

How animals work

by

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1. Respiration and evaporation

Introduction

A simple biological problem may arouse our interest, but as we gain more knowledge the questions ramify and appear to grow in complexity. This may take us to new and seemingly unrelated problems, but in retrospect they are all related to the desire to find out how things work. If we are fortunate we will gain some insight, and when we understand underlying principles, the greatest reward seems to be in the simplicity of the answers.

Twenty-five years ago I had an opportunity to visit the Arizona deserts, and I was much impressed by their abundant animal life, which for me was quite unexpected. In particular, it surprised me that small rodents were quite numerous, in spite of the obvious absence of drinking water. What impressed me equally was that virtually no scientific information, other than a few anecdotal accounts, was available on how these animals could live seemingly without water. It has since become abundantly clear that the water balance of a desert rodent, such as a kangaroo rat, is quite like that of any other animal, that is, for the animal to remain in water balance, the intake of water must equal the total losses. It has become equally clear that they do not eke out a marginal existence during the long periods of drought; they manage as well as any animal that is at home in its natural environment.

Let us briefly consider the water balance of kangaroo rats, which live on seeds and other dry plant material. They do not usually drink, and they do not particularly seek out green and succulent plants to obtain water. A simplified account of their water balance will clarify the questions to be asked (table 1). Since these animals live on dry food, the amount of free water in the food is quite small, and the water which is derived from oxidation of the foodstuffs ('metabolic water') is nearly all that is available. This fairly small amount of water must suffice to cover all losses, which are by

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Table 1. *Water balance of the kangaroo rat. For an animal to remain in water balance, the total gains must equal the total losses*

Gains		Losses	
Oxidation water	90%	Evaporation	70%
Free water in food	10%	Urine	25%
Drinking	0%	Feces	5%

evaporation, in the urine, and with the feces. The two last items can be minimized by excreting a highly concentrated urine and very dry droppings, but the means of reducing evaporation are more limited because the respiratory membranes are moist and air is exhaled saturated with water vapor. As a consequence, evaporation is the major and inescapable avenue for water loss in these animals. For a man in the desert evaporation is far greater because he uses sweating to remain cool in the hot surroundings. For desert rodents the available water would soon be exhausted if they were to sweat; actually, they have no sweat glands and avoid the need to sweat by staying in their relatively cool burrows during the hot desert day, restricting their active life to the cooler nights.

Evaporation, mice and men

We usually assume that air is exhaled saturated with water at close to body temperature, which for mammals and birds is some 37 °C. For reptiles the situation is different because they are 'cold-blooded', which means that their body temperature varies with that of the surroundings. Their temperature, and the water content of the exhaled air therefore, is much more variable, and usually also much lower than in birds and mammals.

When comparing the evaporation from different animals, it will be convenient to use some suitable common measure, for animals are of widely different sizes and their need for oxygen (and thus the ventilation of the lungs) varies greatly. Since lung ventilation, and thus the evaporation, varies with the call for oxygen, it is convenient to examine the amount of water evaporated relative to one unit volume of oxygen taken up. This becomes particularly useful when we consider that the amount of oxygen taken up is a direct measure of the amount of oxidation water formed in meta-

bolism, which again stands for virtually the entire gain of water for the desert rodents we have under consideration.

If we now compare the evaporation of various animals (table 2) we find that those that normally live in deserts evaporate substantially less than non-desert animals or man. Why this difference?

Table 2. *Evaporation in rodents. To permit comparisons, the evaporation is expressed relative to the simultaneous oxygen consumption. For rodents, the figures represent total evaporation from lungs and skin combined, for man from the lungs only.* (Data from Schmidt-Nielsen, 1964)

Species	Evaporation mg H ₂ O ml ⁻¹ O ₂ cons.
Kangaroo rat	0.54 ± 0.04
Pocket mouse	0.50 ± 0.07
Golden hamster	0.59 ± 0.05
White rat	0.94 ± 0.09
White mouse	0.85 ± 0.07
Man (lungs only)	0.84

Presumably both body temperature and lung ventilation are similar in the various species, so how do the differences arise? It should be noted that the figures in this table give the evaporation from the entire animal, and therefore include evaporation from the skin as well as from the lungs, except for man where skin evaporation is considerable and highly variable. It has been said that evaporation from the skin of rodents is small as they have no sweat glands, but in reality it is a substantial amount for white rats, in which nearly one-half of the evaporation is from the skin (Tennent, 1946). If this amount were subtracted, the remaining evaporation for the white rat would be similar to that in the other small rodents, thus eliminating the difference between desert and non-desert species.

The respiratory evaporation as given for man represents air saturated at close to body temperature. If we use this as our standard, the question becomes: How is it possible for other animals to reduce this evaporation? The possible solutions we can imagine would be; (1) that more than the usual amount of oxygen is extracted from the air in the lungs before it is exhaled, or (2) that the exhaled air is not saturated at body temperature.

