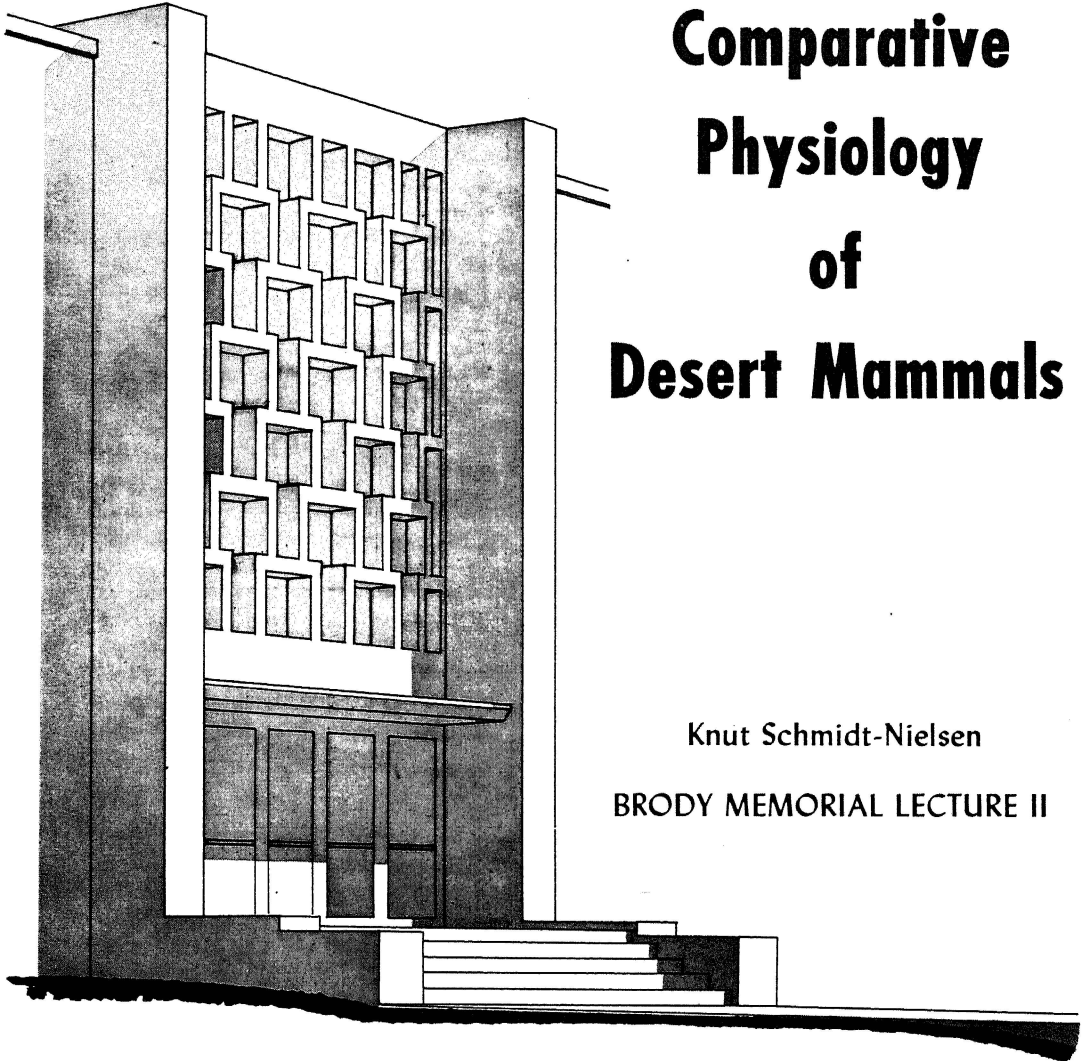# Comparative

Physiology

of

Desert Mammals

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BRODY MEMORIAL LECTURE II

UNIVERSITY OF MISSOURI

AGRICULTURAL EXPERIMENT STATION

TABLE OF CONTENTS

INTRODUCTION

The subject which I have chosen for this lecture is in the field of environmental physiology, and as such it is close to those problems which concerned Dr. Brody and his collaborators the most. It is a privilege and an honor to have this opportunity to present the results of studies concerned with animals that show an extreme degree of adaptation to hot, dry desert conditions, and it is my hope that the research which I will describe can to some small extent lend perspective to the fundamental studies of climatic physiology for which the Missouri group has become so renowned.

It has been estimated that the arid zones comprise between one-fifth and two-fifths of the earth's land surface. In these extensive areas water is at a premium, and temperatures are often excessive. A major physiological problem is to remove excess heat from the body, in contrast to more moderate surroundings where the conservation of body heat is essential for warm-blooded animals. Unless heat is dissipated from the body, its temperature rises to levels incompatible with life.

In a hot environment the usual avenues for heat loss, conduction, convection and radiation to the cooler surroundings, are no longer available. On the contrary, if the environment is warmer than the body, heat flows from the hot surroundings toward the organism, and to keep the body temperature from rising, the excess heat must somehow be dissipated. The only means for removing heat under these conditions is through the evaporation of water. Thus the availability of water becomes a physiological prerequisite in an environment where water is already at a premium.

The possible avenues that can be explored in order to solve this dilemma are limited. Man has penetrated all the major desert areas of the world, but he can do so only because of cultural adaptations. Physiologically, he is capable of living in the hottest deserts, provided sufficient water is available. This he obtains either by bringing it with him or through other technological means such as drilling. Without these adjuncts man is unsuited to subsist under true desert conditions.

The adaptations that permit desert animals to live under such conditions are either physiological or behavioral. The simplest solution is that of escape, but if an animal leaves the desert during the hottest season, it is not a true desert animal and we need not be concerned with it here. However, another route of escape from the scorching heat on the desert surface is to dig into the ground. Many small animals, rodents, reptiles, and insects, do this. In a sense, they are not physiologically adapted to the extreme heat, although they may be well-adapted as desert animals. Large animals, such as camels and gazelles, must remain above ground and endure the torrid environment. Their physiological adaptations, which are limited by the need to prevent the body temperature from rising to a lethal level, must consist in the utmost water economy.

It is my intention to begin this lecture with a brief description of the physiological reactions of man to desert heat and thus lend perspective to the ensuing discussion of two typical desert animals. One is the camel, which uses water in heat regulation and therefore periodically must drink. The other is a

small rodent, the kangaroo rat, which eats only dry food and lives a life without drinking water in one of the driest environments in the world.

MAN

If a man is deprived of drinking water in the hot desert, the use of water for heat regulation will deplete his body of its normal water content. The symptoms soon become noticeable, and their severity increases with increasing water deficit. The information given in Table 1 was compiled by Adolph and his collaborators (1),

TABLE 1-SYMPTOMS CHARACTERISTIC OF DESERT
DEHYDRATION IN MAN (1.)

Water deficit, % of body wt.	Symptoms
1 - 5	Thirst Discomfort and complaints Anorexia Apathy
5 - 10	Stumbling Headache Indistinct speech Dyspnoea Cyanosis
10 - 15	Spasticity Delirium Inability to swallow Shriveled skin Sunken eyes
> 15	Deafness Numb skin Stiffened eyelids Cracked skin Anuria

but only the more moderate effects were observed in experimental work. The information about severe dehydrations in man has been pieced together from observations made when persons have been accidentally lost in the desert. Therefore the exact degree of dehydration that can be tolerated by man is uncertain, but we can conclude from experiments with animals that a water loss corresponding to 18% of his initial body weight is fatal. At this degree of dehydration kidney function stops and the man is virtually dead. With a water deficit of 12 or 14% there is inability to swallow and a man cannot recover without aid. At a 6% deficit movements lack coordination, and the man is in poor condition, both mentally and physically.

If an already dehydrated man is exposed to excessive heat, his tolerance to water depletion is greatly reduced. It has been estimated that in hot surroundings
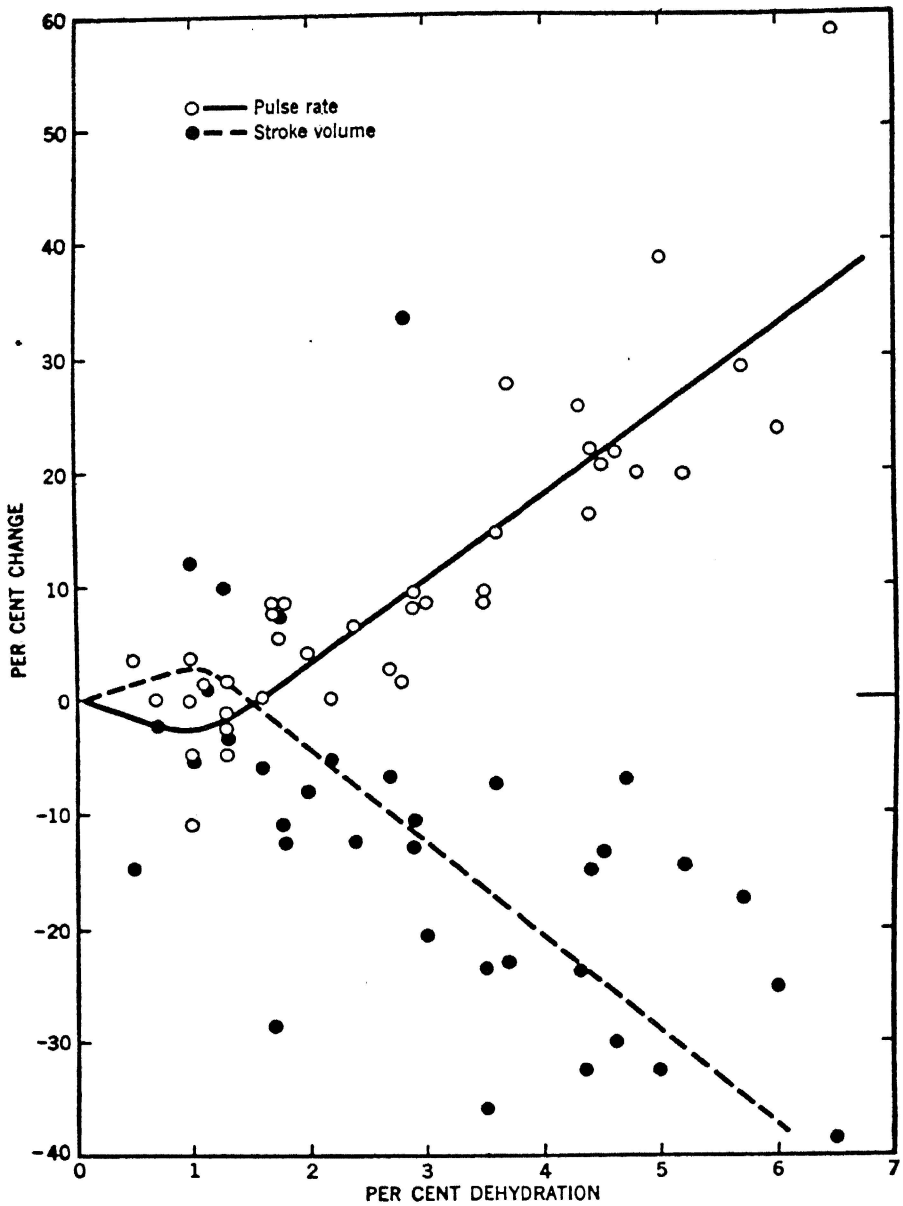
Fig. 1–Cardiac stroke volume and simultaneous pulse rates in relation to dehydration in man. With increasing dehydration the increase in pulse rate is accompanied by a corresponding decrease in stroke volume so that the output of the heart remains constant (1).

