Metabolic rate of camels: effect of body temperature and dehydration

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SCHMIDT-NIELSEN, K., E. C. CRAWFORD, JR., A. E. NEWSOME, K. S. RAWSON, AND H. T. HAMMEL. Metabolic rate of camels: effect of body temperature and dehydration. Am. J. Physiol. 212(2): 341-346. 1967. The effect on metabolic rate (oxygen consumption) of changes in body temperature and state of dehydration was studied in four camels. The data were subjected to multiple-regression analysis. The metabolic rate increased with rising body temperature as expressed by a mean Q_{10} of 2.06. The metabolic rate decreased with increasing dehydration, reaching about 77% of the original value at 77% of the initial hydrated body weight. The rate of respiration (rate of breathing) increased with rising body temperature with a mean Q_{10} of 1.86. The rate of respiration was decreased to 64% of the initial value when dehydration had reduced the body weight to 77% of the initial weight.

oxygen consumption; multiple-regression analysis; Q_{10}; respiration rate; breathing rate

The body temperature of camels may vary considerably. In the absence of heat stress the daily fluctuations are about 2°C, but a dehydrated camel in a hot environment may display fluctuations in excess of 6°C. Under these circumstances the early morning temperature may fall to below 35°C, and during the maximum heat load of the desert day the temperature may reach 41°C. These variations in body temperature are of significance in the water economy of the camel as discussed in previous publications (9, 12).

Since the highest body temperatures occur when the external heat load is maximal, it is of interest to know whether or not the increase in body temperature causes increased metabolic heat production, for this would add substantially to the heat load. It is well known that the metabolic rate of mammals in general increases with increasing body temperature (e.g., fever), and decreases with decreasing temperature (e.g., hypothermia and hibernation). If the metabolic heat production of camels increases to the same extent as in other mammals, i.e., with a Q_{10} of about 2 or 3, a 6°C increase in body temperature should cause an increase in heat production of some 50-100%.

It was the purpose of this study to establish the effect of body temperature on the metabolic rate of camels. Since extreme body temperatures occur only in the dehydrated animal, it was desirable to determine separately the effects of temperature and the degree of dehydration on the metabolic rate. The body temperature fluctuations depend on the degree of dehydration, but the separate contributions of these two interrelated factors can be evaluated by a multiple-regression analysis. We found that an increased body temperature causes an increase in metabolic rate similar to that in other mammals, and that dehydration leads to a decrease in metabolic rate.

MATERIALS AND METHODS

Animal material. These studies were carried out in central Australia (Alice Springs, N.T., 23.4°S) on the one-humped camel (Camelus dromedarius). Camels were originally introduced into Australia from Afghanistan and have since become well established as a feral species in the central deserts. We used four animals, two that were semidomesticated and two that were caught wild (Table 1). All four animals were readily trained to submit to the experimental procedures, which consisted of weighing, temperature measurements, and determinations of oxygen consumption. They were fed on commercially available hay and dried alfalfa, and were kept in the open, either in pens or tethered near the laboratory.

Weighing. The animals were weighed suspended in a canvas sling, using a temperature-compensated Chatillon dynamometer which permitted readings to 0.5 kg. Sur-
RESULTS

Metabolic rate. The oxygen consumption was determined on four camels in a state of normal hydration and in various degrees of dehydration. Due to limited time we chose to obtain more complete observations on two camels (one feral and one domesticated), and supplement this with a smaller number of observations on two additional animals. The observations on each camel numbered 158, 96, 39, and 39, respectively, giving a total of 342.

The data from the one camel (Pete) on which we had 158 observations are plotted in Fig. 1. The oxygen consumption increased with increasing body temperature corresponding to a Q10 of 2.09. These determinations were made with the camel sitting quietly on the ground in the open, outside the laboratory building. The camel showed no obvious struggling, but was at times slightly restless which may explain some of the highest values. However, the data include all observations made, both in the normally hydrated animal and in various states of dehydration, and the variations therefore include the effect of dehydration. The effect of this variable was estimated separately, as will be described below.

