In Cooperation with the University of Arizona School of Natural Resources
and Arizona Game and Fish Department

Literature Review and Annotated Bibliography: Water Requirements of Desert Ungulates

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By James W. Cain III, Paul R. Krausman, Steven S. Rosenstock, and Jack C. Turner

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Executive Summary

Ungulates adapted to desert areas are able to survive extreme temperatures and limited water availability. This ability is largely due to behavioral, morphological, and physiological adaptations that allow these animals to avoid or tolerate extreme environmental conditions. The physiological adaptations possessed by ungulates for thermoregulation and maintenance of water balance have been the subject of numerous studies involving a wide range of species. In this report we review the behavioral, morphological, and physiological mechanisms used by ungulates and other desert mammals to maintain water and temperature balance in arid environments. We also review some of the more commonly used methods for studying the physiological mechanisms involved in water balance and thermoregulation, and the influence of dehydration on these mechanisms.

Introduction and Definitions

For this literature review and annotated bibliography our objectives were (1) to compile available scientific literature on thermoregulation and water balance in desert mammals, particularly studies on ungulates and (2) to review the methodologies available to study the physiological mechanisms involved in thermoregulation and water balance. We were specifically interested in the physiological responses of ungulates to dehydration. This overview and annotated bibliography are intended as a source of references for wildlife biologists, wildlife managers, and others interested in wildlife who have a modest amount of knowledge and experience with animal physiology.

At the outset, it is necessary to define *water balance* and *water flux* because they commonly appear in the literature contained in this bibliography. *Water balance* is the condition where intake of free water, preformed water in food, and metabolic water equals water loss through feces, urine, and cutaneous and pulmonary evaporation over a specific period of time (Louw 1993). Animals may experience positive or negative water balance at a given point in time. *Water flux* or water turnover is the amount of water (ml/day) an animal processes through its body each day (Nagy and Peterson 1988).

We review literature relating to the effects of dehydration on wild and domestic ungulates and also discuss the behavioral, morphological, and physiological mechanisms used by ungulates to maintain water and temperature balance in an arid environment:

- *Behavioral adaptations* reviewed include timing of activities, use of microhabitats, body orientation, migration, diet selection, and social behaviors.
- *Morphological adaptations* include body size and shape, pelage and skin characteristics, and patterns of fat deposition.
- *Physiological adaptations* include adaptive heterothermy and selective brain cooling, as well as adjustments to metabolic rate, renal and digestive water loss, and pulmonary and cutaneous evaporative water loss.

Finally, we review some commonly used methods for the study of the physiological mechanisms involved in water balance and thermoregulation, and the influence of dehydration on these mechanisms. We have included some studies conducted on the physiology of thermoregulation and water balance on small eutherian and marsupial mammals.

Adaptations for Thermoregulation and Maintenance of Water Balance

The physiological adaptations possessed by ungulates for thermoregulation and maintenance of water balance have been investigated using a variety of methods in domestic goats, sheep, horses, donkeys (*Equus asinus*), cattle, camels (*Camelus dromedarius*), guanacos (*Llama guanicoe*), llamas (*Llama glama*), cervids (deer [*Odocoileus* spp.] and elk [*Cervus elaphus*]), pronghorn (*Antilocapra americana*), desert bighorn sheep (*Ovis canadensis mexicana* and *O. c. nelsoni*), reindeer (*Rangifer tarandus*), muskoxen (*Ovibos moschatus*), and a wide range of African gazelles and other bovids.

Ungulates adapted to desert areas are able to survive and even thrive, despite extreme temperatures and scarce water, by (1) avoiding environmental conditions that can result in heat stress and dehydration or (2) tolerating these conditions using behavioral, morphological, and physiological adaptations. (Schmidt-Nielsen 1979; Louw and Seely 1982).

