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Author(s): K. Schmidt-Nielsen, R. C. Schroter, A. Shkolnik

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Desaturation of exhaled air in camels

BY K. SCHMIDT-NIELSEN†, R. C. SCHROTER‡ AND A. SHKOLNIK§

† *Department of Zoology, Duke University, Durham, N.C. 27706, U.S.A.*

‡ *Physiological Flow Studies Unit, Imperial College, London SW7 2AZ, U.K.*

§ *Department of Zoology, Tel-Aviv University, Tel-Aviv, Israel*

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We have found that camels can reduce the water loss due to evaporation from the respiratory tract in two ways: (1) by decreasing the temperature of the exhaled air and (2) by removal of water vapour from this air, resulting in the exhalation of air at less than 100% relative humidity (r.h.). Camels were kept under desert conditions and deprived of drinking water. In the daytime the exhaled air was at or near body core temperature, while in the cooler night exhaled air was at or near ambient air temperature. In the daytime the exhaled air was fully saturated, but at night its humidity might fall to approximately 75% r.h. The combination of cooling and desaturation can provide a saving of water of 60% relative to exhalation of saturated air at body temperature.

The mechanism responsible for cooling of the exhaled air is a simple heat exchange between the respiratory air and the surfaces of the nasal passageways. On inhalation these surfaces are cooled by the air passing over them, and on exhalation heat from the exhaled air is given off to these cooler surfaces. The mechanism responsible for desaturation of the air appears to depend on the hygroscopic properties of the nasal surfaces when the camel is dehydrated. The surfaces give off water vapour during inhalation and take up water from the respiratory air during exhalation. We have used a simple mechanical model to demonstrate the effectiveness of this mechanism.

INTRODUCTION

In the preceding paper (Schmidt-Nielsen *et al.* 1981) we reported that the respiratory water loss was unexpectedly low in camels that were subjected to severe water deprivation, and in fact so low that the results were incompatible with the view that exhaled air is saturated with water vapour. We have previously reported that the respiratory air of camels and several other large mammals may be exhaled at or near ambient rather than body core temperature (Langman *et al.* 1978, 1979). This cooling of the exhaled air results in substantial savings in water, and we now report that camels can further reduce the respiratory water loss by extracting water vapour from the exhaled air, resulting in the exhalation of air at less than 100% relative humidity (r.h.).

METHODS

We studied two mature camels (*Camelus dromedarius*) that were accustomed to human handling. Both animals had been maintained in a healthy and well nourished condition and had been watered regularly. One was a 6 year old female that weighed 575 kg when normally hydrated; the other was a *ca.* 12 year old female that normally weighed 450 kg. The animals were transported by truck to kibbutz Qalia at the north end of the Dead Sea, where we conducted our study in July 1979.

The ambient dry bulb temperature varied from a maximum of 35 to 40 °C in the early afternoon to a minimum around 26 °C in the early morning at sunrise. The ambient relative humidity was around 25% in the afternoon, increasing to over 50% at night, while the absolute humidity remained fairly constant throughout the study at approximately 0.012 kg of H₂O per kilogram of dry air.

The animals were confined to a corral of about 5 m × 10 m with virtually no shade during the day. After becoming familiar with their surroundings they were denied water but were fed dry hay and small amounts of fresh green dates. Both camels were subjected to 16 days of continuous dehydration (except that 5 l of water were given to each animal on day 12). At the end of the 16 days of dehydration each animal was allowed water *ad libitum*. They consumed 92 and 107 l respectively (16 and 24% respectively of their normal body masses).

The animals withstood the dehydration without apparent signs of undue stress. After a few days without water they ate very little hay but took green dates when these were offered. They urinated sparingly and defecated extremely dry faeces. The camels were free to move about, but were brought down to the resting ('sitting') position when measurements were taken. During the daytime, especially as dehydration progressed, they preferred to remain in the resting position throughout the hot day.

Rectal temperature was measured with a copper-constantan thermocouple probe inserted at least 15 cm. Temperature was read on a Wescor TH 60 digital thermometer with the reading noted after the signal remained stable for more than 1 min. In dehydrated camels the rectum tends to become impacted with dry faeces; this required use of petroleum jelly to facilitate insertion of the probe and often several minutes elapsed before the reading became stable, although the nominal time constant of the system was less than 1 s.

Respired air temperatures were measured with welded copper-constantan thermocouples made from wire 0.125 mm in diameter. The small mass of the welded thermocouple and the absence of solder yielded a low time constant (90% response in less than 0.4 s). The thermocouple was connected to a Wescor TH 50 thermometer with analogue output that was recorded on a four-channel rectilinear Physiograph. The thermocouple was mounted in a plastic T-tube with an inside diameter of 1.4 cm. One end of the long arm of the T-tube was inserted into one

of the nares, where it remained, kept in place by the nasal flap. The animals showed very little reaction to the T-tube and could breathe freely through and around the tube.