a dehydration of about 12% is fatal. At this point the blood has lost much water and its viscosity is greatly increased. This means that the resistance to the flow of blood in the vascular system increases, adding to the demands on the heart. When the heart cannot keep up with the demands, the heat produced in the deeper parts of the body is not transported fast enough to the surface. The result is a marked rise in temperature in the deeper parts, and as these symptoms develop at an accelerating rate the result is a fatal increase in body temperature which has been termed an "explosive heat rise."

The fact that explosive heat rise occurs also in the dog has made it possible to study the phenomenon experimentally. It is of interest to note that some desert animals can tolerate a much more severe dehydration than dog and man without becoming subject to explosive heat rise.

As man has been subjected to experimental dehydration, some clarification of his reactions to water loss has been obtained. With increasing dehydration the heart rate goes up (Figure 1). However, at the same time the stroke volume decreases, and in spite of the increased heart rate the cardiac output remains unchanged. Thus the net result is that the work of the heart is increased without any benefit to the circulation of blood. With further dehydration the viscosity of the blood increases the load on the heart until the physiological limit is reached and the explosive heat rise ensues.

As a man becomes dehydrated his body temperature rises above the normal level (Figure 2). The steady rise in body temperature which accompanies increasing water deficits is assumed to be due to a failure of temperature regulation. As we shall see, much greater temperature increases may occur in desert animals under circumstances that suggest a well regulated physiological mechanism rather than a failure of regulation.

In a hot desert a man may sweat as much as 1 or $1\frac{1}{2}$ liters per hour. (Higher sweating rates have been observed under experimental conditions, but at the moment we are concerned with the response to a desert climate.) If a man remains exposed to the desert heat for a full day, the amount of water used for sweat may amount to 10 or 12 liters, or even more. If the water loss is not replaced, a single day in a hot desert can bring the man to the lethal limit of dehydration. Yet, the deserts of the world have a rich indigenous fauna of mammals which are able to subsist under conditions that to man seem incompatible with life.

THE NEED FOR WATER - WATER BALANCE

The brief diagram in Figure 3 lists the various components in the water balance of an animal. When the losses are equalled by the water intake, the animal is in water balance. How this can be achieved in an environment where virtually no water is available will be our major concern in the following discussion.

The losses consist of water eliminated with the urine and the feces, as well as that lost by evaporation. Some water always evaporates from the respiratory tract and from the skin of mammals. When water is used for the dissipation of heat, the evaporation is greatly increased, constituting the most important drain on the water resources.
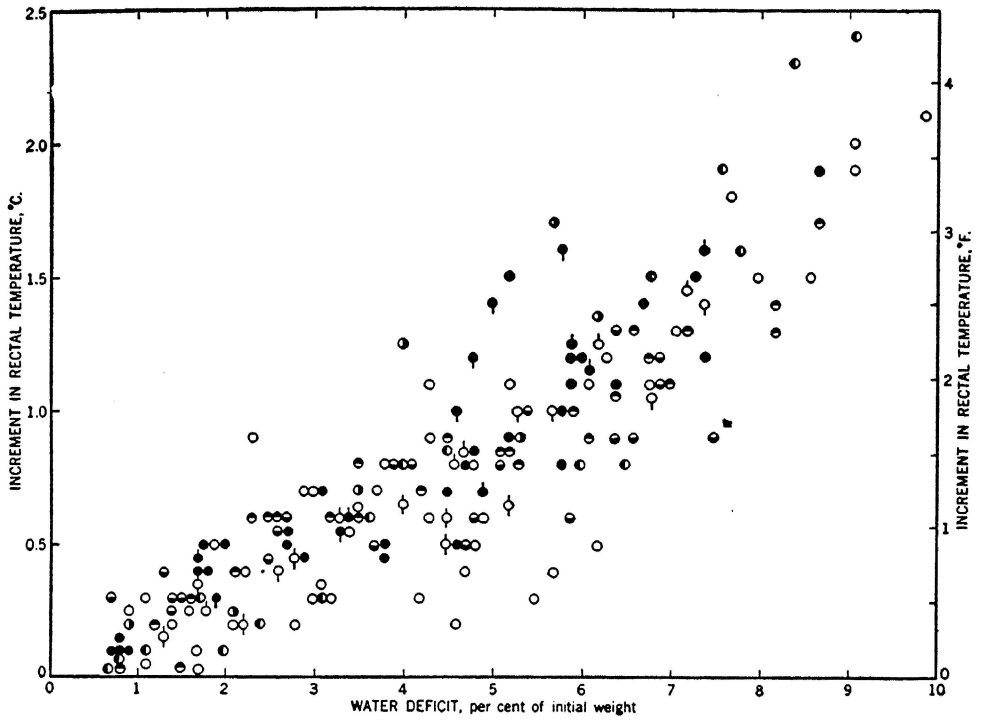
Fig. 2-With increasing dehydration in man the rectal temperature tends to rise above the normal temperature for the same person in hydrated condition (1).

Drinking water Water in food Oxidation water	=	Evaporation $\langle$ Lungs Skin Urine Feces

Fig. 3-When water intake equals the water losses an animal is in water balance.

The intake of water has two major sources, free water taken as drinking water or present in moist foods, and water formed in the metabolism. Even the driest plant materials contain some free water, and succulent plant material may contain as much as 90 or 95%. Less conspicuous is the water formed by the oxidation of foodstuffs, oxidation water or "metabolic" water. The amount depends on how much hydrogen is oxidized in the metabolic processes and therefore on the metabolic rate, and to some extent on the composition of the foodstuffs as well.

Whenever water is used for temperature regulation, evaporation becomes the dominating factor in the water balance. We will therefore briefly discuss the amount of water which is needed for heat regulation in a hot desert. Table 2

TABLE 2-THE EVAPORATION FROM DONKEY, MAN, AND DOG
AS OBSERVED UNDER HOT DESERT CONDITIONS IN THE
SOUTHWESTERN UNITED STATES

	Body weight, kg	Evaporation, % of body weight per hr.	Evaporation, kg per m^2 per hr.
Donkey	96	1.24	0.573
Man	79	1.41	0.60
Dog	16	2.62	0.657

shows observations made by Adolph and Dill in the Nevada desert on three mammals, man, donkey, and dog. It is worth noting that the evaporation due to heat regulation was more than twice as high in the dog as in the larger donkey. However, if the evaporation is calculated per square meter surface, the use of water was of the same magnitude in the three animals. Actually, this could be predicted because the heat load on a mammal is related to the surface of the organism rather than to its weight.

The heat load has two components, metabolic heat and heat impinging from the hot environment. Both are approximately proportional to the body surface. We can therefore from the body surface estimate the amount of water needed for any smaller or larger mammal for temperature regulation in a hot desert. Since the small animal has a larger relative surface, the theoretical need for water is higher. The simplest way to present the estimated need for water is a graph such as shown

in Figure 4. In this graph the actual observations on donkey, man, and dog have been used as a basis for estimating the need for evaporation in larger and smaller animals on the assumption that they are exposed to a similar desert environment and use water to maintain their body temperature.

If an animal is large, such as the camel, it can be estimated that due to its smaller relative surface, its need for water should be about one-half of that in man. Actual measurements on the camel show that its evaporation, when it is exposed to hot desert conditions, is less than shown by this extrapolation. The physiological mechanisms involved in this water economy will be discussed after we have considered the effect of a small body size.

If a small animal should maintain its body temperature in hot desert surroundings there would be a tremendous increase in the calculated need for evaporation (see Figure 4). In fact, the use of water would be so great that a 100 gram kangaroo rat would use 15% of its body weight per hour if it were to keep cool while staying out on the desert surface during the day. This makes it impossible for small animals to depend on evaporation for temperature regulation, and the only way out is to avoid the heat. As a consequence, small desert mammals are nocturnal and have virtually no active defense against overheating.

The difference between a small and a large body could also be expressed by saying that the smaller one has less "thermal inertia." If a pebble and a large rock are placed on the hot desert surface, the pebble heats up much faster - its thermal inertia is less. This is directly related to the relative surface, and the same situation holds for animals. The difference between the camel and the kangaroo rat is illustrated in Figure 5, which shows that the surface, relative to the body weight, is more than 20 times as great as in the kangaroo rat. This effect of body size is of fundamental influence in determining which physiological adaptations can profitably be exploited to enable an animal to live in a hostile desert environment.

THE CAMEL

The camel is known as an excellent desert animal that can traverse the vast expanses of the Sahara with a minimum of water and food. It has been stated that camels can go for a week or even two weeks or more without drinking, but such statements are meaningless unless they include information about such factors as temperature, the load carried, the distance traversed and the speed, and, of course, the water content of any food eaten. In fact, during the winter when the vegetation is fresh and no water is used for temperature regulation, camels need not be watered at all.