Multiple regression analysis. Since the data presented in Fig. 1 include the effect of dehydration as well as of body temperature, the entire set of observations was subjected to a multiple-regression analysis to separate these covariants. The computer determined the constants in equations of the form:

$$\log Q_10 \text{ consumption} = C_0 + C_1(\% \text{ IW}) + C_2(T_B)$$

with the constants $C_0$, $C_1$, and $C_2$ for each camel listed in Table 1.

In these equations $\% \text{ IW}$ means percent of initial body weight, which indicates the degree of dehydration of the animal, expressed as percent of the initial, or hydrated, body weight, and $T_B$ is the body temperature in degrees $\text{C}$. The equations can be used for the calculation of a
TABLE I. Oxygen consumption in four camels in relation to degree of dehydration and body temperature

<table>
<thead>
<tr>
<th>Camel No.</th>
<th>C0</th>
<th>C1 ± se</th>
<th>F Value for C1</th>
<th>C2 ± se</th>
<th>F Value for C2</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 ♂ Feral</td>
<td>-1.9426</td>
<td>+0.002571</td>
<td>13.7963</td>
<td>+0.0598</td>
<td>131.5765</td>
</tr>
<tr>
<td>2 ♀ Domesticated</td>
<td>-0.7872</td>
<td>+0.0005666</td>
<td>0.6089</td>
<td>+0.01737</td>
<td>48.8096</td>
</tr>
<tr>
<td>3 ♂ Domesticated</td>
<td>-0.3745</td>
<td>+0.0001328</td>
<td>0.6153</td>
<td>+0.009666</td>
<td>0.6499</td>
</tr>
<tr>
<td>4 ♀ Feral</td>
<td>-0.2614</td>
<td>+0.0006667</td>
<td>23.6724</td>
<td>+0.03516</td>
<td>0.9076</td>
</tr>
<tr>
<td>All camels</td>
<td>-1.8756</td>
<td>+0.0051035</td>
<td>12.2957</td>
<td>+0.05166</td>
<td>23.1383</td>
</tr>
</tbody>
</table>

Constants are given in the equation log O2 cons = C0 + C1(% IW) + C2(TB), where O2 cons = oxygen consumption; % IW = dehydration expressed as percent of initial weight; and TB = body temperature.

TABLE 2. Estimated rates of O2 consumption (O2 cons.) of camels, computed from equations given in Table 1, for fully hydrated animals at the indicated standard body temperatures (Std. TB)

<table>
<thead>
<tr>
<th>Camel No.</th>
<th>Estim. Init. Body Wt, kg</th>
<th>N</th>
<th>Std. TB, °C</th>
<th>Total O2 Cons., ml/min</th>
<th>O2 Cons., ml/min per kg</th>
<th>O2 Cons., ml/min per m2</th>
<th>Q10</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>295.3</td>
<td>158</td>
<td>38.20</td>
<td>486</td>
<td>1.656</td>
<td>110.1</td>
<td>2.29</td>
</tr>
<tr>
<td>2</td>
<td>552.4</td>
<td>91</td>
<td>39.12</td>
<td>814</td>
<td>1.506</td>
<td>164.0</td>
<td>1.49</td>
</tr>
<tr>
<td>3</td>
<td>532.5</td>
<td>39</td>
<td>39.09</td>
<td>591</td>
<td>1.777</td>
<td>145.5</td>
<td>(1.26)</td>
</tr>
<tr>
<td>4</td>
<td>298.2</td>
<td>39</td>
<td>37.91</td>
<td>477</td>
<td>1.792</td>
<td>115.0</td>
<td>2.29</td>
</tr>
<tr>
<td>All</td>
<td>407.0</td>
<td>330</td>
<td>38.13</td>
<td>673</td>
<td>1.654</td>
<td>122.5</td>
<td>2.06</td>
</tr>
</tbody>
</table>

Last column indicates the effect of change in body temperature as expressed by the Q10. For statistical significance, refer to Table 1. * Not significant.