The relative humidity of the respired air was measured with a solid-state uncoated humidity sensor (Vaisala Oy, Helsinki) and recorded on the physiograph. The sensor is a thin plate that was positioned in the centre of the airstream through the T-tube, orientated parallel to the flow. To protect the sensor from damage or deposition of nasal mucous, it was housed in a fine-mesh wire cage with large free area to allow circulation of air. Air humidity is measured as the capacitance of a thin polymer film, about 1 μm thick, positioned between two thin gold electrodes, mounted on a small glass wafer (4 mm \times 4 mm \times 0.2 mm). The upper gold electrode is an extremely thin, water-permeable, vacuum-deposited gold film, about 10^{-2} μm thick. (The thickness of this electrode is a compromise between that giving short response time and that giving low ohmic resistance loss in the electrode.) The capacitance changes in proportion to the relative humidity of the air, and the temperature dependence is negligible. In other words, the sensor measures relative humidity without significant temperature dependence (the manufacturers quote a value of 0.05 % $^{\circ}\text{C}^{-1}$).

The humidity sensor responds very rapidly to changes in relative humidity (90 % response in less than 0.5 s), provided that the air is not fully saturated. When the sensor is exposed to air at 100 % r.h. its plastic film becomes saturated and the output overloaded. The time taken to remove excess water when the sensor is repositioned in a low humidity depends on the time of exposure to saturated air. The exposure to saturated air encountered in our study was short, and the removal time was about 0.5 s or less. The resulting overall time taken to respond to respiratory air humidity (less than 1 s) was considerably less than the duration of an inspiration or expiration (> 5 s in the dehydrated animal).

The humidity sensor responded very quickly to the change in humidity encountered when switching from inhalation to exhalation, with a time lag of about $\frac{1}{4}$ s behind the temperature and lung volume signals. However, when the humidity changed from 100 % to the low inspiratory level, there was a lag time of a little less than 0.5 s (see figures 1 and 2).

The thermocouple tracings show a temperature profile that contains two artefacts. As the animal begins to breathe in, there is an initial dip in recorded temperature; this is the result of rapid evaporation from the probe tip of moisture deposited during exhalation. This initial dip disappeared when the animals exhaled desaturated air. The other artefact is an initially high temperature during exhalation, caused by the release of latent heat by moisture depositing on the probe, which at that moment was in temperature equilibrium with the inspired air. Both these artefacts, which only appeared when condensation occurred, affect only the initial parts of the temperature profiles.

All thermometers were calibrated over the range 20–50 $^{\circ}\text{C}$ against a pre-

calibrated mercury thermometer and agreed to within 0.2 °C. They were regularly checked against each other to ensure correct readings.

The humidity sensor was checked before, during and after each measurement by suspending it inside a bottle with the bottom covered by 1–2 cm of Drierite (0 % r.h.), a bottle containing a saturated solution of NaCl (75 % r.h.), and a bottle containing distilled water (100 % r.h.). The sensor was also regularly exposed to the ambient air and its reading compared with the relative humidity derived from the wet-and-dry bulb readings. The readings remained extraordinarily stable and suggested that the error was less than 3 % r.h.

On a number of occasions the respiratory frequency was also recorded on the Physiograph, by means of a displacement strain gauge located around the ribcage at a level just above the last rib.

RESULTS

Rectal temperature

When hydrated, the camels' rectal temperatures varied less than 2 °C throughout the day and night. On dehydration the variations in rectal temperature increased with daytime values near 41 °C and night-time values around 36 °C. This pattern is similar to those reported in earlier studies (Schmidt-Nielsen 1964; Schmidt-Nielsen *et al.* 1967).

Ventilation

The respiratory frequency increased during the day, as the body temperature rose, and decreased again at night. The most marked effect, however, was that of progressive dehydration. For example, a fully hydrated camel had a frequency of 9.3 min⁻¹ (body temperature 39 °C), but after 15 days of dehydration the frequency had decreased to 4.3 min⁻¹ (body temperature 38.7 °C). These observations are similar to earlier results of Schmidt-Nielsen *et al.* (1967), although in the present study the respiratory frequencies were considerably lower at all degrees of dehydration when allowance had been made for the effect of body temperature.

Minute ventilation or tidal volume were not measured, but the output of the chest-wall strain gauge provided information on the pattern of ventilation. First, movements of the chest wall were in phase with flow conditions in the nose. Secondly, the strain gauge changes were virtually linear with time (figures 1, 2). Although strictly the gauge indicates chest perimeter, the pattern suggests that the animals were breathing with constant and similar inspiratory and expiratory flow rates, without significant periods of breath holding. This pattern is different from those usually observed in man and other animals.