Does the camel store water?

It has been said that the camel drinks huge quantities of water before a long desert journey. How it understands and anticipates the needs is never explained but the belief in water storage is firmly rooted. Support for the hypothesis has been sought in the unusual structure of the camel's stomach. Being a ruminant, the camel has several stomachs. The foremost of these, the rumen, has a special structure. In two areas, the smooth wall forms pockets or sacs that are subdivided into smaller chambers. Since this structure is absent in other ruminants, it has
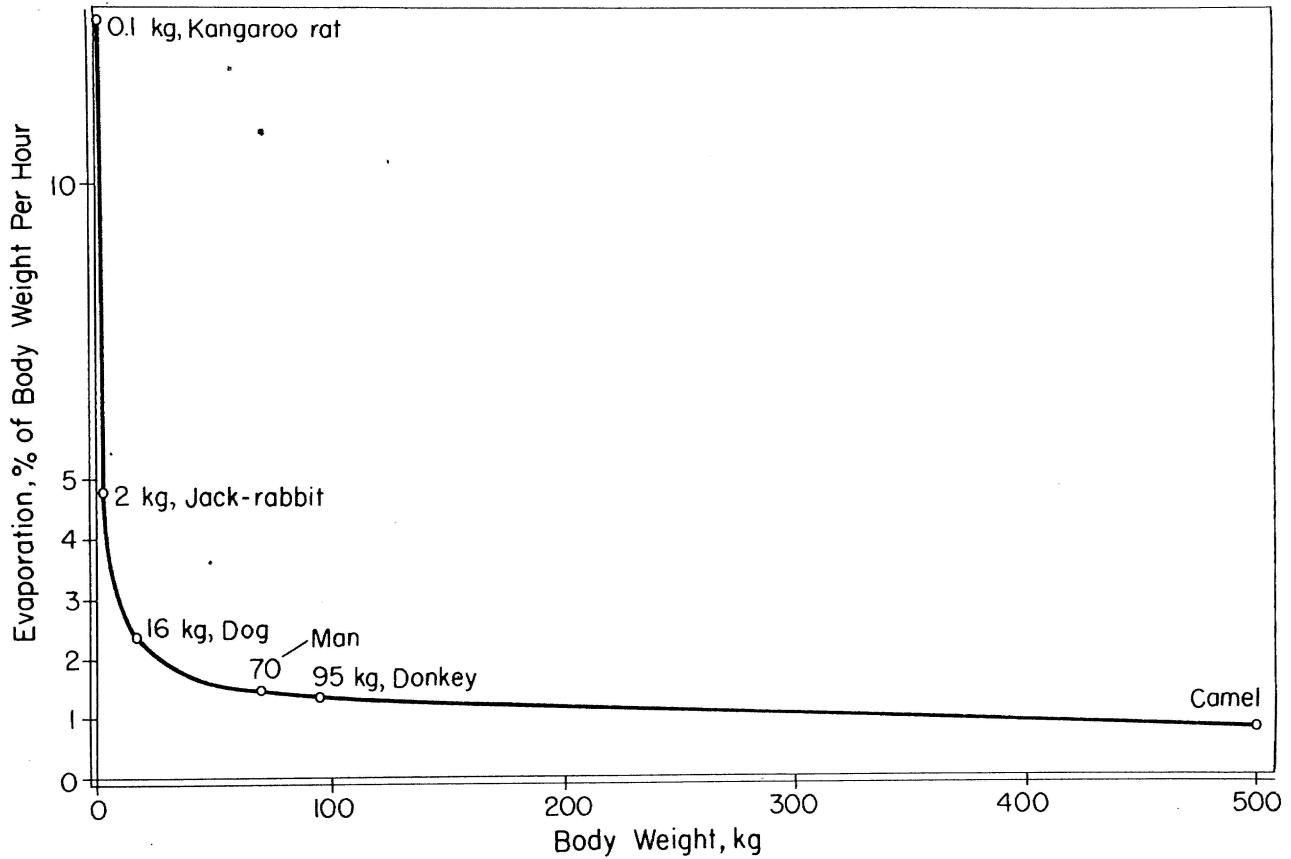
Fig. 4—The calculated need for evaporation in an animal which is assumed to use water for heat regulation when exposed to a hot desert environment. The curve is calculated on the basis of actual observations on dog, man, and donkey (see Table 2). The extrapolation to larger and smaller body size has been carried out as described in the text (8).

IN HOT ENVIRONMENT HEAT GAIN IS PROPORTIONAL TO BODY TEMP.

CONDUCTION +
CONVECTION   } ALL THESE
RADIATION   } APP. PROPORTION-
METABOLISM   } AL TO SURFACE

"THERMAL INERTIA"

LOW   HIGH

HEAT GAIN RAPID   HEAT GAIN SLOW
3000 cm^2/Kg   130 cm^2/Kg
(X20)

Fig. 5—An animal the size of a kangaroo rat has a relative surface more than 20 times as large as the camel, and its thermal inertia is therefore correspondingly low (12).

been associated with the reputed water storage, and the compartments have been called "water sacs." The edges of the sacs have muscular bands which have been interpreted as sphincters capable of closing off the sacs to prevent contamination of the water with the fermenting feed in the rumen.

In reality, there is no support for the water storage hypothesis. The total volume of the compartments is less than a gallon, a minimal quantity for an animal that can consume more than 25 gallons in a single drinking session. The so-called "sphincters" are straight muscular bands which could not possibly close the sacs. When the rumen from normal camels is examined, the compartments always contain coarsely masticated feed, and of some 20 camels I have examined, I have found none which had water in these compartments. Their walls are covered with glands; in this respect, also, the camel is different from other ruminants, whose rumen contains no glands (4). This suggests that the function of the sacs is digestive. It is true that the rumen of the camel contains appreciable quantities of liquid, but in proportion to its body size the amount is rather less than found in, for example, cows. The liquid is isotonic with blood and has undoubtedly the same funcation as the rumen liquid in other ruminants--that of providing a suitable medium for the microbial flora which aids in digestion of the feed.

Another structural characteristic of the camel is its hump. This also has been related to water storage. The hump consists of adipose tissue, and as the camel travels in the desert on a scanty supply of feed, the fat is gradually used up. When fat is metabolized, 1 gram yields 1.1 gram of oxidation water. The immediate conclusion is that a camel which consumes most of the fat in its hump during an extensive desert travel gets a large quantity of oxidation water in the process. For example, if 40 kg of fat is used, 44 liters of water is formed. This is a great deal of water, but unfortunately, it is not a net gain. Since the metabolism of fat requires uptake of oxygen, the necessary ventilation of the lungs entails a certain water loss as relatively dry air is taken into the lungs and exhaled again saturated with water vapor. It is possible to calculate the approximate respiratory water loss, and we obtain a rather interesting result which is summarized in Table 3.

TABLE 3-COMPARISON OF OXYGEN UPTAKE AND WATER FORMATION
IN THE METABOLISM OF FAT AND OF CARBOHYDRATES
FOR A METABOLIC LEVEL OF 10,000 KCAL

	Foodstuff used, kg	Oxygen used for oxidation of food, liter	Oxidation water formed, kg	Approximate evaporation from lungs in dry air kg
Fat	1.06	2130	1.13	1.8
Starch	2.39	1980	1.33	1.7

If we assume that a camel has a metabolic rate of 10,000 kcal per day, slightly more than 1 kg of fat is used and 1.13 liters of water is formed. Since more than 2,000 liters of oxygen is needed, there is a considerable respiratory water loss which in dry air will be approximately 1.8 liters. In other words, the formation of oxidation water inevitably involves a respiratory loss of water in excess of that formed.

It is interesting to compare this result with the hypothetical situation of energy being stored not as fat, but as carbohydrate (see Table 3). The caloric value of carbohydrate is about one-half that of fat, and a greater amount of carbohydrate is therefore needed to cover the 10,000 kcal. Thus, although carbohydrate yields less oxidation water per gram, the total yield of water would be greater than in fat metabolism. Furthermore, since carbohydrate requires less oxygen for its metabolism, the respiratory water loss would be somewhat lower. Nevertheless, there would still be a net loss of water, and we therefore find that in either case the evaporation from the lungs exceeds the amount of oxidation water formed.

Although it remains true that water is formed in the metabolism of fat, there is no net gain, and we are therefore not justified to say that stored fat constitutes a water storage. Of course, oxidation water is formed in the metabolism of all animals, but this does not enable them to live in the desert. Fat is the usual form of energy storage in animals in general, the only unusual thing about the camel is the location of the fat in a hump and this can make no difference to formation of oxidation water.

Since neither the stomach nor the hump can be assigned any role in water storage, what other possibilities are there? There are no other anatomical features of the camel that would be suitable for water storage and the only possibility that remains is that the camel could be able to overhydrate its body in general and distribute excess water in all tissues and body fluids. During our work in the Sahara we found no indication that this takes place. Camels that had been exposed to water deprivation would afterwards drink sufficiently to restore their original water content, but there was no evidence that they overdrank or overhydrated in order to have available an excess of water in anticipation of future physiological needs.

Temperature regulation and water economy

Since the camel is unable to seek underground shelter to avoid exposure, it can keep its body temperature from rising only by evaporation of water. Two different mechanisms can be employed, either sweating, as in man, or panting as displayed by the dog. It is of interest to examine the relative importance of these two mechanisms in the camel. Table 4 shows some respiratory rates observed in dogs

TABLE 4-BREATHING RATES IN DOG AND CAMEL

| | Respirations per min. | |
	Normal	Hot
Dog	8 – 40	350 – 400
Camel	6 – 11	8 – 18

and in camels under heat stress. When the dog is exposed to a heat load, its respiration increases from a normal level of some 20 to 40 respirations per minute to open-mouthed breathing at rates between 300 and 400 per minute. The respiratory rates found in the camel are slightly increased, but the animal continues to breathe with the mouth closed, and the changes are insufficient for any appreciable cooling.