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The first possibility would seem quite reasonable, in fact more likely than the second. More oxygen could be removed in the lung if the oxygen affinity of the blood hemoglobin were increased. We know that in some animals this may be so; the llama, for example, has hemoglobin with a high oxygen affinity which enables it to take up oxygen more easily in the rarified atmosphere of high altitude in the Andes where it lives (Hall, Dill and Guzman Barron, 1936). A higher oxygen affinity is expressed as a shift to the left of the oxygen dissociation curve, but no such shift is found for kangaroo rat blood; on the contrary, the dissociation curve is located rather to the right, showing a low oxygen affinity as is usual for mammals of small body size.

This alone does not prove that there can be no increase in oxygen extraction in the lung, but other evidence strongly supports it. If, say, twice the usual amount of oxygen were to be removed from the lung air, the carbon dioxide concentration in the exhaled air would become twice the usual. Thus the blood carbon dioxide tension would be doubled, which would be reflected either as severe acidosis or as a change in the bicarbonate buffer system. The blood buffer system of kangaroo rats is as in other mammals, and we must therefore abandon the hypothesis of an increased oxygen extraction (Gjønnes and Schmidt-Nielsen, 1952).

We must now consider the second possibility, that the exhaled air is not saturated at body temperature. On examination we find that although the air is saturated, its temperature is far below body temperature. In the lung the air is at body-core temperature, on its passage from the lung to the outside it undergoes substantial cooling, and in the process water vapor is recondensed on the walls of the passageways.

A cold nose

If we measure the temperature inside the nasal passage of a kangaroo rat, we find the lowest temperature at the tip of the nose, with a longitudinal gradient extending inwards until body temperature is reached at a depth of about 20 mm (figure 1). When the animal breathes saturated air, the temperature at the tip of the nose approaches that of the surroundings; in dry air, however, the temperature at the tip is several degrees below the ambient air temperature. The air that flows through the nasal passages attains, within a few tenths of a degree, the same temperature as the wall,

and an animal which inhales dry air thus exhales air at a temperature even lower than the inhaled. We should remember, of course, that the air as it leaves the lung is at body temperature, 38°C , and is cooled as it flows out through the nose.

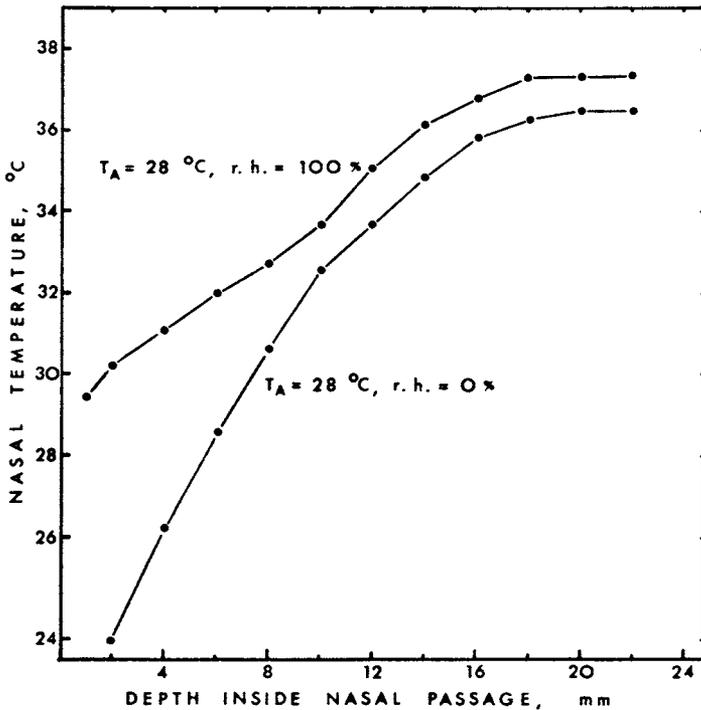


Figure 1. Temperatures in the nasal passage of the kangaroo rat (*Dipodomys merriami*). Upper curve: breathing air of 100% relative humidity at 28°C . Lower curve: breathing completely dry air, also at 28°C . Body temperature 38°C . (From Jackson and Schmidt-Nielsen, 1964.)

To understand how this temperature gradient along the nasal passageway is established, it is useful to look at a simple model of the nose (figure 2). Let us assume that there is no evaporation to complicate things. During inhalation the walls of the passageway are cooled by the air passing by, and the wall temperature will approach that of the inhaled air, in this case, 28°C . During exhalation, as warm air from the lungs passes over these cool surfaces, the air is cooled, and if the heat exchange is complete, the exhaled air temperature will approach that of the surface,

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28 °C. The measurements on the kangaroo rat in moist air (see figure 1, upper curve) showed approximately this situation, the exhaled air temperature was nearly that of the ambient air. In completely dry air (also at 28 °C) the exhaled air was about 23 °C,