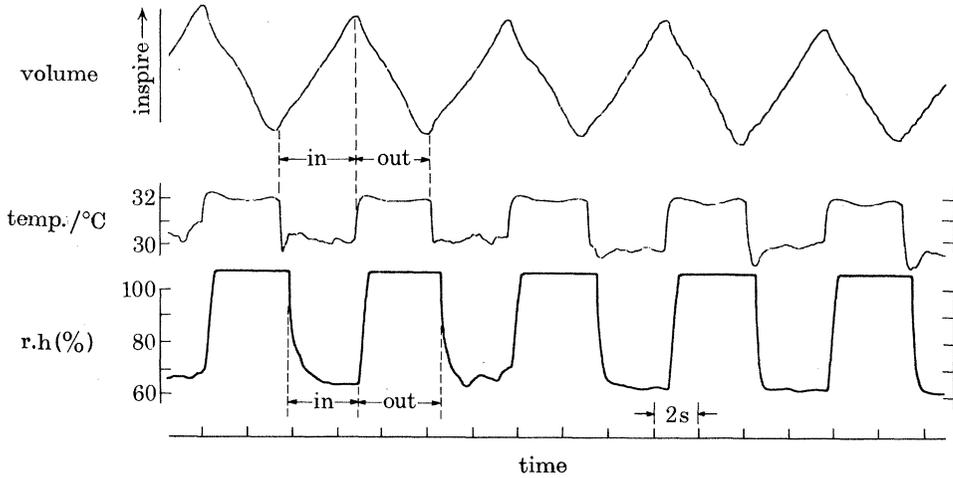


FIGURE 1. Recordings of respiratory movements (top), temperature of respired air (middle) and relative humidity of respired air (bottom) of a normally hydrated camel (rectal temperature 37.5°C , ambient air temperature 30.0°C). The records were obtained in the evening after sunset. Exhaled air was at 32.0°C and 100% r.h. (It is an inherent characteristic of the otherwise linearly responding humidity sensor that at 100% r.h. it continues to absorb water vapour, with the record going off scale.)

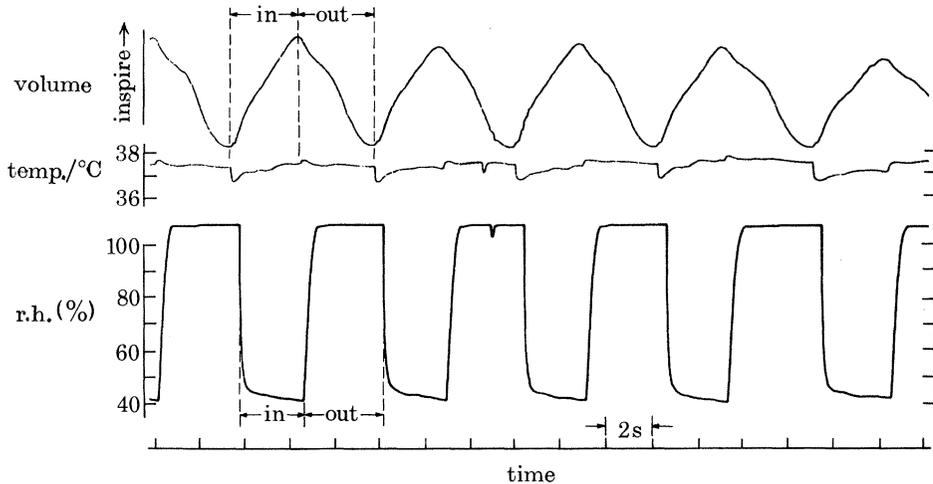


FIGURE 2. Recordings of respiratory parameters, similar to those in figure 1, obtained from a normally hydrated camel in the middle of the day (rectal temperature 39.0°C). Exhaled air was close to ambient air temperature (37.5°C) and at 100% r.h.

Exhaled air temperature

When the camels were fully hydrated or only moderately dehydrated the exhaled air was fully saturated (figures 1, 2). In the daytime, when the ambient air was hot and near body temperature, the animal breathed out air at a temperature near to body temperature. At night, when the air temperature fell, the exhaled air temperature also fell (as reported by Langman *et al.* 1979).