Behavioral Adaptations

Desert ungulates reduce heat loads and maintain water balance using daily timing of activity, diet selection, microhabitats, body orientation, migration, seasonal timing of reproduction, and social behaviors (Jarman 1977; Berry et al. 1984; Skinner and van Jaarsveld 1987; Fryxell and Sinclair 1988*a*; Alderman et al. 1989; Sargeant et al. 1994; Costa 1995). Although described separately here, behavioral adaptations function in combination with both morphological and physiological adaptations.

Timing of Activity. Seasonal changes in the duration or timing of daily activities can reduce heat loads and minimize evaporative water loss. During the hottest, driest periods of the year some species reduce diurnal activity and become more crepuscular, foraging and moving during the cooler periods of the day and thereby reducing daily heat loads (Jarman 1977; Alderman et al. 1989; Vrahimis and Kok 1992; Hayes and Krausman 1993; Sargeant et al. 1994). Nocturnal activities, including feeding have been documented for cattle, pronghorn (Ellis and Travis 1975; Lewis 1977), oryx (*Oryx beisa*), eland (*Taurotragus oryx*), African buffalo (*Syncerus caffer* – Lewis 1977), desert bighorn sheep (Miller et al. 1984), and desert mule deer (*Odocoileus hemionus eremicus* – Hayes and Krausman 1993).

In addition to the thermoregulatory benefits of restricting activities to cooler nighttime periods, ungulates in some areas also increase the intake of preformed water by foraging at night. In areas where relative humidity increases at night, plants absorb moisture from the cool night air, thereby increasing preformed water content of forage (Taylor 1969*a*). For example, in northern Kenya, the Namib Desert, and Aldabra Atoll in the Seychelles Islands, as ambient temperatures decrease at night, the air loses its capacity to hold water and excess condensates on vegetation (Taylor 1968*a*, 1969*a*, 1972; Burke 1988). Nocturnal feeding in these areas can provide animals with forage containing up to 40% more water than is available in these same plant species during the day (Taylor 1968*a*, 1969*a*). Furthermore, the general behavior of selecting forage plants with higher moisture content, regardless of time of day, may provide a means to reduce the amount of free water needed to maintain water balance (Taylor 1969*a*; Carlisle and Ghobial 1968: Jarman 1973).

Use of Microclimates. The use of cooler microclimates also reduces heat loads and the need for evaporative cooling, thus conserving water. Use of shaded, lower temperature microhabitat is a common behavior during midday when temperatures are highest, and has been observed in a variety of wild ungulates, including dik-dik (*Rhynchotragus kirkii* – Kamau and Maloiy 1985), desert bighorn sheep (Simmons 1969; Hansen 1982), desert mule deer (Sargeant et al. 1994; Tull et al. 2001), collared peccary (*Pecari tajacu* – Sowls 1997), dorcas gazelle (*Gazella dorcas* – Wilson 1989), eland (Taylor and Lyman 1967), oryx (Lewis 1978), springbok (*Antidorcas marsupialis* – Bigalke 1972; Hofmeyr and Louw 1987), domestic cattle (Lewis 1978), and sheep (Johnson and Strack 1992).

Ungulates that are active during the hotter periods of the day and those that inhabit areas lacking shade are able to reduce the amount of solar radiation absorbed by adjusting body position relative to the location of the sun (Taylor 1969*a*; Berry et al. 1984; Hofmeyr and Louw 1987; Vrahimis and Kok 1992). To minimize heat gain and water loss, animals in shadeless areas stand with the long axis of the body parallel to the direction of the sun with the rump pointed towards the sun or lie down in this position with head down, shaded by their body, thereby reducing solar radiation loads (Jarman 1977; Berry et al.

1984; Hofmeyr and Louw 1987; Vrahimis and Kok 1992). For example, springbok using this body orientation can reduce estimated solar radiation load by 62% during the day (Hofmeyr and Louw 1987). Social interactions also facilitate reduction of heat loads. For example, camels (Wilson 1990) and collared peccaries (Sowls 1997) create shade for each other and reduce the amount of surface area exposed to solar radiation by bedding down in small groups.