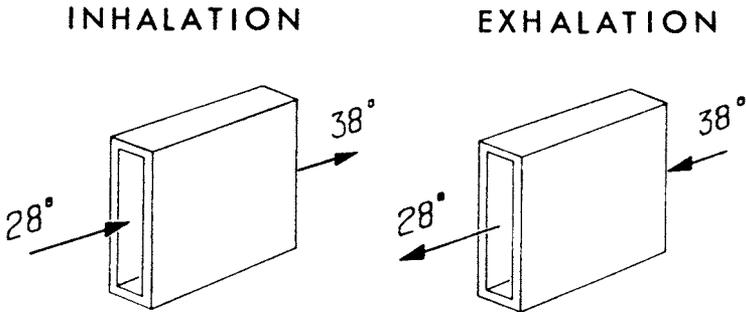


Figure 2. Model of heat exchange in the nasal passageways. Ambient air is 28 °C and saturated, body temperature is 38 °C. As inhaled air flows through the passageways (*left*) it gains heat and water vapor, and is saturated and at 38 °C before it reaches the lungs. On exhalation (*right*) the air flows over the cool walls, gives up heat, and water recondenses. As heat and water exchange approaches completion, exhaled air approaches 28 °C, saturated. (From Schmidt-Nielsen *et al.* 1970b.)

or 5 degrees below ambient air temperature (figure 1, lower curve). This is because during inhalation water evaporates from the moist nasal mucosa, which therefore becomes cooler than the air, just as the 'wet-bulb' thermometer of a sling psychrometer.

Flukes and flippers, or Countercurrent heat exchange

The heat exchange in the nose has a great similarity to the well-known countercurrent heat exchange which takes place, for example, in the extremities of many aquatic animals, such as in the flippers of whales and the legs of wading birds. The body of a whale that swims in water near the freezing point is well insulated with blubber, but the thin streamlined flukes and flippers are uninsulated and highly vascularized and would have an excessive heat loss if it were not for the exchange of heat between arterial and venous blood in these structures. As the cold venous blood returns to the body from the flipper, the vessels run in close proximity to the arteries, in fact, they completely surround the artery, and heat from the arterial blood flows into the returning venous

blood, which is thus re-heated before it enters the body (figure 3). Similarly, in the limbs of many animals both arteries and veins split up into a large number of parallel, intermingled vessels each with a diameter of about 1 mm or so, forming a discrete vascular bundle known as a rete (Scholander, 1958; Scholander and Krog, 1957). Whether the blood vessels form such a rete system, or in some other way run in close proximity, as in the flipper of the whale, is a question of design and does not alter the principle of

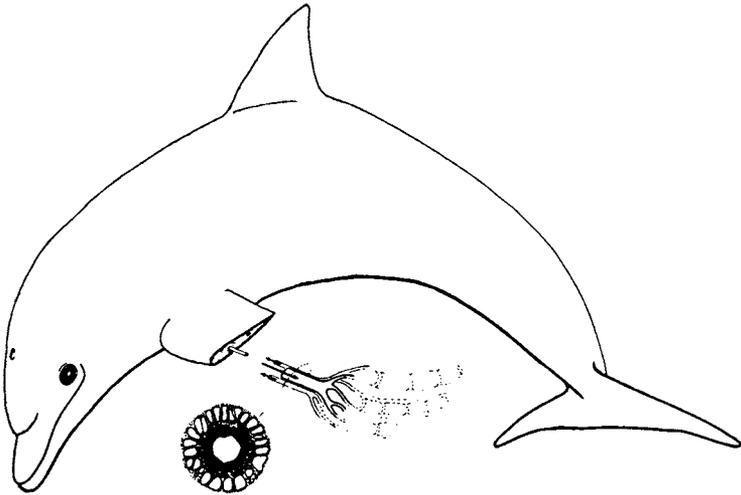


Figure 3. Heat loss from the extremities of whales is reduced by a special arrangement of the blood vessels. This cross-section of a porpoise flipper shows how an artery is completely surrounded by veins. As a result, the warm arterial blood gives up heat to the venous blood, which thus is pre-heated before it re-enters the body. (Drawing by D. E. Murrish, reproduced by permission from Schmidt-Nielsen, 1970.)

the heat recovery mechanism. The blood flows in opposite directions in arteries and veins, and heat exchange takes place between the two parallel sets of tubes; the system is therefore known as a countercurrent heat exchanger.

In principle, the heat exchange in the nasal passage is similar. In the limb the blood flows in opposite directions in two separate tubes, in the nose the flows in and out take place in the same tube. They are separated in time, however, and we can therefore speak about a *temporal separation* in the countercurrent heat exchanger of the nose, as opposed to the *spatial separation* of the blood vessels in

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the extremities. This difference is shown diagrammatically in figure 4.