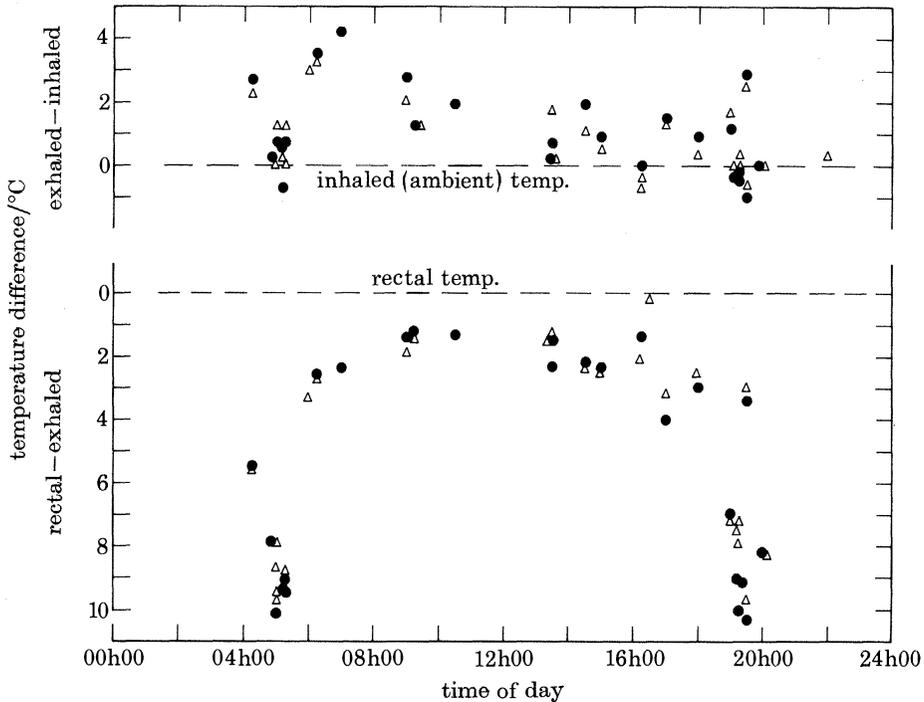


FIGURE 3. Exhaled air temperature of camels in relation to ambient and rectal temperatures.

Upper panel: the temperature of the exhaled air remained within a few degrees of that of the inhaled (ambient) air. At night exhaled air temperature could fall below that of the inhaled air. Lower panel: in the daytime the exhaled air temperature was close to body temperature but in the early morning and evening it could fall to more than 10 °C below body temperature.

The manner in which the exhaled air temperature varied with inhaled (ambient) temperature and rectal temperature can be seen in figure 3, in which these are plotted in relation to the time of day. During the hot day, when the solar heat load was considerable, the exhaled air temperature was close to rectal temperature and slightly higher than ambient temperature. However, at night the exhaled temperature fell to as much as 10 °C below rectal temperature and could even be lower

than the temperature of the inhaled (ambient) air. Such low exhaled air temperatures relative to ambient have previously only been observed in small mammals (Jackson & Schmidt-Nielsen 1964; Schmidt-Nielsen 1972).

Exhaled air humidity

When the camels were moderately dehydrated they exhaled fully saturated air, but as the dehydration period extended beyond about ten days the animals began to exhale unsaturated air (figure 4). At the beginning of an exhalation that lasted

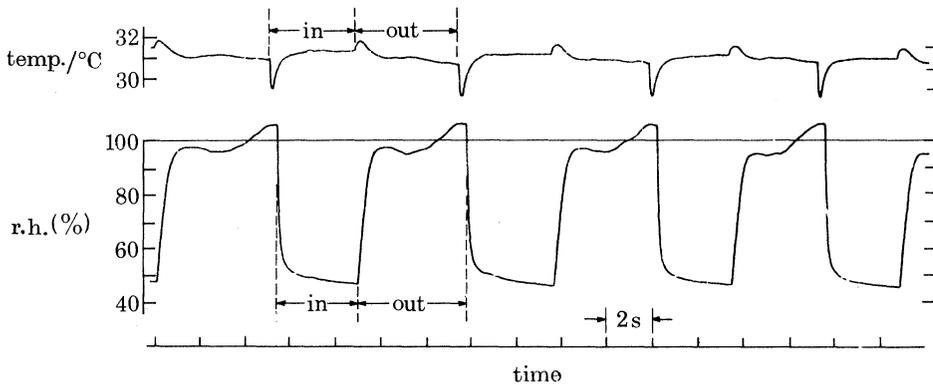


FIGURE 4. Recordings from a camel after 12 days of water deprivation (rectal temperature 40.1 °C). The temperature of the exhaled air (31.0 °C) was slightly below that of the inhaled ambient air (31.5 °C). The exhaled air was, at the beginning of each exhalation, less than fully saturated, but reached 100% r.h. towards the end of the breath. (For a note on the response characteristics of the humidity sensor, see figure 1.)

about 5 s, the air was well below 100% r.h., but towards the end of the exhalation the relative humidity rose to full saturation. Exhalation of unsaturated air was only observed at night or in the early morning, and not during the daytime, when the animals were subjected to a heat load.

Obtaining records of unsaturated exhalation required very gentle and quiet handling of the animals. Excessive restraint, sudden noise or other disturbances caused the camels to switch to fully saturated exhalation. An example is shown in figure 5, in which a nervous and rapidly breathing animal suddenly changed from unsaturated to fully saturated exhalation. The change in humidity of the exhaled air is reflected in the temperature trace, where the condensation and evaporation artefacts suddenly appeared as the exhaled air was fully saturated.