The camel has been reputed not to sweat, but this is incorrect (5). Water evaporates easily in the dry desert air, and since the camel does not sweat more than needed for temperature regulation, the fur remains dry. However, if evaporation is prevented, such as under a saddle, the fur will be soaked with perspiration on a hot day.

When a man is exposed to hot conditions the body temperature is kept from rising by the production of an appropriate amount of sweat, and he is able to maintain a nearly constant body temperature, even in the hottest deserts.

In contrast, the camel permits some increase in the body temperature and thereby accomplishes a considerable economy with water. Instead of evaporating sufficient water to keep the body temperature constant, a limited rise is permitted. Thus heat is stored in the body, and in the cool night this heat can be dissipated by means of radiation and conduction. The water which would otherwise be used for evaporation is therefore conserved.

This simple means of saving water by temporarily storing heat is further amplified by the fact that the camel frequently has a particularly low morning

temperature after a cool night. The difference between the low morning temperature and the afternoon maximum may be as much as 6°C (see Table 5). This means that in an animal weighing 500 kg about 2500 kcal may be stored in the body during the day and dissipated again at night. This equals the heat otherwise required to evaporate between 4 and 5 liters of water, in other words, a considerable economy in the use of water.

TABLE 5-MINIMUM AND MAXIMUM RECTAL TEMPERATURE OBSERVED
IN A DEHYDRATED CAMEL WITHIN ONE DAY

Morning low	34.2^{O}C	$(93.6^{O}$F)
Evening high	40.7^{O}C	$(105.3^{O}$F)

However, the increase in body temperature during the day has a further effect on the water economy which is very important. When the body is warmer, the temperature difference between the hot environment and the body is less. Therefore, the flow of heat from the environment to the body is correspondingly reduced.

The diagram in Figure 6 depicts a hypothetical example of this effect. If a man is to maintain a constant core temperature of 37°C he must, in order to dissipate the metabolic heat, maintain a surface temperature of about 35°C. This is done by sweating. If the environmental temperature is 45°C, the temperature gradient over which heat flows to the surface of the body is 10°C. However, a
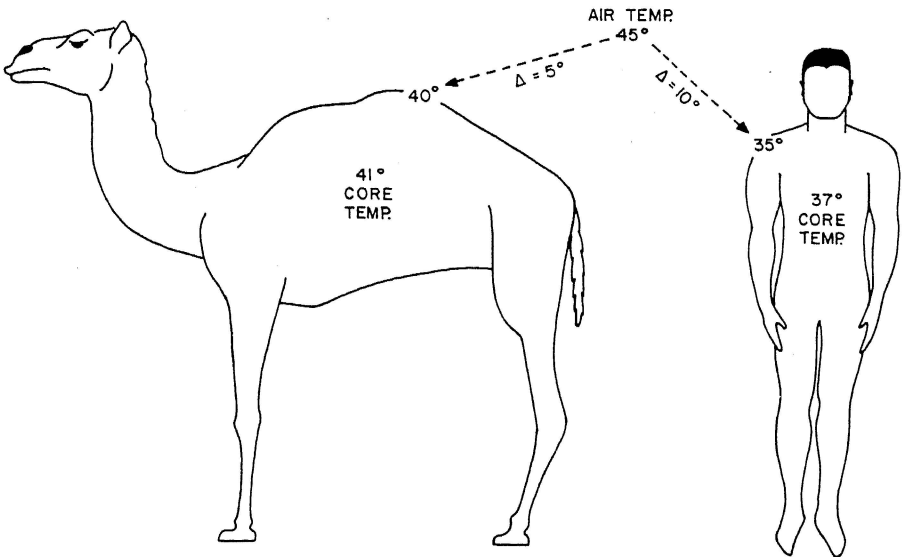
Fig. 6-The elevated body temperature of the camel results in a reduced environmental heat load. In this diagram the temperature gradient between the hot air and the body surface is 10°C in the man, but only 5°C in the camel.

-14-

hat permits its temperature to rise to 41°C can dissipate the metabolic heat
in temperature is at 40°C. In the same 45°C environment the temperature
t is now only 5°C; in other words, the gradient over which heat flows is
only half as great as in man. Thus the increase in body temperature in the camel
has a two-fold advantage: while the temperature rise takes place there is little
sweating, and when a high body temperature has been established, the environmental
heat gain is reduced.

The extreme variations in body temperature occur only in the dehydrated
camel. When a camel is watered daily the temperature fluctuations are only some
2°C (Figure 7). The water-sparing mechanism is therefore fully utilized only when
needed in the water economy.
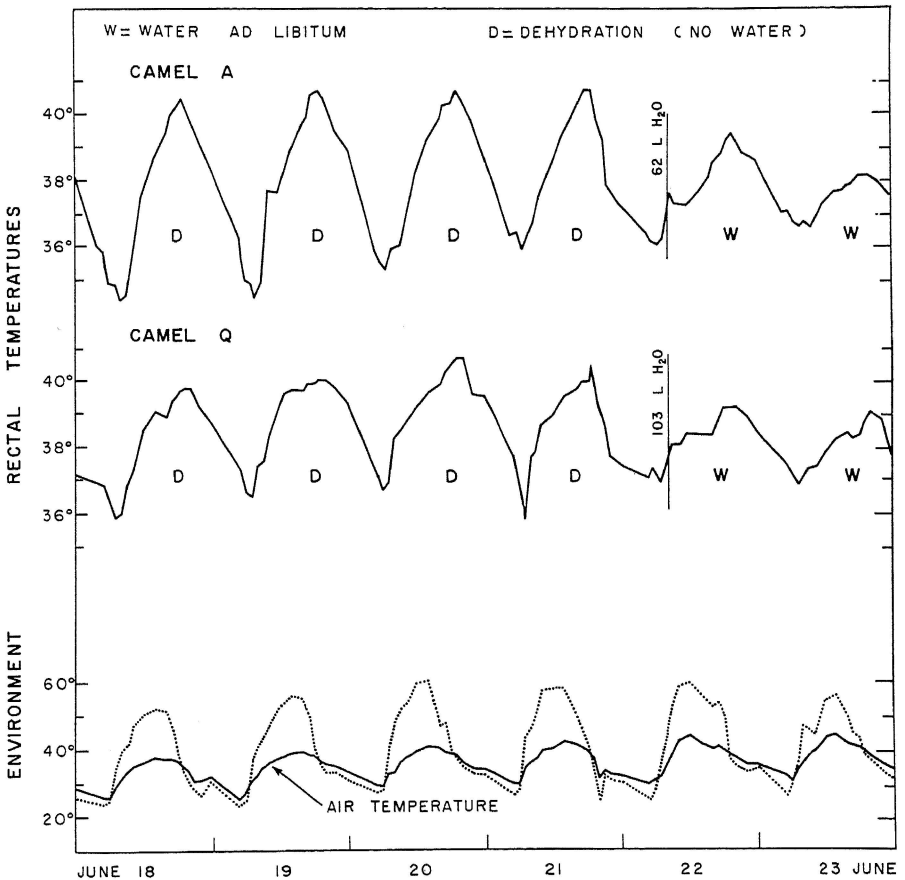
Fig. 7-In a camel deprived of drinking water (D) the rectal temperature may
vary as much as 6°C. When the same camel is given drinking water (W), the
temperature fluctuations are reduced (11). Dotted line indicates additional
heat load due to radiation from sun and ground.

There is, of course, a limit to the rise in body temperature. Even during a long severe heat load the body temperature is not permitted to rise above 41°C. This means that the increase cannot be considered simply as a failure of heat regulation, it must regarded as a part of the water conserving mechanisms employed by the camel. This may have some bearing on the use of the rectal temperature as the only criterion for heat tolerance in livestock. Undoubtedly, the animal which is unable to keep its body temperature from rising when it is exposed to a hot climate is a poor heat regulator, and in this animal the body temperature is a measure of its failure to resist the environmental heat load. However, the observations made on the camel suggest that a well controlled rise in body temperature may also be an important mechanism in water conservation, and in this animal the rise in body temperature can by no means be regarded as a lack of tolerance to a hot climate.

In addition to the advantages the camel enjoys through the rise in its body temperature, the environmental heat gain is decreased by the insulation of its fur. It is obvious that the flow of heat from warm surroundings to a cooler body is reduced if an insulating layer is imposed in between. The value of the camel's fur in this respect can best be established by comparing the use of water in a camel that has its natural wool intact with one that has been shorn (Figure 8). It appears that the unshorn camel "A" evaporates about 2/3 the amount used by camel "Q". To assure that there were no individual differences between these two camels that could account for the different evaporation, camel "A" was shorn, and it now turned out that the evaporation was identical in the two camels. (The increased evaporation in both animals was because the second test was made later in the summer and the environmental temperature was higher.) It has been repeatedly demonstrated that the use of water in a hot climate is increased when animals such as sheep have their coats clipped. Conversely, adding surface insulation has, within limits, a water sparing effect, such as demonstrated by the use of clothing in man by Adolph and his associates (1).

In addition to the rise in body temperature and the insulating value of the fur, a number of minor factors contribute to the water economy of the camel. Some of these are listed in Table 6. A camel that needs to economize with water will always tend to seek shade in order to avoid radiation from the sun. It orients its body lengthwise to the rays of the sun, and it remains sitting on the ground exposing as little surface as possible. The long legs are folded under the body so that these thinly haired surfaces are in shade and unexposed. The camel remains sitting in this position throughout the day without moving to another place where the ground has been heated by the sun. The thickest fur is on the back and over the hump where the incident solar radiation is maximal. Unfortunately, the quantitative role of these adjustments has not been established.

A characteristic of the camel is its ability to withstand an exceptional degree of depletion of its body water. The lethal limit for dehydration is unknown, but some that had lost as much as 30% of the body weight did not appear to be in serious condition. The donkey can also withstand similar dehydration.