I shall now proceed to discuss the general nature of heat exchange in the respiratory passageways and its importance for the water balance of mammals and birds. The system is not peculiar to desert animals, it is an inevitable consequence of the geometry of the

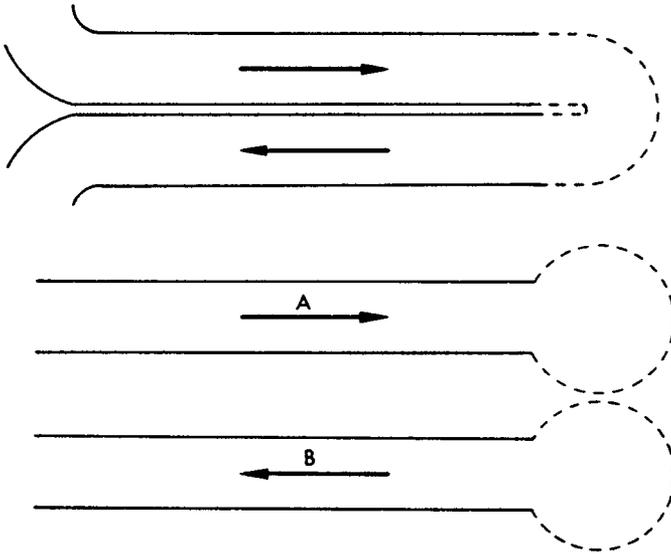


Figure 4. *Top*: Model of countercurrent heat exchanger as in the whale flipper or bird leg. The blood flows in opposite directions in the two tubes, which are separated in space (spatial separation). *Bottom*: Countercurrent heat exchanger as in nasal passageways. On inhalation (A) heat is removed from the wall; on exhalation (B) air flowing in the opposite direction returns heat to the wall. The nasal heat exchanger thus uses one tube in which the two flows are separated in time (temporal separation). (From Schmidt-Nielsen *et al.* 1970b.)

passageways, and I shall try to analyze its general features. I shall also show how even cold-blooded animals have something to be gained from cooling of the exhaled air, and finally, I shall show how the type of heat exchanger functioning in the nose of a kangaroo rat can be used to design an engine which appears to be a perfectly feasible *perpetuum mobile*.

Measurements on birds

The observation that air is exhaled, not at body temperature, but at some lower temperature close to the ambient air, can be

made on birds as well. We made such measurements on cactus wrens, which are about the same size as kangaroo rats (35 grams), over a range of ambient air temperatures of 12 to 30 °C (see figure 5).

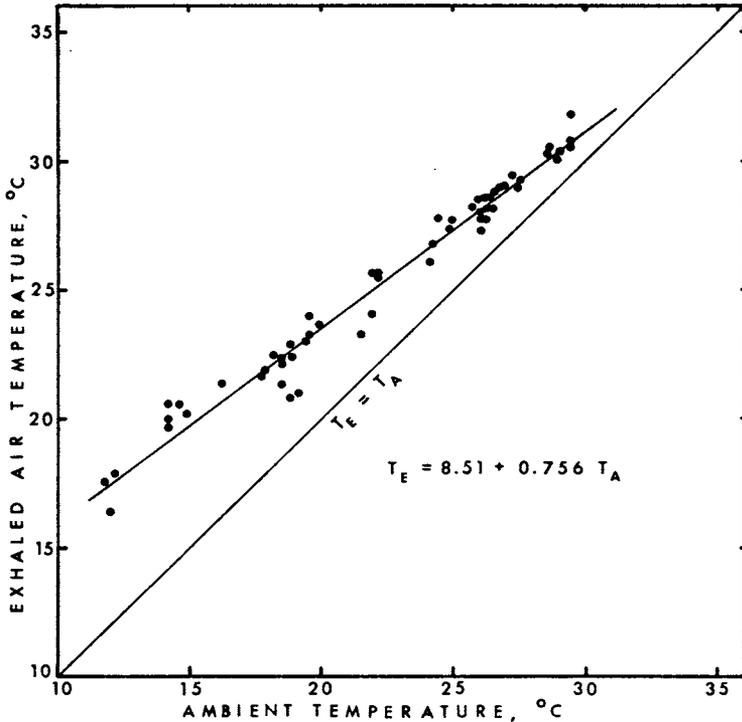


Figure 5. Temperature of the exhaled air of the cactus wren (35 g) at ambient air temperatures between 12 and 30 °C. Body temperature remained constant at 41 °C. (From Schmidt-Nielsen *et al.* 1970b.)

The exhaled air was always below body temperature, which was 41 °C, and the extent of cooling ranged from 8 to as much as 23 °C below body temperature (Schmidt-Nielsen, Hainsworth and Murrish, 1970b). In other words, over this entire range of ambient temperatures the exhaled air was within a few degrees (1 to 7 °C) of the inhaled air. The cactus wren, like the kangaroo rat, is a desert animal, and cooling of the exhaled air reduces evaporation from the respiratory tract, an obvious advantage in their water balance.

If we compare desert birds with non-desert birds, we might expect to discover some difference between the two groups which

may give an advantage in water conservation to the desert species. The results for seven species of birds, which are summarized in figure 6, give no indication that the desert birds are different from