As the animals became more severely dehydrated, the exhaled air became more unsaturated, with a relative humidity around a fairly constant value of 75 to 80% (figure 6). Under the most severe dehydration studied (15 days) the ventilation pattern changed somewhat. The inspiratory time remained similar to that in the

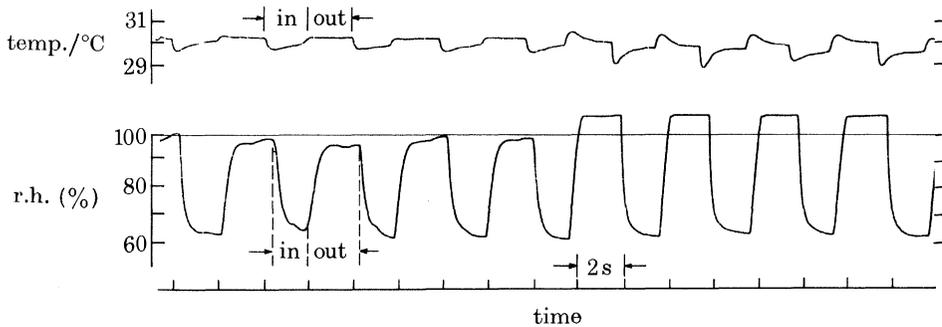


FIGURE 5. Recordings from a camel after 11 days of water deprivation (rectal temperature 38.7 °C). The temperature of the exhaled air (30.0 °C) was nearly equal to that of the ambient air (29.5 °C). The humidity of the exhaled air was initially below 100% r.h. but suddenly changed to full saturation after a slight disturbance to the relaxed animal (cf. text).

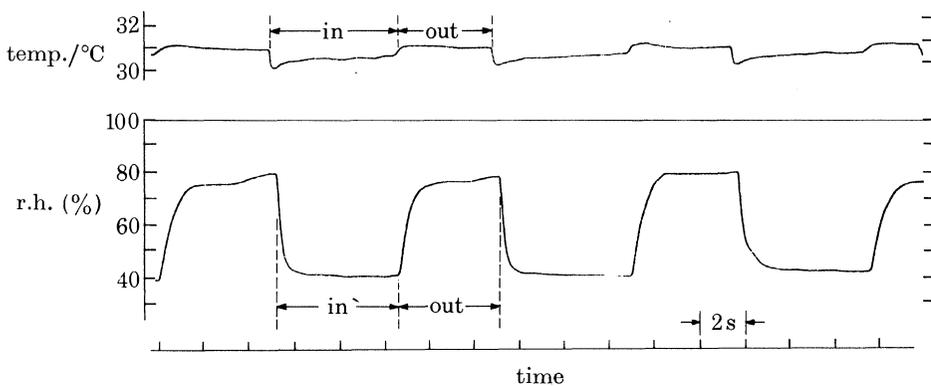


FIGURE 6. Recordings obtained at night from a severely dehydrated camel after 13 days of water deprivation (rectal temperature 38.9 °C). The exhaled air was clearly unsaturated throughout the period of exhalation of approximately 4 s.

less severely dehydrated animal, but the expiratory time increased markedly, respiratory rate falling to 4.3 min^{-1} . We do not know whether this was due to slow exhalation or to an end-expiratory pause. The exhaled relative humidity, which in the beginning of each exhalation was approximately 75%, increased towards the end of the exhalation. (The thermocouple record indicated a cooling artefact at the beginning of the inspiratory limb that may have resulted from an end-expiratory pause with air in the vicinity of the sensor becoming saturated with moisture.)

DISCUSSION

Cooling and desaturation of exhaled air

It is well known that the respiratory air of mammals and birds can be exhaled at temperatures far below body temperature, but it has been assumed that the exhaled air is always saturated with water vapour at the temperature at which it leaves the nasal passageways. The observation that water vapour can be removed from the exhaled air as it passes through the nose is new, and helps to explain the extremely low respiratory water losses that have been observed in camels.

The temperature and humidity relations of the respiratory air of humans have been the subject of numerous studies (see, for example, Ingelstedt 1956). Many investigators have been concerned with the heating and humidification of the air on inhalation, processes that are nearly complete in the nasal or oral passageways before the air reaches the trachea. In the lungs the air is at body temperature and fully saturated (Cole 1953), but it is exhaled at a somewhat lower temperature because the exhaled air loses heat as it passes over the nasal mucosa. In the process the air also gives up some water vapour and remains at 100 % r.h. This can be restated as: during exhalation some heat and water are reclaimed in the nasal tract (see, for example, Walker *et al.* 1961).

The cooling of the exhaled air and recovery of water is strikingly important in desert rodents, such as kangaroo rats (Jackson & Schmidt-Nielsen 1964). Kangaroo rats live on seeds and other dry plant material. Usually they do not drink, and they do not seek out green and succulent plants to obtain water. Their total water supply consists of the small amount of free water adsorbed in their dry food and the water derived from oxidation of the food ('metabolic water'). This water must suffice to cover all losses: by evaporation and in urine and faeces. Losses in urine and faeces are minimized by excreting highly concentrated urine and very dry faeces, and the respiratory water loss is reduced by cooling of the exhaled air and the resultant recovery of water. The mechanism is simple. The surfaces of the nasal passageways are cooled by the inhaled air and because of evaporation they may be cooled to below the temperature of the inhaled air. On exhalation the air that passes over the cool surfaces gives up heat, water recondenses, and the exhaled air may even be below ambient temperature. For example, a kangaroo rat that inhales air at 30 °C and 25 % r.h. is able to exhale air at 27 °C and 100 % r.h. Under these conditions 54 % of the water that was added to humidify the air on inhalation is recovered on exhalation (Schmidt-Nielsen, *et al.* 1970).