When an animal becomes dehydrated water is lost from all fluid compartments of the body, but to different degrees. When man becomes dehydrated the reduction in volume is relatively greater in the plasma than in the other fluids.
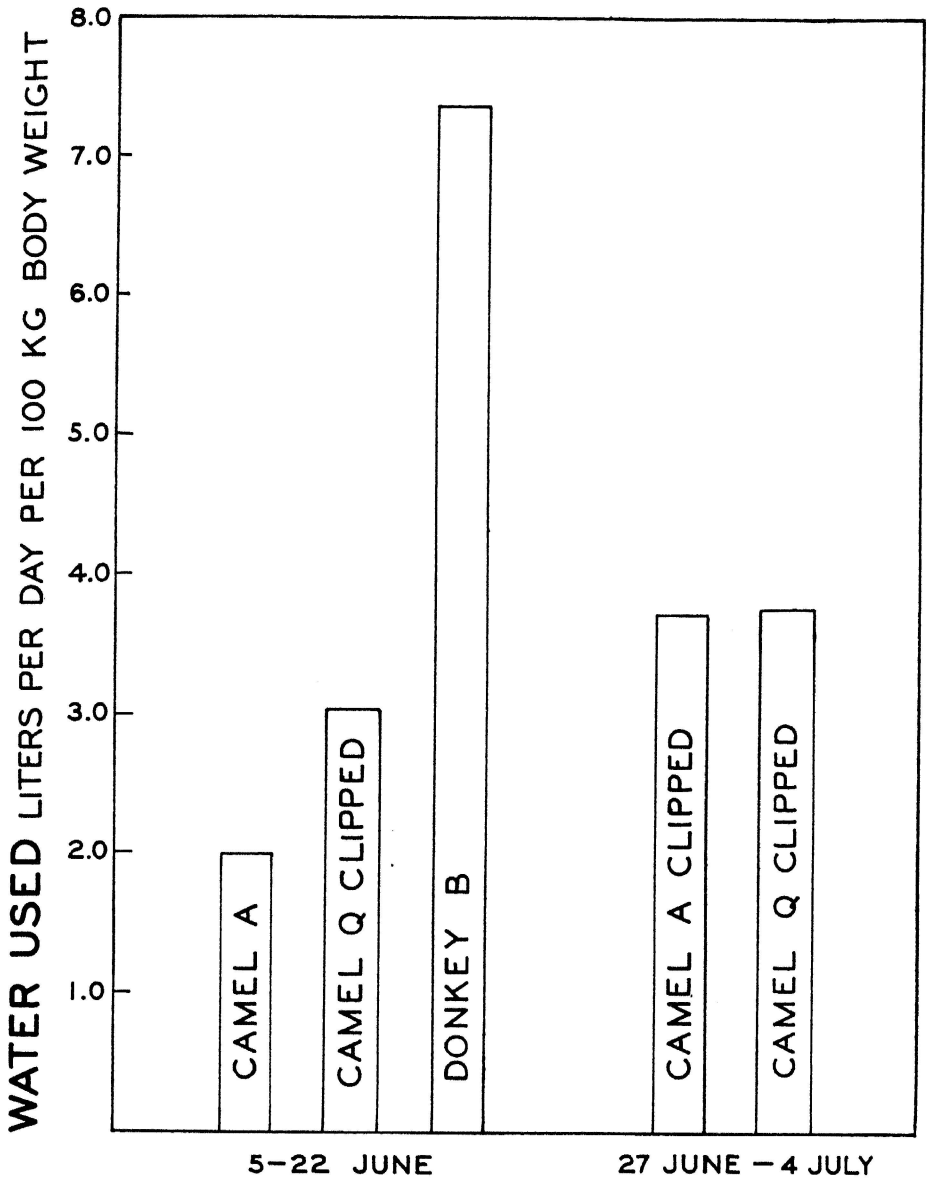
Fig. 8–The insulating value of the camel's fur contributes to its water economy. In the left side of the graph the camel that had been clipped (camel Q) used about 50% more water than a camel with its natural fur (camel A). When camel A was clipped, its evaporation increased to the same level as camel Q (right side of graph). The fact that both camels in the latter period evaporated more than earlier was due to a general increase in environmental temperature (11).

When men were dehydrated by 1 to 11% of their body weight, the reduction in plasma volume was about 2½ times as great as expected from the total water loss.

TABLE 6–BEHAVIORAL CHARACTERISTICS THAT CONTRIBUTE
TO THE WATER ECONOMY OF CAMELS

A. Seeking shade
B. Orienting lengthwise to sun's rays
C. Sitting with legs folded under body
D. Exposing minimal surface
E. Remaining sitting on same spot of ground,
    thus avoiding contact with hot surface
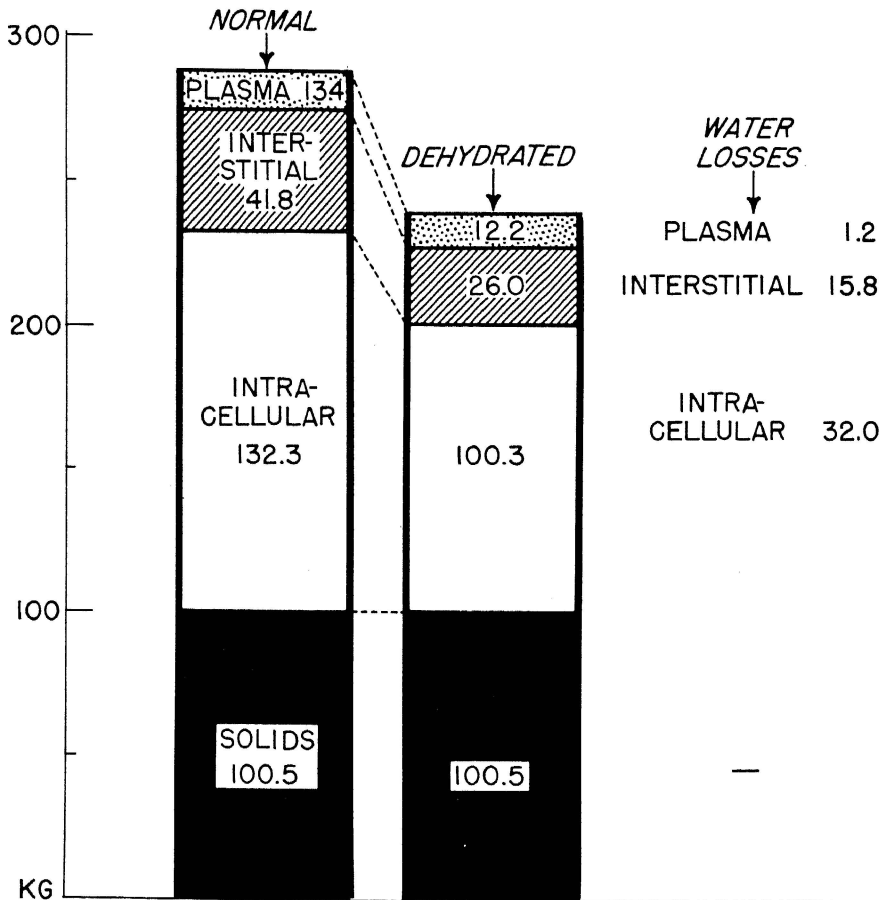
Fig. 9–When a camel is dehydrated the major part of the water loss occurs in the intra-cellular water compartment. The reduction in plasma volume is very small. This may have considerable influence on the maintenance of normal circulation in the dehydrated animal.

In the camel the situation is different. The distribution of the water loss in a camel that had been without water for 8 days is given in Figure 9. The camel originally weighed 288 kg and had lost 49 liters of water, in other words about 17% of the body weight. Of this water loss, only slightly more than 1 liter had been taken from the plasma volume, about 16 liters had been removed from the interstitial fluid, while the remaining 32 liters came from intra-cellular water.

This is not surprising, for the intra-cellular water is by far the largest volume to begin with. However, it is interesting that the plasma volume, which is so greatly reduced in dehydrated man, is not much reduced in the camel. This is perhaps one reason that explosive heat rise did not occur in the dehydrated camels, although they were exposed to much more severe dehydration than tolerated by man or dog. Since the blood is not severely dehydrated, its volume is maintained and its viscosity does not increase much. The circulation is therefore maintained more easily, the heart is not subjected to a severe load, and heat dissipation is not impeded to the extent that it is in animals where loss of plasma volume is characteristic in the dehydration syndrome.

Both the camel and the donkey can drink in a short time sufficient water to cover a severe water deficit. The drinking pattern in man is different; he is unable to drink much more than a liter at a time. A record of the fluid intake of a man during one day is shown in Figure 10. This particular individual drank 6 liters, or somewhat less than 10% of the body weight. Characteristically, most of the liquid was consumed during the meals with smaller amounts between meals throughout the day. In general, even when water is freely available, man tends to drink less than the amount needed to cover his water deficit, and not until meal-time does he make up completely for the losses. He thus undergoes a certain "voluntary" dehydration.

During the summer in the Sahara a donkey which was watered daily usually drank some 8 liters. This took about 60 seconds. For a man, who weighs about two-thirds as much as the donkey, it is barely possible to drink 1 liter within the same period of time. The amazing drinking capacity of the donkey is even better demonstrated in a severely dehydrated animal. When our donkey had been without water for 3 days it drank 27 liters in about 10 minutes (Table 7). Eight liters were consumed in one minute, 6 in the second minute, and the remainder was consumed more slowly. When the animal started drinking, its body weight was 73 kg; it therefore consumed more than 1/3 of its body weight. The dehydrated camel can drink a similar quantity, about one-third of its body weight.

The relative merits of sweating and panting

Both in man and in the camel the main burden of heat dissipation in hot surroundings is on the sweating mechanism. This is an excellent method for cooling the body surface and thus reducing the heat load on the organism. The dog, on the other hand, depends for heat dissipation on the characteristic increase in respiration which is known as panting. What are the relative merits of these two types of temperature regulation?

