Ṁ run for bipedal animals which differs from the quadrupedal relationship by a factor of 2, it appears that man may have paid a high price in freeing his hands for purposes other than locomotion. Further investigations on the energetics of bipedal running are necessary before this can be decided.

* Slope for man calculated using data from Margaria et al. (4).
suggestion can be regarded as more than speculation. Such work is in progress in our laboratory.

In the running rhea, heat storage is important. The body temperature increases during running even at an air temperature of 25°C. At higher air temperatures and high running speeds, rheas store large amounts of heat. Body temperature continues to climb, either until the rhea is no longer able to run, or until non-evaporative heat loss is increased enough by the steeper temperature gradient between body and air for body temperature to equilibrate. Almost 75% of the heat produced during a 20-min run at 10 km hr⁻¹ is stored when the air temperature is 43°C and 57% when air temperature is 35°C (Fig. 6).

Increased evaporation does not appear to be involved in temperature regulation of the running rhea. When the rhea ran at 10 km hr⁻¹, roughly the same amount of heat was lost by respiratory evaporation whether the air temperature was 25, 35, or 43°C. Because storage of heat was so important at high air temperatures (see above), the evaporation was correspondingly unimportant in the heat balance. Thus, the percentage of the heat production lost by respiratory evaporation at high air temperature decreased rapidly with increasing speed (Fig. 7). For example, at 10 km hr⁻¹ when air temperature was 43°C only about 27% of the heat produced was dissipated by evaporation.

An important consequence of the high body temperature of the running rhea is the increase in non-evaporative heat loss due to more favorable temperature gradients between body and air. If the body temperature of the running bird had remained at 39-40°C when the air temperature was 43°C, as was the case in the resting bird, then the heat load on the running bird would have been potentiated by increased convection. Instead, the increase in body temperature to above-the-air temperature maintains a positive gradient for heat loss during a large part of a 20-min run. Thus, while the resting bird gained heat from the environment amounting to nearly 60% of its metabolic heat production, the running bird gained almost no heat during a 20-min run (Fig. 8). The high body temperature is also important for heat dissipation after a bird stops. For example, in the experiments of 20 min running followed by 40 min recovery at 43°C, not only was there no additional heat gain from the environment as a result of the run, but also about 25% of the heat generated by the run was lost by non-evaporative means (Fig. 5).

This investigation was supported by National Institutes of Health Research Grant HE-02228 and National Institutes of Health Research Career Award 1-K6-GM-21,522 to K. Schmidt-Nielsen.

REFERENCES