The processes of heat exchange and water recovery in the nasal passageways have been the subject of careful theoretical analysis (Collins *et al.* 1971), which has confirmed that the water recovery under favourable circumstances may exceed 75 %. This recovery of water is an essential component of the water balance of kangaroo rats and other small desert mammals and their ability to subsist without free water.

The heat exchange in the nose of humans is less effective because of the much wider passageways and a relatively small surface area. It has therefore been assumed that in other large animals nasal heat exchange would be relatively ineffective, but we have recently shown that in the giraffe and several other large East African ungulates the respiratory air may be cooled substantially, resulting in considerable recovery of water in the nasal passageways (Langman *et al.* 1979). These measurements indicated that nasal recovery of water in giraffes can explain their relative independence of drinking water on the semi-arid East African savanna. In camels the recovery of water caused by nasal heat exchange might reach 70% of the potential respiratory water loss (Langman *et al.* 1978).

The main site at which the heat and water exchange occurs has been identified as the turbinate structures of the nasal passages. The reasons why heat exchange and therefore water recovery are unexpectedly effective in large animals are that the surface area of their turbinate structures is much larger than in humans and that the wall-to-wall distance (the width of the passageways) is much smaller than in humans, thus permitting rapid heat exchange during the flow of air.

The turbinates of the camel have been studied by Arnautovic *et al.* (1970), who found that their surfaces are covered with a moist secretion that serves to humidify the dry inspired desert air. To obtain a quantitative measure of the area of the turbinate system we studied the heads of two adult camels, one formalin-fixed and the other deep-frozen immediately after death. A section across the turbinates shows them to be an extremely elaborate scroll-like structure. The manner in which they develop from the nasal entrance to the level of the olfactory sinus can be seen in figure 7. The structure is, in fact, more complex than suggested by Arnautovic *et al.* (1970).

Measurements of the perimeter of the turbinates in serial sections suggest that the total surface area that is exposed to respired air exceeds 1000 cm². The gap between adjacent surfaces in the air passages is only 1–2 mm. The remarkably large surface area for exchange may be compared with an area of approximately 12 cm² in humans and in rabbits (Negus 1958). In a study of rabbits in which thermocouples were implanted in the turbinate system it was found that the inhaled air, even when inhaled at 0 °C, is brought close to body core temperature as it passes over the turbinate system (Caputa 1979). Similar measurements have not been made in the camel, but the large surface of the turbinates and the narrowness of the passageways gives assurance that on inhalation the air is heated and fully humidified to body core conditions.

In our measurements we found a conspicuous difference in the temperature of the exhaled air between day- and night-time conditions. In the daytime the exhaled air is close to rectal temperature and at night the exhaled air was cool and approached and might even be below ambient air temperature. During the cool night this aids in water conservation while in the daytime the heat load makes it necessary for the camel to dump heat. In part this is achieved by exhaling warm air with a correspondingly high water content.

The difference between day and night temperatures of the exhaled air must be achieved primarily through changes in the blood flow within the turbinates. At night the blood flow may be minimal, thus adding little heat to the cooled tissues, and in the daytime a high blood flow will reheat the turbinates, the blood itself being cooled in the process. This results in exhalation of air close to the temperature of the blood and thus to the animal's body core temperature.

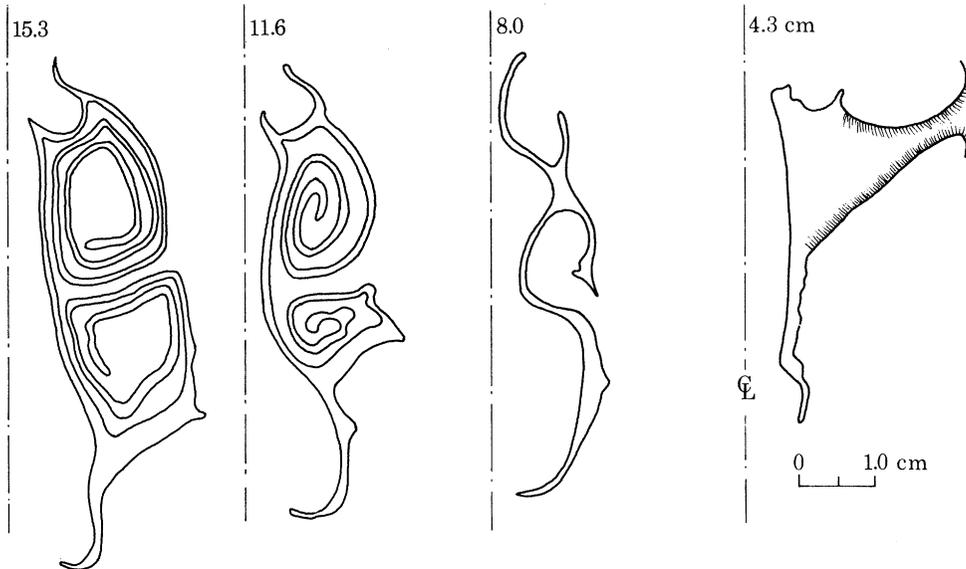


FIGURE 7. Tracings of cross sections of the nasal turbinate passages of a camel, made at the indicated distances from the anterior end of the naris.