It has repeatedly been shown that the dog has excellent powers of temperature regulation. A classical experiment was carried out about 200 years ago by the secretary of the Royal Society, Mr. Blagden. A room was heated as much as
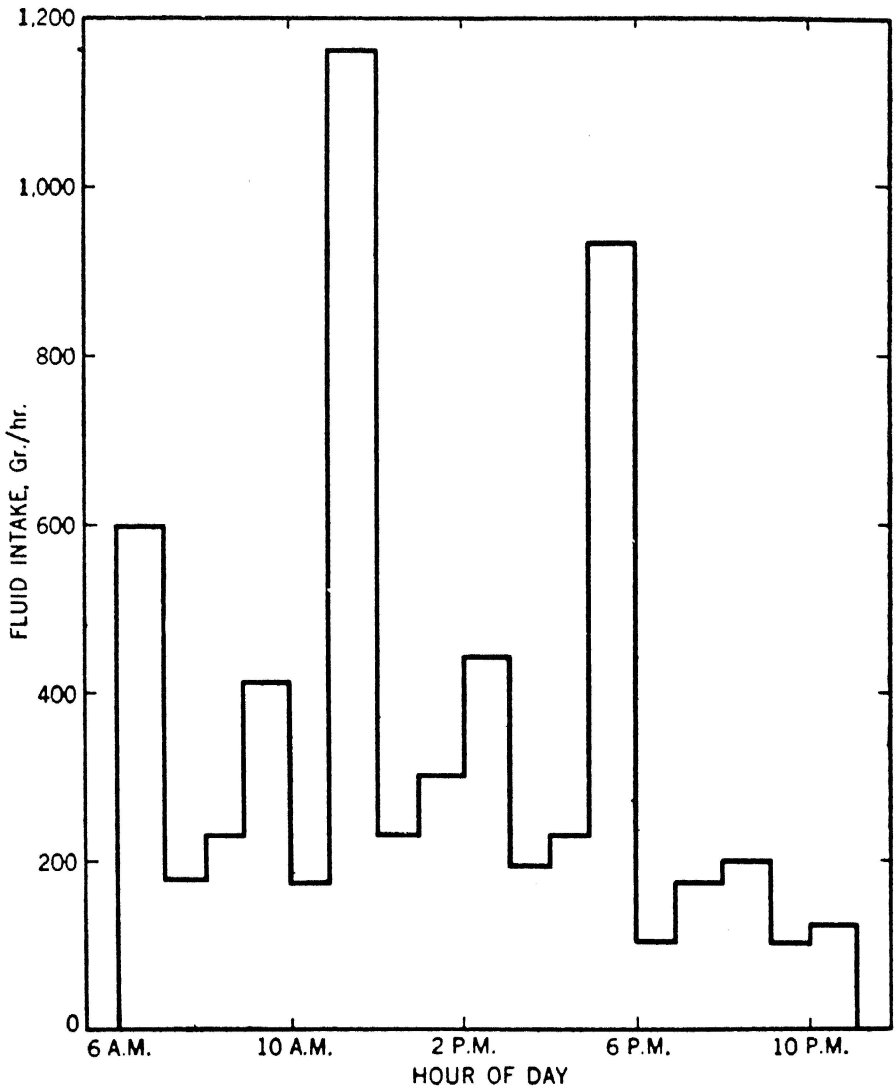
Fig. 10–The usual drinking pattern of a man in the desert shows that he tends to concentrate the drinking around meal time. During the remainder of the day he does not drink sufficiently to cover his water losses, even if water is freely available, and he thus undergoes some degree of voluntary dehydration (1).

TABLE 7–AMOUNT OF WATER CONSUMED IN A SINGLE DRINKING SESSION
BY CAMEL AND DONKEY

	Body Weight, kg	Water Consumed, Liter	Water consumed, % of Body Wt.
Camel	325	103.5	32.2
Donkey	73	26.9	37

possible, and when the temperature had been brought to 260°F (126°C) he entered the room and took with him a dog and a raw steak. After 3/4 hour Mr. Blagden and the dog were none the worse for the experience (the dog had been kept in a basket to keep its feet from being scorched), but the steak was cooked after 20 minutes and quite overdone by the time Mr. Blagden left the room. This experiment is a classical contribution to environmental physiology, and it is a superb demonstration of the ability of animal and man to dissipate heat. It is also evident from Mr. Blagden's experimentation that panting must be an efficient means for heat dissipation.

The act of breathing depends on the work of the muscles of the chest and diaphragm. It seems obvious that the work performed by these muscles must increase as the rate of respiration increases. This is, however, a very interesting aspect to the energetics of panting which has recently been brought out by Eugene Crawford of Duke University (3). Crawford has suggested that the panting takes place at the resonant frequency of the respiratory system. This means that the muscular work is less than would otherwise be required to maintain the high respiratory frequency. Respiration at the resonant frequency means that advantage can be taken of the elastic rebound of the system and only a small amount of muscular work is needed to keep the system moving at this frequency.

The evidence presented by Crawford for his hypothesis was supported by determinations of panting frequency and the resonant frequency of the respiratory system in the same dogs. In 10 dogs the mean panting rate was 320 ± 42 cycles per minute. In the same animals the resonant frequency was determined to be 316 ± 18 cycles per minute. This good correspondence suggests that panting may be more economical than could otherwise be expected.

Although panting is an efficient way of increasing evaporation, it has one major disadvantage. The increased ventilation of the lungs leads to an excessive removal of carbon dioxide from the blood and the development of severe alkalosis. The dog is, however, much more tolerant to alkalosis than man. If a man overventilates his lungs he will develop severe muscle cramps and lose consciousness at a loss of carbon dioxide which is only a small fraction of that which a dog can tolerate without any apparent ill effects.

There is another form of temperature regulation which I would like to mention in this connection. When exposed to high temperature, some Australian marsupials salivate copiously and lick their extended legs and the belly. In particular, the large kangaroos show this response to heat stress. These marsupials are efficient temperature regulators, but since they have not been studied

in detail, it is not possible to say to what extent they depend on the licking response as a major mechanism for heat dissipation. However, this mechanism of heat dissipation has at least one serious disadvantage – it cannot be employed while running. In this connection it is useful to remember that no large carnivores are native to Australia, and the present marsupial fauna has evolved where fleeing from carnivorous predators has not been a major factor in evolution. To what extent this may have contributed to the evolution of mechanisms of temperature regulation different from those in placental mammals is a subject where speculation takes the place of experimentation.

THE KANGAROO RAT

It has been known for long that some desert rodents, both in the southwestern United States and in the Old World deserts can live for indefinite periods without drinking water, eating only dry food such as grains and other seeds.

It can easily be demonstrated that the American kangaroo rats do not utilize any kind of physiological water storage in order to survive long periods of dry feed. If this were so, the water content of their bodies should gradually be depleted as they are kept on a dry diet. However, the water content of animals kept for up to 7 weeks on dry barley remained close to a mean of 66% (Figure 11). Furthermore, in this particular experiment the animals had increased in weight. Since the percentage of water remained constant, the total quantity of water in their bodies had actually increased. We can therefore conclude that kangaroo rats, although they eat dry seeds which contain almost no free water, are able to remain in water balance and even increase their water content.

Since the kangaroo rats remain in water balance, let us briefly examine again the components of water balance given in Figure 3. On the intake side of the account drinking water is nil, and other sources must therefore suffice. Dry pearled barley, such as we used for feeding kangaroo rats in the laboratory, contains some 5 to 10% of water absorbed in the grain, the exact amount depending on atmospheric humidity. A large quantity of water is formed in the oxidation of the food. One hundred grams of barley (dry weight) will yield about 54 grams of water when metabolized in the mammalian body. This means that the animals rely almost entirely on oxidation water to cover the needs for urine formation, feces, and evaporation.

We will therefore discuss the means by which the kangaroo rat can reduce these losses to a level where the water intake suffices to cover all needs.

The kangaroo rats have no sweat glands and normally do not use water for temperature regulation. In an emergency situation a kangaroo rat exposed to excessive ambient temperature can, to some extent, counteract a lethal rise in body temperature through a copious salivation which wets the fur under the chin and throat. This emergency heat regulation can suffice only for short periods because of the large quantities of water necessary to cool a small animal.

The kangaroo rat avoids the excessive temperatures of the desert day by remaining in its underground burrow. Recordings of temperatures in the burrows of various desert animals made throughout the year showed that the burrow tempera-
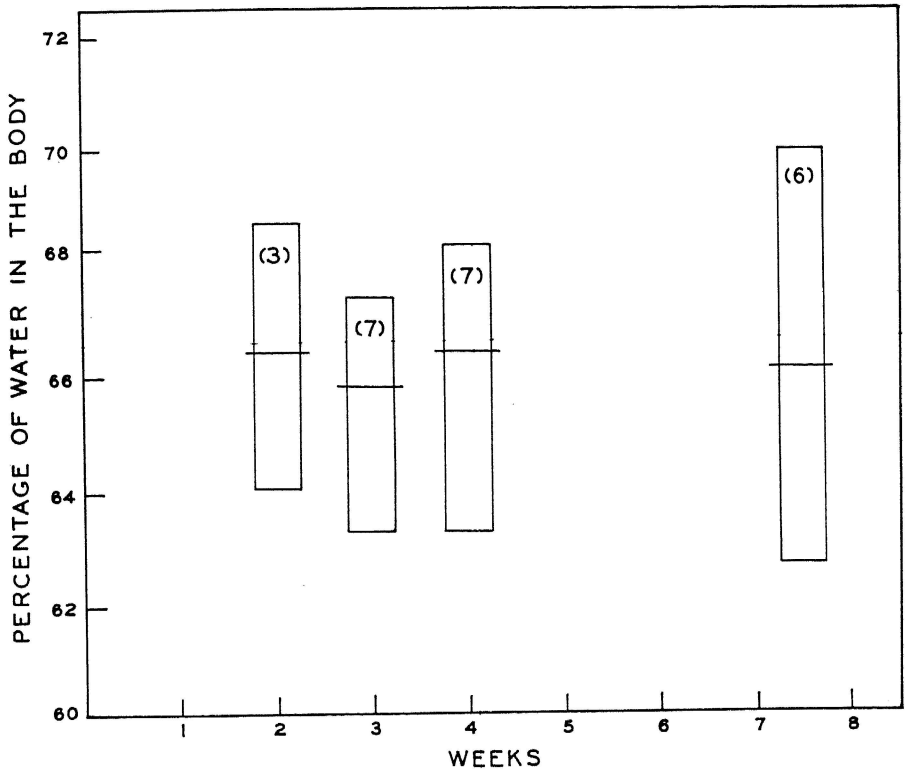
Fig. 11-Kangaroo rats kept for increasing periods of time on dry food without any drinking water maintain a constant water content in their bodies of about 66%. Horizontal lines = mean; vertical bars = range; number in parentheses = number of animals in each group.

ture of the kangaroo rat remains below 30°C even during the hottest summer (15). At this temperature there is no need for use of water in temperature regulation, and we need only be concerned with the inevitable evaporation from the respiratory tract and the skin.