Migration. Migration is also used by some species to avoid high temperatures, limited water availability, and poor forage conditions. Ungulate species that currently have or had migratory populations, include eland, gazelles, gemsbok (*Oryx gazella*), springbok, wildebeest (*Connochaetes taurinus*), elephant (*Loxodonta africana*), and zebra (*Equus* spp.) in Africa; elk, pronghorn, bison (*Bison bison*), mule deer, and caribou in North America; and chamois (*Rupicapra rupicapra*), saiga (*Saiga tatarica*), Mongolian gazelle (*Procapra gutturosa*), and Tibetan antelope (*Pantholops hodgsoni*) in Europe and Asia (Grzimek and Grzimek 1960; Field 1971; Talbot and Talbot 1978; Fryxell and Sinclair 1988*a*). While ungulates in different areas show varying patterns of migration, some migrate across the landscape (e.g., wildebeest). and others migrate altitudinally (e.g., elk). Quantity and quality of forage resources, avoidance of predation, and availability of drinking water may be reasons to vary migration patterns (Fryxell and Sinclair 1988*a*; Rautenstrauch and Krausman 1989). Ungulates commonly move to areas of recent rainfall to take advantage of the increasing quantity and or quality of vegetation and leave areas when drought conditions prevail (Sinclair and Fryxell 1985; Fryxell and Sinclair 1988*b*). Species inhabiting arid or semi-arid environments may also respond to changes in the availability of surface water (Western 1975; Sinclair and Fryxell 1985; Fryxell and Sinclair 1988*b*).

Timing of Reproduction. Reproduction in ungulates is timed to insure that parturition occurs at a favorable time of year thus increasing the likelihood of offspring survival (Skinner and van Jaarsveld 1987). The predictable seasonal environmental conditions in temperate and mesic tropical areas favors regular seasonal breeding in ungulates, with young being born over a relatively short time period (Skinner and van Jaarsveld 1987). Conversely, species that inhabit arid and semi-arid areas with unpredictable environmental conditions display a more opportunistic breeding pattern, where young are born over a more extended period of time (Skinner and van Jaarsveld 1987). For example, the young of springbok (Skinner and Louw 1996; Skinner and van Jaarsveld 1987), gemsbok and eland in Africa (Skinner and van Jaarsveld 1997), and desert bighorn sheep in North America (Thompson and Turner 1982; Witham 1983), can be born almost any month of the year.

Morphological Adaptations

Desert-adapted ungulates possess a variety of morphological adaptations that aid in the reduction of heat loads and minimize water loss. Morphological adaptations that reduce heat loads and minimize water loss include body size and shape, pelage and skin characteristics, and patterns of fat deposition (Louw and Seely 1982). Although described separately here, morphological adaptations to life in arid areas do not function in isolation, but work in combination with both physiological and behavioral adaptations.

Body Size and Shape. Major morphological characteristics that regulate heat gain and water loss in ungulates are body size and shape. Large bodied animals gain heat from the environment at a slower rate than do smaller animals because they have a lower surface-area-to-volume ratio and higher thermal inertia (Scholander et al. 1950; Herreid and Kessel 1967; McNab 1983; Bradley and Deavers 1980; Phillips and Heath 1995). The relatively small surface area of large animals reduces the proportion of the animal exposed to solar radiation, thereby reducing potential environmental heat loads.

Although their overall energy requirements are higher, large animals also have lower mass-specific metabolic rates than do small animals; these low metabolic rates contribute relatively less metabolic heat to the total heat load (Kleiber 1932; Schmidt-Nielsen 1979; Louw and Seely

1982). While having a large body reduces the rate at which heat is gained from the environment, it is disadvantageous because it also reduces the rate of heat loss to the environment and shaded microclimates of sufficient size are often more limited in areas that are sparsely vegetated or lack other types of cover (Louw and Seely 1982).