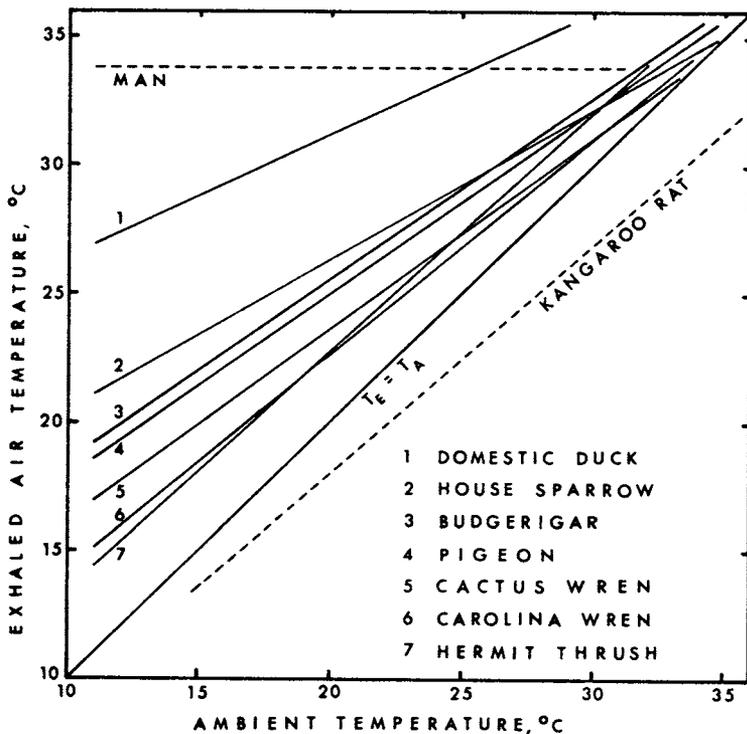


Figure 6. Temperature of exhaled air in seven species of birds. Regression lines obtained from data similar to those in figure 5 and calculated by least squares method. The dashed line for kangaroo rat shows that cooling of the exhaled air is more effective in this animal than in birds. The line labelled *Man* is for one individual; other persons would be represented by somewhat different lines, usually with a positive slope. (From Schmidt-Nielsen *et al.* 1970b.)

non-desert birds. In fact, the cactus wren had slightly higher exhaled air temperatures than its close relative, the Carolina wren. Similarly the Australian budgerigar (parakeet), a typical inhabitant of arid lands, was practically indistinguishable from the ordinary house sparrow.

One species of bird distinguished itself by being outside the general range, the domestic duck had considerably higher exhaled air temperatures than the other birds. This is undoubtedly related

to the fact that the nasal passages are much wider, and the conditions for heat exchange are therefore far less favorable. The exhaled air temperatures of man would be substantially higher again (although his body temperature is some 3 or 4 degrees below that of the birds), usually in the range of 34 to 35 °C. The reason is the same; the wide passageways are not favorable to heat exchange between air and the surfaces over which it flows.

The kangaroo rat, as we saw before, cools the exhaled air to temperatures below those of the ambient air, and its regression line is therefore located well below the group of birds of similar size. This difference between the birds and the kangaroo rat is easy to understand in terms of the structure of the nasal passageways and the conditions for heat exchange between the respiratory air and the nasal walls. Cross-sections of the nose of a kangaroo rat (figure 7) show a very narrow passage with a large wall surface;

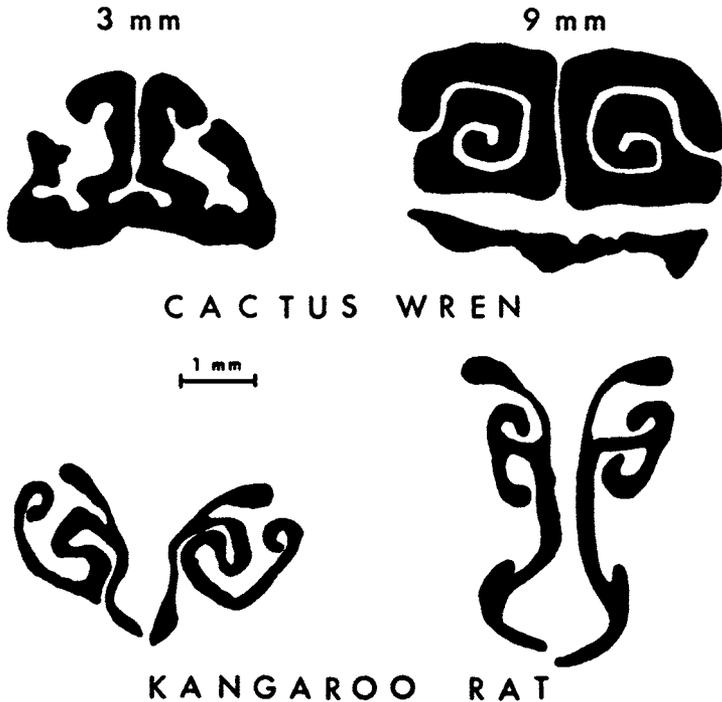


Figure 7. Cross-sections of the nasal passageways of cactus wren and kangaroo rat. The passages are wider and the wall area smaller in the bird than in a mammal of the same body size (about 35 g). In both animals the profiles were obtained at a depth of 3 mm and 9 mm, respectively, from the external openings. (From Schmidt-Nielsen *et al.* 1970b.)

this facilitates to the utmost exchange of heat between the air and the nasal tissues as it flows closely over the surface. In the birds, where the passageway is wider and shorter, the surface area is smaller, and conditions for heat exchange are less favorable. In the duck the passageways are larger again, and in man the heat exchange between air and nasal walls is so incomplete that under most circumstances it is of only minor importance. Thus, the statement, that air is exhaled saturated at body temperature or very nearly so, is quite true for man and is in accord with actual observations. The mistake has been to generalize by assuming that this would hold true for all other warm-blooded animals.