“normal” oxygen consumption in the four camels, eliminating the effect of dehydration and referring the value to a “standard” body temperature for which we used the mean of the body temperatures at which the observations were made. The result of this computation of the oxygen consumption in resting, fully hydrated camels is given in Table 2. Since the body weights of the camels differed considerably, the information is given not only as total oxygen consumption, but also as oxygen consumption per kilogram body weight and per estimated body surface area.

Temperature effect. The regression lines for the relationship between oxygen consumption and body temperature, including all data for all four camels are given in Fig. 2. Since the animals had different body weights, these results have been calculated per kilogram body weight to make them more directly comparable. It will be seen that there are no gross differences between the animals, which all showed an obvious temperature effect on the metabolic rate.

The simplest way to express the temperature effect is by the Q10, as listed in Table 2, column h. It should be noted that the over-all Q10 for all camels is weighted in favor of camel 1 because this animal was represented by more determinations than the others. The Q10 is apparently lower in the two large domesticated animals (2 and 3) than in the two young feral camels (1 and 4), but the material is insufficient to conclude whether any real difference existed.

Effect of dehydration. The equation for the effect of dehydration on oxygen consumption, when the data from all camels are combined, gives the regression line shown in Fig. 3. The maximum degree to which any of these camels was dehydrated was to 77% of the initial body weight (fully hydrated weight). Not all camels were exposed to equally severe, or the same number of, dehydration periods. The slope of the regression line is therefore determined primarily by those two camels on which most data were obtained, 1 and 2.

The regression line indicates that when dehydration had resulted in a decrease in body weight to 77% of the original the metabolic rate had decreased to 76.5% of that in the fully hydrated animal. The time required to reach this degree of dehydration does, of course, depend on heat load, exposure to sun, work, etc., and on individual differences between the animals. In these particular experiments (central Australia in February) the rate of water loss was such that 23% of the body weight was lost after about 12 days of feeding on dry feed without any watering. In a hotter desert, such as the Sahara, the rate of dehydration would be faster in summer, while in winter the rate would be much slower.

Respiration rate. It has previously been established that the main mechanism for heat dissipation in the camel is sweating, rather than panting (10). However, there still is a noticeable increase in respiratory rate with increasing body temperature. The increase is from about 7 cycles/min at a body temperature of 35°C to about 30 cycles/min at 41°C body temperature (see Fig. 4). Part of this increase should be due to the increase in oxygen consumption at higher body temperature, but if this factor alone is considered, the respiratory rate should only increase to about 11 cycles/min. Since tidal volumes and carbon dioxide in the blood were not determined, it remains uncertain to what extent the animal hyperventi-
FIG. 2. Oxygen consumption per kilogram body weight in relation to body temperature (rectal or vaginal) in four camels. Regression lines refer to normally hydrated animals as derived from computer analysis. Number of observations, camel 1-158, 2-96, 3-39, 4-39; total 332 observations.

lated and what fraction of the total heat dissipation could be accounted for by respiratory means.

The multiple regression analyses for the information on respiratory rate gave the following equation for all camels combined:

\[ \log \text{resp. rate} = -3.6140 + 0.008502 \times \text{(} \% \text{ IW)} + 0.1036 \times (T_B) \]

The regression line in Fig. 5 shows the relationship between respiratory rate and dehydration (as expressed by the decrease in body weight), with all figures referred to a standard body temperature of 38.13°C.

At a dehydration involving 25% loss of body weight, the respiratory rate would be decreased by 36%. This decrease is somewhat larger than the decrease in oxygen consumption (23.5%) which results from the same degree of dehydration (see Fig. 3).

DISCUSSION

This investigation was undertaken to study the influence of degree of dehydration and of body temperature on the metabolic rate of camels. It has earlier been established that camels can tolerate an exceptional degree of dehydration. While other mammals, if exposed to heat, are likely to succumb when the water loss corresponds to some 12–15% of body wt, camels have tolerated water losses exceeding 25% of body wt without apparent ill effect (9, 11).