The shape of the body and appendages also influences the rates of heat gain and loss in animals; thin appendages minimize radiant heat gain and maximize convective heat loss (Louw 1993). Compared to similar species inhabiting mesic areas, desert-adapted species often have longer, thinner appendages with a higher surface-to-volume ratio that facilitates heat loss (Bradley and Deavers 1980; Philips and Heath 1992). Changes in the rate of blood flow from the body core to the surface by vasodilatation and vasoconstriction affects the rate of heat loss from the body surface. Thus, areas of the body surface where the changes in blood flow occur are analogous to windows that can be opened or closed to regulate heat loss (Philips and Heath 1992; de Lamo et al. 1998). The highly vascularized horns of bovids may have a thermoregulatory function (Taylor 1966; Picard et al. 1996, 1999). Bovid species from arid areas have relatively larger horn cores and thinner keratin sheaths than temperate species (Picard et al. 1999). Both the thin keratin sheath and larger, vascularized horn core would facilitate heat loss from horns of tropical bovids compared to temperate species (Picard et al. 1996, 1999).

Pelage Characteristics. Pelage also affects the maintenance of heat and water balances in ungulates. Both the thickness and color of the pelage affect heat transfer between the body and the environment (Hofmeyr 1985). Pelage thickness affects heat gain and loss of an animal from the environment; thin pelage allows more heat to reach the body, whereas thick pelage provides maximum insulation from solar radiation. However, thick coats limit the use of sweating for evaporative cooling (Hofmeyr 1985). Conversely, thin pelage allows for maximum heat loss but provides relatively little insulation.

There is a decrease in pelage thickness as body size increases in desert-adapted ungulates, which may facilitate heat loss and compensate for the disadvantage of large body size (Hofmeyr 1985; Hofmeyr and Louw 1987). Pelage color also affects rates of heat gain and loss. Desert-adapted ungulates are typically light colored. Light colored pelage reflects more radiation than does dark colored pelage (Hofmeyr 1985). However, while dark colored pelage may absorb more solar radiation than light colored pelage, reduced radiation reaches the skin of the animal, and animals with dark pelage (e.g., black Bedouin goats – Shkolnik et al. 1972) can have lower metabolic rates in winter than animals with light colored pelages (Louw and Seely 1982; Louw 1993).

Fat Deposition. The location of fat deposition also affects rates of heat loss and gain. Fat stored subcutaneously throughout the body may inhibit the loss of heat to the environment (Louw and Seely 1982). The storage of fat in localized areas may be an adaptation to reduce the impact of fat reserves on an animal's ability to lose heat to the environment by minimizing the insulative effect of fat to small areas of the body, thus facilitating heat lost over other body surfaces. Examples of animals that have highly localized fat storage include the camel, zebu cattle, and arid–adapted fat-tailed sheep (Degen 1977*c*; Louw and Seely 1982; Wilson 1989).

Physiological Adaptations

Physiological adaptations function to minimize cutaneous and pulmonary water loss and water loss in feces and urine. Physiological mechanisms used by desert ungulates to minimize water loss include adaptive heterothermy, changes in metabolic rate, reduction in renal and digestive water loss, and reduction in pulmonary evaporative water loss by cooling exhaled air (Louw and Seely 1982; McNab 2002).

Water Loss. There are four primary routes of water loss in mammals: cutaneous and pulmonary evaporation, feces, and urine. Lactation is an additional route of water loss for females nursing young. Desert-adapted ungulates have evolved physiological adaptations that reduce the amount of water lost through each of these routes or are able to tolerate significant amounts water loss. Some species (e.g., camels and Bedouin goats) can survive water losses amounting to 30 – 40% of body mass, whereas in others (e.g., waterbuck) a 15% loss can result in mortality (Taylor et al. 1969b; Louw 1984).