The combined evaporation from lungs and skin has been determined in kangaroo rats and is compared with that from some other rodents in Table 8. To make the figures comparable the evaporation is related to the oxygen uptake. It appears that the kangaroo rat evaporates much less water than white rats and mice, and also less than the pulmonary evaporation in man.

The mechanism which is responsible for the relatively low evaporation in kangaroo rats is understood, but it has not been the subject of detailed studies. It has been found that the nose temperature of these animals is lower than that in man, and since the expired air leaves the respiratory passages saturated with water vapor, its water content will be lower in the kangaroo rats. White rats also have low nasal temperatures, and their higher level of evaporation is explained by the fact that they have a considerable loss of water vapor from the skin (14).

TABLE 8–TOTAL EVAPORATION FROM VARIOUS RODENTS AS RELATED
TO THE SIMULTANEOUS OXYGEN CONSUMPTION (6)

	Evaporation, mg H_2O per ml O_2
Kangaroo rat	0.54 ± 0.01
Pocket mouse	0.50 ± 0.03
Canyon mouse	0.54
Albino rat	0.94 ± 0.03
Albino mouse	0.85 ± 0.03
Man (lungs only)	0.85

Since the body temperature of these rodents is in the usual mammalian range, the temperature of the nasal mucosa must somehow be lowered. The mechanism can be regarded as an intermittent countercurrent heat exchanger. As dry outside air, during inspiration, passes over the nasal mucosa, the surface is cooled by evaporation of water. As saturated warm air from the lungs passes over the same surfaces during expiration, part of the water condenses again on the cool surfaces as the temperature of the air is lowered. During the next inspiration water again evaporates and cools the surface, and during expiration part of it is again recondensed. This intermittent flow of air in opposite directions makes the system perform as a modified counter current heat exchanger. It can work only in small animals with narrow air passages. In man the dimension of the air stream is so large that sufficient heat exchange between air and the surface of the nasal passage cannot take place.

The use of water for urine formation is lower in desert rodents than in most other mammals because the kidneys can produce an exceptionally concentrated urine (Table 9). This means that for a given amount of excretory products, a correspondingly smaller amount of water is used for urine formation.

TABLE 9–MAXIMUM URINE CONCENTRATIONS AND URINE:PLASMA
OSMOTIC RATIOS IN VARIOUS MAMMALS

	Electrolyte conc. mEq per liter	Urine:Plasma Osmotic ratio
Man	460	4.2
White rat	600	8.9
Kangaroo rat (Dipodomys merriami)	1200	14
Gerbil (Gerbillus gerbillus)	1600	14
Sand rat (Psammomys obesus)	1900	17
Sea water	600	

Since the kangaroo rat can produce a urine about twice as concentrated as sea water, could it drink sea water and still excrete the large amounts of salt it contains? Man cannot drink sea water with impunity because the kidneys can produce urine only about 2/3 the concentration of sea water. If a man drinks, for example, one liter of sea water, the excretion of the salt it contains will require the formation of $1\frac{1}{2}$ liters of urine. In other words, an extra one-half liter of water is needed, and the ingestion of sea water therefore merely leads to increased dehydration.

The exceptionally powerful kidney of the kangaroo rat suggests that it should be able to drink sea water. Since it normally does not drink at all, it must somehow be induced to do so. A diet of soybeans, which have a very high protein content, leads to the formation of large amounts of urea. The excretion of this urea requires additional water, and the animals will now drink water (or sea water) if it is available. Initially, they will lose some weight but will soon learn to drink, and those that drink sea water get along as well as control animals that are given fresh water (Figure 12).
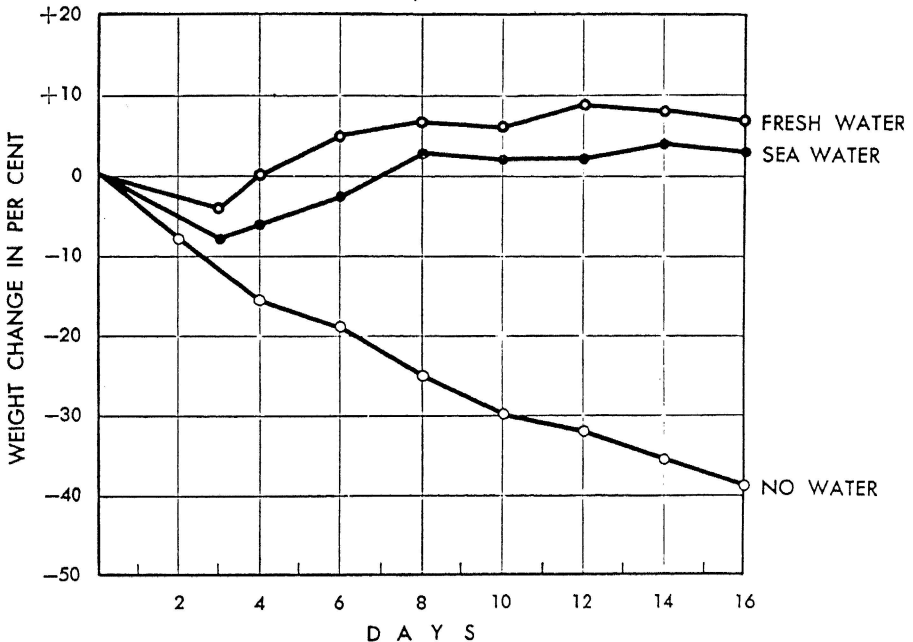

Fig. 12-The weight curves of kangaroo rats which were given either fresh water or sea water to drink shows that these animals can drink sea water without ill effects. Although kangaroo rats normally do not drink, they were induced to do so by a diet of soybeans. Due to the high protein content of this diet extra water is needed for the excretion of urea and the animals soon learn to drink (7).

Some other desert rodents also have a very powerful kidney. T. W. Burns of the School of Medicine at the University of Missouri has investigated the Egyptian Gerbil (Gerbillus gerbillus), which has an even more efficient kidney than the kangaroo rat (2).

The mechanism for formation of a concentrated urine depends on the structure of the kidney. It was pointed out by Sperber that the kidneys of desert rodents in general have a very long renal papilla (13). This is associated with the fact that in these animals the loop of Henle, the structure responsible for producing a concentrated urine in mammals, is exceptionally long. Figure 13 shows the difference in the length and size of the papilla in white rats and two typical desert rodents, the kangaroo rat and the sand rat. The latter is a rodent from North Africa which normally eats juicy plants that grow in wet places with saline soil. The juice of these plants may have a salt content twice as high as sea water, but the kidney of the sand rat can readily excrete these salts.

The last component in the water balance sheet of the kangaroo rat, the fecal water loss, should also be mentioned. The kangaroo rat produces small firm pellets of feces that have a low water content. Furthermore, the animal reingests its feces, and this coprophagy has some bearing on the water balance. The re-ingestion means that the utilization of the food is increased, and the final bulk of the feces is therefore reduced. Hence, the amount of water lost with the feces is correspondingly lowered.

If we summarize the account of the water balance of a kangaroo rat, we find that the water intake, which is about 0.5 grams per gram of food eaten, will just suffice to cover the needs for evaporation, urine formation and production of feces.

I would like to compare this water balance account as given for the kangaroo rat with similar accounts for a number of other mammals. This comparison is presented in Figure 14. The water balance of each animal has been related to its metabolic rate, the unit of comparison being the formation of one liter of oxidation water. (In this connection the time required for this level of metabolism can be disregarded.)

The account of the water balance for the kangaroo rat as given in the preceding shows that the sum of water expenditure for urine, feces, and evaporation adds up to an amount almost equal to the oxidation water. Let us next look at the white rat. Its kidney is less powerful and more urine is formed. Its feces has more bulk and a higher water content. The evaporation is also higher than in the kangaroo rat. The sum exceeds the amount of oxidation water, and the animal obviously cannot remain in water balance on dry food only. This is, of course, well known to all of us. In man, the water balance is still less favorable, his urine is more dilute, the bulk of feces is higher, but the evaporation (in the absence of increased cutaneous water loss) is about as in the rat.

The large herbivores included in Figure 14 are not strictly comparable to the smaller animals. In particular, the fecal water loss is considerable in these animals. They eat fibrous plant material which gives a high bulk of feces and therefore a relatively high water loss. The data for the cow refer to a grazing animal on pasture, which forms tremendous quantities of moist feces and dilute urine. Cows on a drier regimen form less urine and feces, but studies of their water expenditure when deprived of water have not been made.