The body temperature of the camel can fluctuate daily by some 6 or 7°C, from about 34 to 41°C. However, such extreme variations occur only in the severely dehydrated animal when exposed to high environmental heat loads (12). The rise in body temperature during heat load is advantageous to the water balance of the camel in two ways. First, the increase in body temperature during the day constitutes a storage of heat which can be dissipated at night without expenditure of water. If the body temperature were to be kept constant during the day, an equivalent amount of water would have to be evaporated. Second, as the body temperature is allowed to rise, the temperature gradient (and heat flow) from the hot environment to the cooler body surface is correspondingly reduced, and thus the external heat load and the use of water is reduced. Although it has not been possible to establish the exact amount, it has been estimated that the increase in body temperature cuts the amount of water needed to dissipate heat gain from the environment to about one-half (12).

It is well known that an increase in the body temperature of mammals leads to an increase in metabolic rate (heat production). The metabolic heat production of the camel also increases at high body temperature, and the internal heat production thus adds to the heat load when the external heat load is at its maximum. The reduction in external heat load achieved by permitting a rise in body temperature is thus partly offset by the increase in metabolic heat load.

The effect of a temperature increase on a physiological process is most conveniently expressed as the Q10, i.e., the increase that occurs with a temperature rise of 10°C. The temperature fluctuations in mammals are usually so small that the Q10 cannot be established with precision, but it is commonly stated that Q10 for man is about 2 or 2.5. This information is based on the work of DuBois, who reported an average Q10 of 2.3 for fever in man (4). More recently a Q10 of 2.1 was found in a human subject where an intracerebral lesion had destroyed the temperature regulation (2). Q10 for dogs has been reported to be 2.3 between 36 and 38°C (7), and for rats 2.01 between 38 and 18°C (5). The reduction in metabolic rate which occurs in hibernating mammals can also be used for a calculation of Q10, which usually is in the order of 2–4 (8). However, it could be argued that this is a special
Our present results show that there is indeed a reduction in metabolic rate due to dehydration when the observations are referred back to the same body temperature (Fig. 3). Our camels, when dehydrated to 77% of the initial body weight, had metabolic rates reduced to about 77%. (This does not mean that the dehydrated camel always has a lower metabolic rate than if it were fully hydrated, because during the day it will have a high body temperature which, due to the Q_{10} effect, gives a rise in metabolic rate.)

It is interesting that the metabolic rate decreases as water is lost, although there should be no decrease in dry tissue weight, protein mass, etc. The camel continues to eat as water is lost (until seriously dehydrated), and when water is offered it will drink until its body weight has been restored to the initial value.

Respiration rates. The respiratory rate of the camel increased about threefold as its body temperature increased from 35 to 41°C (Fig. 4). The change was gradual, and even at the highest rates there was no open-mouthed breathing similar to the panting of dogs.

In dogs when panting begins there is a sudden change in frequency from some 30 to 40 cycles/min to some 300–400 cycles/min. It has been suggested that dogs pant at the resonant frequency of the respiratory system, thus reducing the muscular work (and the heat production) required for the high respiratory frequencies (3). The gradual change in the respiratory frequency in the camel indicates that a similar principle of a resonant frequency is not involved in the increased respiratory rates at high body temperature.

An increased ventilation may of course be expected with the increased oxygen consumption at high body temperature. However, the Q_{10} for the increase in metabolic rate is about 2, whereas the Q_{10} for the increase in respiration is about 10 (mean for all camels Q_{10} = 10.86). A decrease in tidal volume could possibly take

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**FIG. 4.** Respiratory rates in four camels in relation to body temperature. Regression lines refer to normally hydrated animals as derived from computer analysis. Number of observations, camel 1—48, 2—94, 3—37, 4—38; total—317 observations.

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**FIG. 5.** Mean respiratory rate in relation to dehydration in four camels. Estimated from equations given in text for a standard body temperature of 38.13°C.
The respiratory rate did decrease with dehydration of the camels, as shown by multiple-regression analyses, which eliminated the temperature effect from the computation. This decrease, which was about 36% for a 23% loss of body weight, was somewhat greater than the decrease in oxygen consumption (23.5%).