Desert-adapted ungulates employ facultative use of cutaneous evaporation, depending on their extent of hydration. Cutaneous evaporation involves both insensible water loss (water loss from moist surfaces) and sensible water loss (i.e., sweating). The latter is controlled by a neural response to heat. In hydrated animals, the rate of cutaneous evaporation generally increases with body temperature. However, when dehydrated, Grant's gazelle (*Gazella granti*), Thomson's gazelle (*Gazella thompsonii*), oryx, eland, wildebeest, hartebeest, African buffalo, zebu steer (Taylor 1969*a*, 1970*a*, *b*), impala (*Aepyceros melampus* – Maloiy and Hopcraft 1971), east African goat (Schoen 1968), donkey (Maloiy 1970), and camel (Schmidt-Nielsen et al. 1957) reduce the rate of cutaneous evaporation. Cutaneous evaporation rates of hydrated animals declined by 12 – 89% when dehydrated. The body temperature at which dehydrated animals begin sweating is often higher than that of normally hydrated animals (Schmidt-Nielsen et al. 1957; Taylor 1969*a*, 1970*a*, *b*). At very high ambient temperatures (45 ºC), species such as the oryx stop sweating entirely, with the exception of insensible water loss from the skin, and use adaptive heterothermy (see below) to reduce evaporative water loss (Schmidt-Nielsen et al 1957; Taylor 1969*a*, 1970*a*, *b*).

Pulmonary evaporation is another major avenue of water loss in mammals. Similar to the rates of cutaneous evaporation, pulmonary evaporation tends to increase with increasing body temperature. In normally hydrated animals, respiratory rates increase with increasing ambient temperature, resulting in increased rates of pulmonary evaporation (Taylor 1969*b*, 1970*a*; Maloiy and Hopcraft 1971; Finch 1972). Dehydrated animals often have lower respiratory rates and initiate panting at higher ambient temperatures than do normally hydrated animals. However, some species (e.g. dik-dik and wildebeest) increase respiratory rates with increasing ambient temperature regardless of their water status (Taylor 1969*a*, 1970*a*, *b*; Maloiy 1973*a*). By breathing slowly and deeply some ungulates may be able to extract more oxygen per breath, therefore reducing the amount of air needed to move through the lungs and thus reducing respiratory water loss (Taylor 1969*a*). Another mechanism that can result in the reduction of water loss via pulmonary evaporation is the reduction in water content of expired air. Expired air is cooled as it passes over the relatively cool nasal turbinates, allowing extraction of water and reducing respiratory water loss (Taylor 1969*a*; Langman et al. 1978, 1979; Schmidt-Nielsen et al. 1981*a*, *b*).

Reduction in water content of feces and urine, and increases in urine osmolality are mechanisms by which ungulates reduce water loss (Maloiy et al. 1979). Considerable interspecific variation in the moisture content of feces exists in normally-hydrated ungulates. Fecal water content ranges from 40- 50% in arid-adapted species (e.g., springbok, gemsbok) to 70-80% in species adapted to more mesic areas (e.g., cattle, waterbuck [*Kobus ellipsiprymnus*] – Maloiy et al. 1979; Louw and Seely 1982; Woodall et al. 1999). Reductions in fecal moisture content of 17-50% have been found in some ungulates (e.g., dorcas gazelle, eland, cattle, camel, impala, desert bighorn sheep) when dehydrated (Ghobrial and Cloudsley-Thompson 1966; Taylor and Lyman 1967; Maloiy and Hopcraft 1971; Turner 1973). Water is reabsorbed in the colon, and species possessing large intestines that are longer and have more surface area with smaller circumferences of the proximal and distal colon are able to produce drier feces (e.g., springbok, eland, impala versus wildebeest, waterbuck---Woodall and Skinner 1993).