The cooling of the blood that drains from the turbinates is probably of importance in protecting the brain from overheating, as suggested by Baker & Hayward (1968). The approximate blood flow to the brain of camels can be estimated to be approximately 0.4 l/min, based on an estimated brain mass of 700 g (Brody 1945) and a minute blood flow of 0.5 l/kg brain, similar to that in humans (Folkow & Neil 1971). If air is inhaled at 35 °C (25 % r.h.) and exhaled at 38 °C (100 % r.h.), then the change in enthalpy of the air is 93 kJ per kilogram of dry air. If one assumes that the ventilation volume of the camel is 40 l/min (as measured in the daytime in a 500 kg camel under heat stress), the amount of heat removed per minute would be 3.42 kJ. This is sufficient to cool about 410 ml blood by 2 °C. The cool venous blood from the nasal region drains via the cavernous sinus, where it cools the arterial blood flowing to the brain. Such cooling of the arterial blood to the brain depends on the presence of a carotid rete, which the camel possesses (Ask-Upmark 1935), and its importance has been amply documented in sheep and

several other species (see, for example: Baker 1972; Baker & Chapman 1977; Taylor & Lyman 1972). Thus, the exhalation of warm, saturated air in the daytime can permit selective cooling of the brain relative to body core temperature, while at night, when the surroundings are cool, this mechanism is not needed and the role of water conservation takes over.

The ability of the camel to desaturate the exhaled air has not been observed before, and no similar phenomenon has been reported for other mammals. However, the mechanism explains the observations of extremely low respiratory water losses reported in the accompanying paper (Schmidt-Nielsen *et al.* 1981). The low respiratory water losses were observed only in severely dehydrated camels, as was the directly measured desaturation of the exhaled air. This fact helps to explain the mechanism responsible for the desaturation of the exhaled air.

Mechanism for desaturation of exhaled air

Any hygroscopic surface will take up water when moist air passes over it, and water vapour will be given off again when dry air passes over it. This characteristic of a hygroscopic surface appears to be the basis for the mechanism in the camel, an assumption that is supported by observations with a simple mechanical model that effectively achieves the same result.

When a camel is reasonably well hydrated the turbinate surfaces are kept moist by secretions from the numerous glands in the mucosal lining, and especially by secretion from the lateral nasal gland. (This gland, also known as Steno's gland, is absent in man but present in many other mammals, such as dogs, in which its importance in nasal secretion and heat exchange is substantial.) The nasal gland is of appreciable size in camels (Abdalla & Arnautovic 1970), but its function has not been studied in detail. In the well watered camel one can observe small quantities of fluid flowing from the nose within the split in the upper lip. However, as dehydration progresses, the secretion subsides and the turbinate surfaces presumably dry up. These large areas will then be covered with a layer of dried mucous containing salts from glandular secretions, epithelial cells, etc.

The key to the desaturation of the air is that the dry surfaces take up water from the exhaled air and give off water during inhalation. The mechanism is similar to the nasal heat exchange that has been demonstrated in a variety of animals (Schmidt-Nielsen 1972), except that in this case water vapour is deposited on exhalation and removed from the surface on inhalation.

To demonstrate that this mechanism can work, we designed a simple mechanical model in which air of different humidities was made to flow in alternating directions (figure 8). Various materials were used for lining of the narrow space over which air was passed. To avoid condensation anywhere in this system, we used air of 90% r.h. to represent exhaled lung air, and for simplicity 0% r.h. to represent inhaled ambient air. The system was kept at constant temperature to avoid complications from temperature gradients along the system.

We found that ordinary filter paper convincingly demonstrated the effectiveness of the model. A single sheet of filter paper, 6.8 cm \times 24.2 cm (164 cm²), was tacked with rubber cement to a brass plate and inserted, leaving an air space of 1 mm. Passage of air in alternate directions over this system at a flow rate of 0.6 l/min gave the results suggested in figure 8. The frequency of 'breathing' was kept at 6 cycle/min, the 'inhalation' and 'exhalation' each lasting 5 s. When dry air passed through the model (figure 8, top), it arrived at the 'trachea' at 85% r.h.;