Effects on water balance

If we wish to examine the importance of cooling of the exhaled air for the water loss from an animal, it is helpful first to recall that the water vapor content of saturated air is highly dependent on the temperature. The curve shown in figure 8 illustrates the rapid

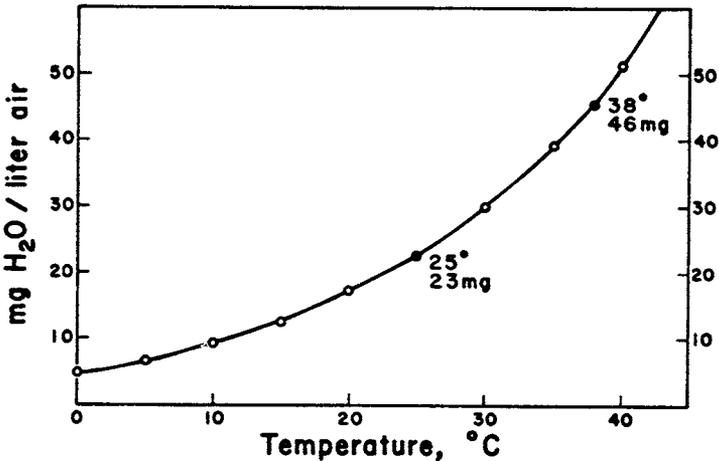


Figure 8. Water vapor content in air at saturation (100% relative humidity). The slope of the curve becomes increasingly steep around the body temperature of birds and mammals, thus greatly increasing the amount of water required for saturation of lung air.

increase in the amount of water vapor that can be held in air at higher temperatures. As a rule of thumb, I have found it convenient to remember that saturated air at body temperature contains

exactly twice as much water vapor (46 mg l^{-1}) as saturated air at room temperature (23 mg l^{-1}). Cooling of the exhaled air from body temperature to room temperature therefore reduces by one-half the amount of water vapor that the air can carry away, indeed a substantial water saving when we remember that evaporation is responsible for the major water loss from the animals we have under consideration.

The effect of cooling the exhaled air on the water balance of the kangaroo rat is shown in figure 9, and this graph can be used

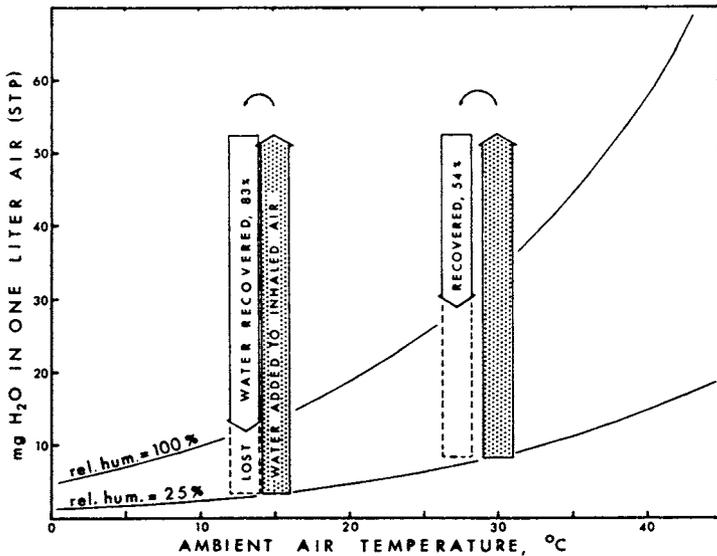


Figure 9. Diagram showing recovery of water from exhaled air in the kangaroo rat. When air is inhaled at 15°C and 25% relative humidity, the amount of water needed to bring this air to saturation at body temperature (38°C) is indicated by the shaded bar placed at 15°C on the abscissa. Under these atmospheric conditions the kangaroo rat exhales air at 13°C , and the amount of recondensed water is represented by the unshaded column. The bars to the right in the diagram give evaporation and recovery at ambient air of 30°C , 25% relative humidity. (From Schmidt-Nielsen *et al.* 1970b.)

as an illustration of the effect on small rodents in general. These calculations are for two arbitrarily selected air temperatures, 15 and 30°C , both at the equally arbitrarily chosen 25% relative humidity. In this diagram the shaded bars indicate the amount of water vapor that must be added to one liter of outside air as it is inhaled and brought to saturation at body temperature (38°C).

The unshaded bar which is placed next to each shaded bar is located at the corresponding temperature of exhaled air under the selected conditions. If air is inhaled at 15 °C, for example, exhaled air will be at 13 °C. In this case the cooling of the exhaled air causes the recondensation of 83% of the water that was added on inhalation, i.e. only about one-sixth of the water needed to saturate the respiratory air is lost by the animal. At 30 °C the savings are smaller, but even so, 54% of the evaporated water is saved as compared to what would be lost had the air been exhaled at body temperature.