Arid-adapted ungulates typically have reduced urine output and greater urine concentration than do non arid-adapted species (Louw and Seely 1982). Reductions in urine volume are the result of reduced glomerular filtration rates and renal plasma flow (Siebert and Macfarlane 1971; Maloiy et al. 1979; Wilson 1989). The ability of the mammalian kidney to produce hyperosmotic urine relative to the blood is related to the length of the loop of Henlé in the nephron; mammals with longer loops of Henlé are capable of producing a more concentrated urine (Louw and Seely 1982; McNab 2002). Arid-adapted mammals, which produce more concentrated urine, have longer loops of Henlé than do other species (Schmidt-Nielsen and O'Dell 1961). Because most of the loop of Henlé is in the medulla of the kidney, the thickness of the medulla is correlated with the length of the loop of Henlé. The thickness of the medulla relative to kidney size, called the relative medullary thickness, is often used as an index of kidney concentrating ability and is correlated with the environment and diet of the animal (Zervanos 2002; McNab 2002). In desert bighorn sheep, the relative medullary thickness is nearly twice that of domestic sheep and urine concentrations of 3,900 mosm have been measured (Horst and Langworthy 1971; Turner 1973).

Water is conserved when dehydrated ungulates reduce total urine volume and increase concentration (Taylor and Lyman 1967; Schoen 1969; Maloiy and Hopcraft 1971; Maloiy et al. 1979; Ali et al. 1982; Mohamed et al. 1988). Reductions in urine volume ranging from 0 to 76% and increases in urine osmolality ranging from 3 to 239% have been documented in comparisons of normally hydrated and dehydrated ungulates (e.g., camels, goats, sheep, dorcas gazelle, Grant's gazelle, Thomson's gazelle, and rock hyrax – Taylor et al. 1969*a*; Khan et al. 1978; Maloiy et al. 1979; Ali et al. 1982; Olsson et al. 1982; Etzion and Yagil 1986; Mohamed et al. 1988; Wilson 1989).

Role of the Rumen in Water Balance. The relatively large volume of fluid in the alimentary tract of ruminants may maintain water balance for blood and body tissues for the first few days of water deprivation (Hecker et al. 1964, Maloiy et al. 1979, Louw and Seely 1982). After dehydration, some desert-adapted species are able to drink water in amounts equivalent to a large proportion of their body mass. For example, Bedouin goats (Choshniak and Shkolnik 1977), donkey (Maloiy 1970), camels (Schmidt-Nielsen 1979), and desert bighorn sheep (Turner 1973) are able to drink water in amounts equivalent to 40, 30, 30, and 20% of their body mass, respectively. However, other species, such as oxen and cattle, are not able to rapidly imbibe water because of problems associated with hemolysis (Bianca 1970; Louw 1984).

The function of the rumen during rehydration differs among species that are able to ingest large volumes of water over short time periods. For example, in camels, water ingested rapidly passes from the alimentary tract to the blood and body tissues (Schmidt-Nielsen 1979; Etzion et al. 1984). In desert-adapted goats, large volumes of rapidly ingested water are released more slowly to the blood and other body tissues, thus minimizing hemolysis and osmotic shock to tissues (Choshniak and Shkolnik 1977; Louw 1984). Osmotic fragility of red blood cells decreases and life span of red blood cells increases in some ungulates (e.g., camel and desert bighorn sheep) when dehydrated (Yagil et al. 1974; Turner 1979). Those mechanisms may reduce water requirements by minimizing the need to replace red blood cells more often; they allow for rapid rehydration while minimizing hemolysis (Yagil et al. 1974; Turner 1979).

Body Water Pools And Water Turnover. Total body water of mammals is often viewed as being composed of separate compartments: the intracellular fluid consisting of fluid within cells and the extracellular fluid consisting of rumen fluid, blood plasma fluid and interstitial fluids; water can move between body fluid compartments (Lockwood 1966; Maloiy et al. 1979; Louw 1993). The relative distribution of water and the contribution to total fluid loss during dehydration varies for each compartment depending on species and state of hydration (Maloiy et al. 1979; Louw 1993). The loss of water from water compartments varies for dehydrated animals. Ungulates (e.g., camels, Bedouin goats) that are able to withstand severe dehydration (i.e., 20 – 30% of body mass) typically lose relatively less water from blood plasma fluid than from other compartments, or are able to move fluid from other compartments to maintain plasma volume at a level that prevents circulatory failure during dehydration (Macfarlane et al. 1961; Yousef et al. 1970; Choshniak and Shkolnik 1977; Turner 1979; Choshniak et al. 1984). During the first few days of dehydration, fluid contained in the rumen provides a large portion of the water lost, and may buffer ungulates against short-term water deprivation (Hecker et al. 1964; Hoppe et al. 1975; Maloiy et al. 1979; Turner 1979).