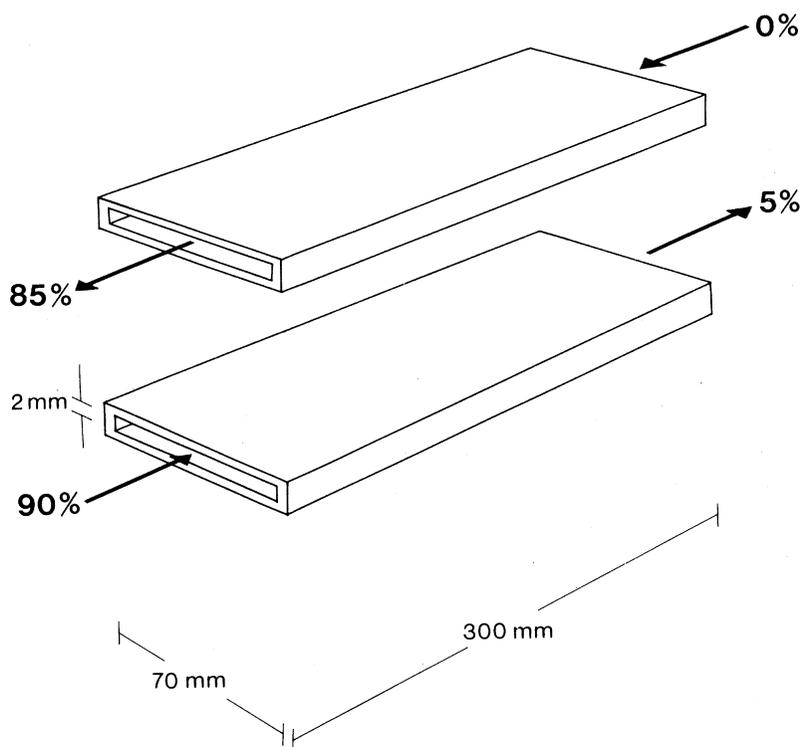


FIGURE 8. Mechanical model used to demonstrate the ability of a hygroscopic surface to give off or absorb water vapour in analogy to the camel's nose (cf. text).

when 'exhaled' air at 90% r.h. passed over the filter paper, it exited from the 'naris' at 5% r.h. The results were similar when 10 or 100 mg NaCl were added to the filter paper.

The ability of a single sheet of filter paper to alternately humidify and dry the air that passes over it makes us believe that this principle is effective in the nasal region of the camel, which has an area approximately ten times as large as that in our model. The air flow rates used in our model were 0.6 and 1.2 l/min. In the camels for which we reported observations in the preceding paper, the respiratory minute volume was 10–42 l/min (measured at ambient temperature and pressure),

or some 10 to 40 times higher than in the model. We therefore conclude that the ability of severely dehydrated camels to desaturate the exhaled air can be explained by a simple exchange system, based on a hygroscopic surface and in principle analogous to the well known exchange of heat in the nasal passageways.

Effect on water balance

The question of greatest relevance to the water balance of the camel is: how much water is saved when the exhaled air is cooled and desaturated, compared to the loss that would occur if the respiratory air were exhaled saturated at core temperature? The potential loss is the amount of water added on inhalation; the actual loss is less. The amount of water saved can be computed as (water recovered on exhalation)/(water evaporated on inhalation), or

$$\text{saving} = \frac{\text{mass H}_2\text{O in sat'd air at core temp.} - \text{mass H}_2\text{O in exhaled air}}{\text{mass H}_2\text{O in sat'd air at core temp.} - \text{mass H}_2\text{O in inhaled air}} \times 100 \%$$

The recovery of water depends on several variables, such as the camel's core temperature, the temperature of the exhaled air and its humidity, and, of course, the amount of water already present in the inhaled air. As an example we can consider measurements on camels under actual desert conditions.

Consider the record shown in figure 6. The ambient air was at 30.5 °C, 40 % r.h.; this air therefore had a water content of 12.3 mg/l. The exhaled air was at 31 °C, 75 % r.h., and had a water content of 23.8 mg/l. Had the air been exhaled at core temperature, 38.9 °C, and 100 % r.h., it would have had a water content of 47.9 mg/l. The recovery on exhalation caused by cooling and dehydration of the air was therefore 68 % of the potential water loss. (If the air had been exhaled cooled to 31 °C but fully saturated, the recovery would have been 46 %.)

The ability of severely dehydrated camels to desaturate the exhaled air represents a considerable increase in the animal's ability to conserve water. In the present study the animals exhaled air at 75 % r.h. as the lowest observed value, but we do not know whether this is the limit that can be achieved. The humidity of the ambient air at the site of our study was never very low, the water content remaining at approximately 12 mg/l, which in the night-time made the relative humidity increase to around 40–50 %. It is not known whether the inhalation of air at lower ambient humidities can result in exhalation at less than 75 % r.h.

It can be concluded that during the daytime the dehydrated camel copes with the heat load both by storing heat (permitting its body temperature to rise) and by dumping heat via exhalation at the expense of water conservation. Sweating also occurs, but it is probable that the substantial increase in evaporation from the nasal tract is of importance in keeping the brain temperature from increasing to intolerable levels. At night, when the environmental temperature is low, the dehydrated camel cools down, reduces the temperature of the exhaled air, and desaturates this air. This reduces the respiratory water loss to a minimum, thus conserving water.

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