It may seem surprising that the water expenditure in the camel is of the same magnitude as in man. However, the information used for Figure 14 concerns the water balance in the absence of heat stress. In the winter, the camel manages
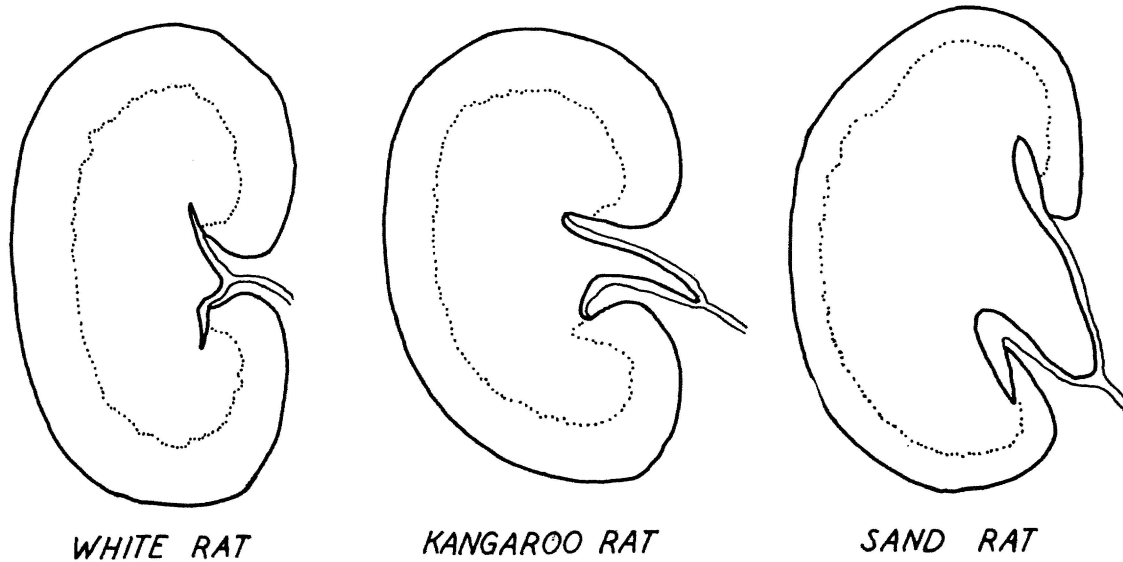
WHITE RAT   KANGAROO RAT   SAND RAT

Fig. 13–Cross-sections of the kidney of three rodents, white rat, kangaroo rat (Dipodomys merriami) and sand rat (Psammomys obesus). The ability to produce a concentrated urine is directly related to the thickness of the medulla and the length of the renal papilla. The two desert rodents both have exceptionally long renal papillae. The sand rat, which normally eats large quantities of succulent plants with a highly saline sap, has an unusually thick papilla as well. Its diet requires the formation of large volumes of highly concentrated urine. The length of the papilla permits the high concentration and its great diameter permits the formation of larger volumes of concentrated urine than would otherwise be possible.
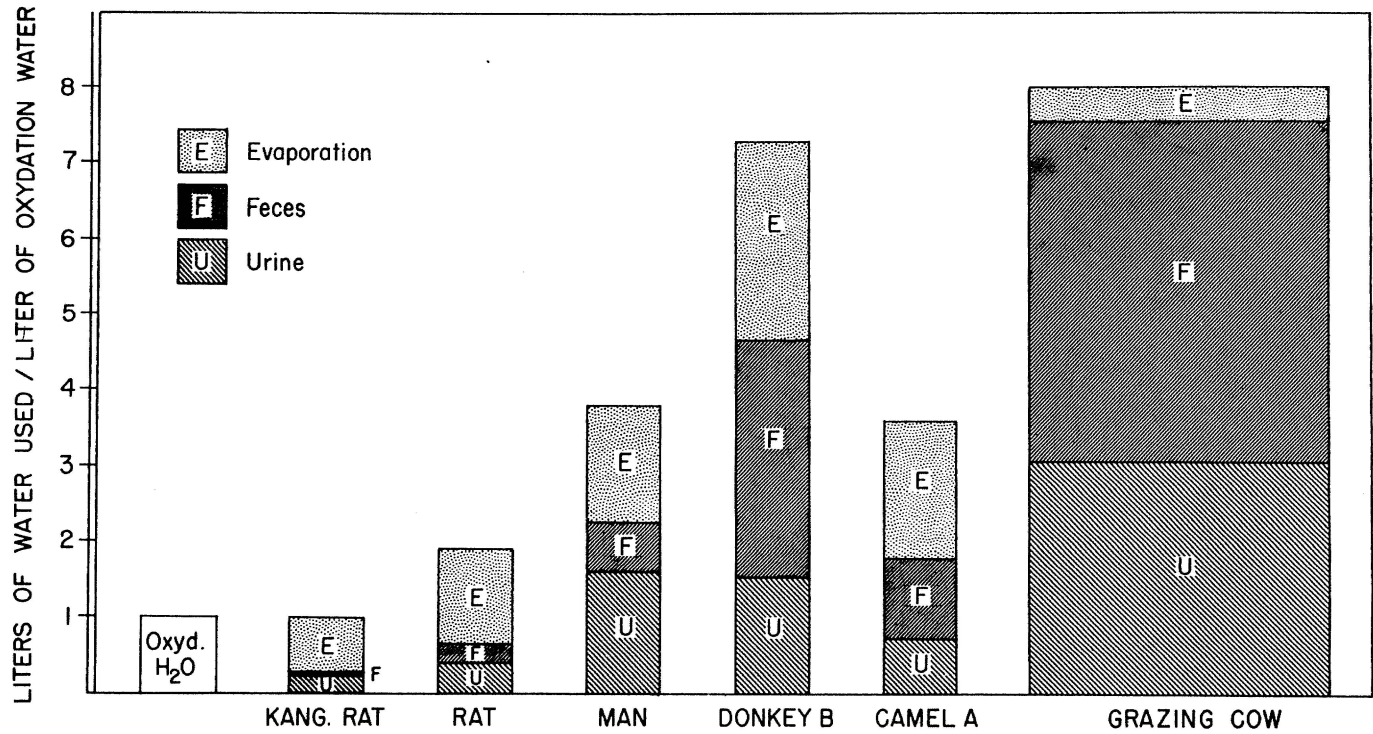
Fig. 14—A comparison of the water expenditures in various mammals as related to the same metabolic level (indicated as the formation of 1 liter of oxidation water). In the kangaroo rat the total water expenditure is about equal to the oxidation water. This shows the unique ability of the kangaroo rat to cover all its needs for water without drinking. In all the other mammals shown here the minimal water expenditure exceeds the oxidation water (10).

well on the free water present in fresh plant material and does not need to drink at all. In summer, when water is needed for heat regulation, the difference between camel and man becomes evident. Figure 15 shows the water needed for heat regulation under hot conditions by camel, donkey, and man. It now becomes obvious that the greatest difference is in the economy the camel has been able to achieve in use of water for heat regulation. The main causes for this economy are the fluctuations in body temperature, the decreased gradients from the hot environment, the insulation of the fur, and a number of behavioral adaptations which reduce the environmental heat gain. Through these means the camel is able to live in the desert with an expenditure of water roughly 1/7 that in man. However, the camel
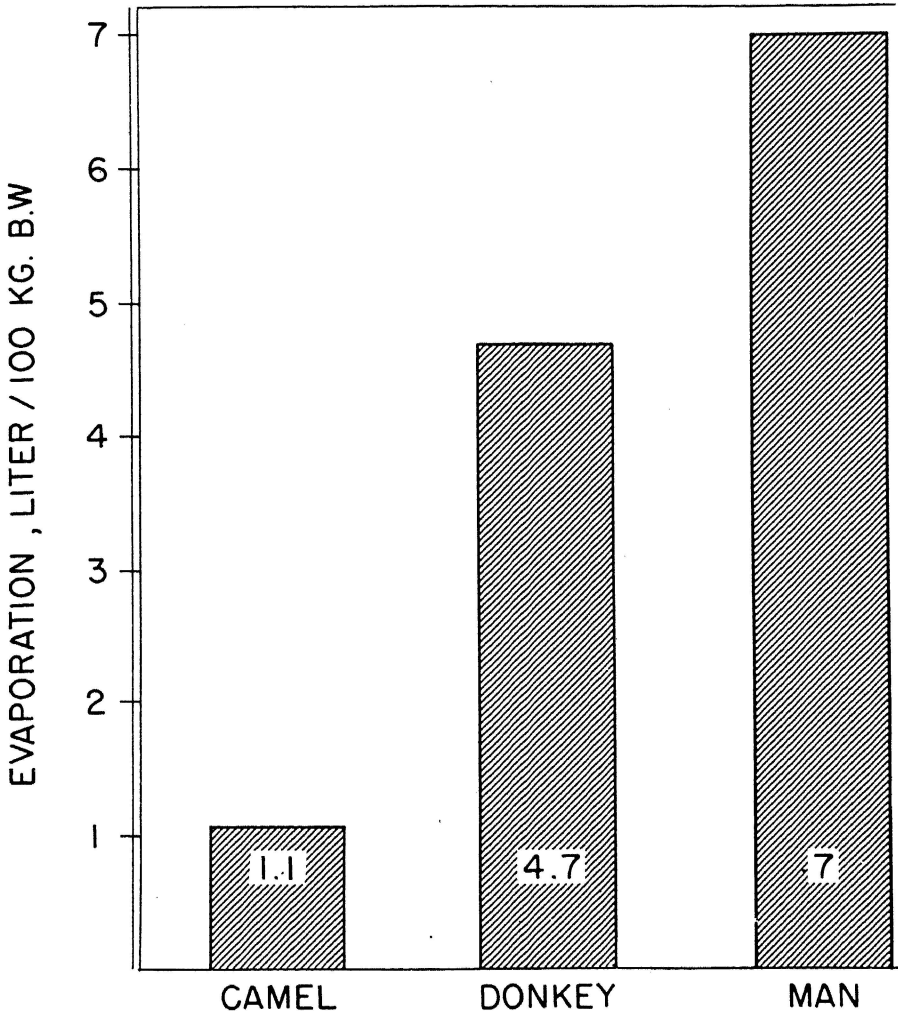
Fig. 15-The amount of water used for heat regulation during a hot desert day is about seven times as high in man as in the camel. The major reasons for this difference are discussed in the text (10).

has to drink in order to survive in the desert, while the kangaroo rat, by avoiding the heat of the day, is able to manage without drinking at all.

In summarizing my discussions I would like to emphasize that the basic physiological principle of water balance is the same in all mammals. The differences appear in the modifications of the basic pattern found in various characteristic desert animals. Through the study of the comparative physiology of these animals we frequently find that a general mechanism may be particularly well developed or may be present in an extreme form. However, instead of emphasizing the specialized features of this function, its clarification frequently reveals aspects of basic mechanisms which are difficult to discern in the study of less highly specialized animals. Thus comparative physiology lends a valuable perspective to the study of physiological function in general.

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