In a typical bird, the cactus wren can be an example, the water savings will be less because the cooling of the exhaled air is not as effective, yet they will be substantial. For conditions similar to those used for the kangaroo rat, an air temperature of 15° and 25% relative humidity, the water saving will be 74%, and at 30° it will be 49% (Schmidt-Nielsen *et al.* 1970b). It should be remembered, of course, that the body temperature of birds is higher than in mammals (41 °C *v.* 38 °C) and more water is required to saturate the lung air.

What effect do these water savings have on the heat budget of these small animals? Table 3 shows an account of the heat that a

Table 3. *Comparison, for the kangaroo rat, of the amount of heat required for warming and humidification of one liter of inhaled air with that recovered by cooling of the same air on exhalation. Under the chosen atmospheric conditions (15 °C, 25% relative humidity, as in figure 9, left), 88% of the added heat is recovered. The recovered heat is 16.1% of the metabolic heat produced concurrently with the breathing of 1 liter of air (192 cal.).*

	Added upon inhalation	Recovered on exhalation	% Savings on exhalation
Heat of vaporization	28.5 cal	23.5 cal	83%
Heating of air	6.8 cal	7.4 cal	107%
Total heat	35.1 cal	30.9 cal	88%

Savings in % of metabolic heat production = 16.1%

kangaroo rat adds to the air during inhalation, and how much is recovered again on exhalation. It turns out that, at 15 °C, 35 calories are used to heat and humidify one liter of respired air, but

of this heat 31 calories are recovered on exhalation. Thus, some 88% of the heat used to warm and humidify exhaled air is recovered again, and therefore does not constitute a drain on the body heat. It is evident that this is quite significant, for it is 16% of the simultaneous metabolic heat production. At higher ambient temperatures the relative importance of heat savings will be less, but at lower temperatures it will be greater.

In man the large dimension of the nasal passage and a laminar air stream cause a far less complete heat exchange between the stream of respired air and the nasal walls, the distance from the center of the stream to the wall is too great. Man exhales air at close to body temperature, and the recovery of heat and water vapor is usually insignificant. At very low air temperatures, however, the amount of heat that is lost due to heating and humidification of inhaled air becomes a substantial item in the heat budget even in man. For example, for a man breathing dry air at 0 °C, nearly one-fifth of his metabolic heat is used to heat and humidify the respiratory air. At even lower air temperatures the passageways begin to cool off substantially, for example at 30 °C, recovery of heat and water from the exhaled air becomes quite important in reducing the drain on the heat resources of a man (Walker, Wells and Merrill, 1961; Webb, 1951, 1955).

Mathematical model of nasal heat exchange

If we wish to examine the nasal passageway as a heat exchanger, we find that there is a formidable number of variables to be considered. As heat diffuses between air and wall, water is either evaporated or condensed, and in the process binding or releasing substantial amounts of latent heat. Of obvious importance for heat and water flux are such geometrical variables as the total surface available for heat exchange, and the distance from the core of the air stream to the wall. External physical conditions, air temperature and humidity, must be important, for both influence heat transfer and evaporation. We also have a number of physiological variables to consider; the rate of respiration and the volume of respired air can vary, and both influence the linear velocity of the air stream flowing over the nasal surfaces, a velocity which is continuously changing during each respiratory cycle. Then there is the blood stream that not only supplies the water that is evaporated, but also carries heat from the body core to the nasal region.

During inhalation heat flows transversely from the wall to the air stream, and water vapor flows into the air along the transversal temperature gradient thus established. On exhalation this process is reversed, heat flows from the air to the nasal wall, and, as the temperature decreases, water vapor diffuses transversally and recondenses on the surface. To describe these processes adequately during the constantly changing linear flow rates during a single breath has proved an unmanageable problem.

One of my former students, Dr J. Collins, has shown that this intractable number of variables can be disregarded and the nasal passage can be analyzed as a relatively simple steady-state model. Figure 10 shows in diagrammatic form a model of the nasal passage,

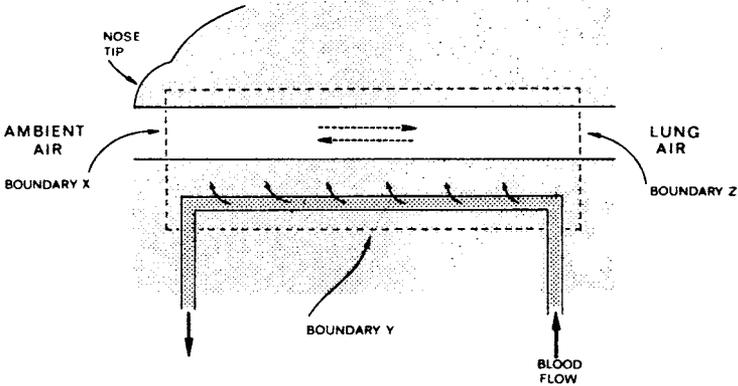


Figure 10. Heat and water exchange in the nasal passageway can be analyzed as a steady-state model by examining the energy transfer across an imaginary boundary indicated by the dashed line in this diagram. A mathematical model, as described in the text, can be used to predict nose temperatures and efficiency of water recovery as given in tables 4 and 5.

a liquid flow stream (blood), and an imaginary boundary indicated by a dotted line. This imaginary boundary encloses the nasal passage and its moist surface, beginning at a given distance from the the nose tip at Boundary X, and extending along Boundary Y to Boundary Z where the temperature equals body-core temperature. Energy transported across this boundary can be separated conceptually into several components. First of all, the air crossing Boundary Z undergoes no change in energy content, for by definition this boundary is where the air is at body temperature and saturated. The energy crossing Boundaries X and Y can be separated into four components:

- (a) change in air temperature,
- (b) evaporation of water,
- (c) thermal conduction to outside,
- (d) change in blood temperature.

This permits the development of a mathematical model which describes the steady-state energy balance of the system, in which the rate of energy transfer from the liquid stream (designated *(d)* above, representing blood flow and heat diffusion from the body core to the nasal region) is equated with the sum of energy transfer (*(a)*) by a change in the temperature of respiratory air, (*(b)*) by evaporation, and (*(c)*) by direct conduction from the nose tip itself to the environment, or $(a) + (b) + (c) = (d)$. All the variables which enter the equation, except the flow rate of the liquid stream (*(d)*), can be measured or estimated from physiological measurements. This permits the solution of the equation for the liquid stream flow rate. After having obtained an empirical solution for the liquid stream flow rate, this variable can be eliminated and a general energy balance equation can be completed, which in turn can be used to compute values for expired air temperatures, rates of water loss, and efficiency of vapor recovery, for a variety of ambient air conditions.

I shall omit a discussion of how the mathematical model was justified and tested against physiological measurements, for the lengthy details have been given elsewhere (Collins, Pilkington and Schmidt-Nielsen, 1971). Instead I give two tables which show the computer print-out for predicted nose temperatures of kangaroo rats under a variety of atmospheric conditions, and the efficiency of predicted water recovery in the nose. Table 4 shows model-predicted nasal temperatures. It contains no great surprises, the exhaled air temperature depends very much on ambient conditions, and especially the relative humidity of the inhaled air is important. At high humidities, cooling of the exhaled air, as expected, is uniformly not as great as in dry air.

More surprising is the model-predicted efficiency of water recovery in the nasal passages (table 5). Under the wide variety of ambient air temperature from 10 to 36 °C, and relative humidities from 0 to 100%, the predicted efficiency of water recovery varied only from 66 to 77%. In other words, in spite of changing ambient conditions the model predicts that the efficiency of water recovery should remain fairly close to three-quarters, a finding that without the aid of a computer would require an inordinate amount of

Table 4. *Computer-predicted nose tip temperature of the kangaroo rat as a function of ambient conditions. (From Collins et al. 1971)*

Amb. temp. (°C)	Ambient relative humidity (%)					
	0	20	40	60	80	100
10	9.8	11.8	13.7	15.3	16.8	18.1
12	10.7	12.9	14.8	16.5	18.1	19.5
14	11.7	14.0	16.0	17.8	19.4	20.9
16	12.6	15.1	17.2	19.1	20.8	22.4
18	13.6	16.2	18.4	20.4	22.2	23.9
20	14.6	17.3	19.7	21.7	23.6	25.3
22	15.6	18.5	21.0	23.1	25.1	26.9
24	16.6	19.6	22.2	24.5	26.5	28.4
26	17.7	20.8	23.5	25.9	28.0	29.9
28	18.8	22.0	24.9	27.3	29.5	31.4
30	19.7	23.2	26.1	28.6	30.9	33.0
32	20.6	24.3	27.4	30.0	32.4	34.5
34	21.6	25.4	28.6	31.4	33.8	36.0
36	22.6	26.6	29.9	32.8	35.3	37.6

Table 5. *Computer-predicted efficiency of nasal vapor recovery in the kangaroo rat as a function of ambient conditions. (From Collins et al. 1971)*

Amb. temp. (°C)	Ambient relative humidity (%)					
	0	20	40	60	80	100
10	0.755	0.756	0.758	0.760	0.763	0.766
12	0.749	0.750	0.753	0.755	0.758	0.762
14	0.743	0.745	0.747	0.750	0.754	0.757
16	0.736	0.739	0.741	0.745	0.749	0.753
18	0.730	0.732	0.735	0.739	0.743	0.748
20	0.723	0.725	0.729	0.733	0.737	0.743
22	0.715	0.718	0.722	0.726	0.731	0.737
24	0.707	0.710	0.714	0.719	0.725	0.731
26	0.698	0.702	0.706	0.711	0.717	0.724
28	0.688	0.692	0.697	0.703	0.709	0.715
30	0.682	0.686	0.692	0.697	0.703	0.710
32	0.675	0.680	0.685	0.691	0.697	0.704
34	0.667	0.672	0.678	0.684	0.690	0.696
36	0.659	0.665	0.671	0.677	0.682	0.686