Water turnover rates vary among species and are lower in animals from arid areas than those adapted to more mesic conditions; this trend is also observed in domestic ungulates with breeds adapted to arid areas having lower water turnover rates than European breeds (Macfarlane et al. 1971; Macfarlane and Howard 1972; Degen 1977*a*; Maloiy et al. 1979; Nagy and Peterson 1988). In normally hydrated ungulates (both wild and domestic), water turnover rates increase with increasing temperature and are lower in winter than in summer (e.g., mule deer [1,750 – 8,050 ml/day – Longhurst et al. 1970; Nagy and Peterson 1988], pronghorn [1,940 – 2,420 ml/day – Wesley et al. 1970], camel [Siebert and Macfarlane 1971; Yousef 1971], feral burro [Tomkiewicz 1979], collared peccary [1,170 – 1,360 ml/day – Zervanos and Day 1977], desert bighorn sheep [4,850 – 7,010 ml/day], horse, and cattle – Macfarlane and Howard 1972).

In arctic areas, water availability is limited more in winter than in summer resulting in higher water turnover rates in arctic ungulates (e.g., caribou, muskoxen) in summer than in winter (Cameron and Luick 1972; Cameron et al. 1982). When ungulates are dehydrated, water turnover rates decrease regardless of ambient temperature (Maloiy 1973*b*). Those rates have also been found to differ between captive and free-living animals of the same species (Nagy and Peterson 1988). For example, captive mule deer have significantly lower water turnover rates than do free-living mule deer (Nagy and Peterson 1988; Parker et al. 1993).

Water turnover rates also vary with reproductive status. Water turnover rates are 40 – 50% higher in pregnant and lactating animals than in nonlactating animals (Siebert and Macfarlane 1971; Macfarlane and Howard 1972; Degen 1977*b*; Maloiy et al. 1979; Hassan et al. 1988). Water deprivation during lactation can decrease milk production (Maltz and Shkolnik 1980; Wilson 1989; Hossaini-Hilali et al. 1994). Dehydration during lactation can also result in a reduction in the concentration of fat and nonfat solids and an increase in water content of milk. This composition change is viewed as an adaptation to insure that nursing young receive adequate water during times of limited water availability (Mittal 1980; Yagil and Etzion 1980*a*, *b*; Yagil et al. 1986).

Maloiy et al. (1979) classified ungulates into three functional groups based on water turnover rate, metabolic rate, and renal concentrating ability. African buffalo, cattle, pig, waterbuck with increased rates of water turnover and metabolism and poor renal concentrating ability comprise Group I; sheep, wildebeest, hyrax [*Procavia habessinica*], donkey with intermediate water turnover and metabolic rates and moderate renal concentrating abilities comprise Group II; and camel, goat, oryx, gazelles that have lower metabolic and water turnover rates and higher renal concentrating abilities comprise Group III.

Blood Plasma Constituents. Reductions in plasma fluid volume caused by dehydration affect blood constituents. The reduction in plasma volume results in an overall increase in plasma osmolality due to increases in plasma Na^+, Cl^-, K^+, chloride, urea, packed cell volume, hemocrit, and hemoglobin concentrations (Bianca et al. 1965; Ghobrial and Cloudsley-Thompson 1966; Laden et al. 1987; Ben Goumi et al. 1993; Abdelatif and Ahmed 1994; Al-Toum and Al-Johany 2000). Severe hemoconcentration due to loss of plasma fluid can result in death from circulatory failure (Schmidt-Nielsen et al. 1956; Macfarlane et al. 1961).

Adaptive Heterothermy and Selective Brain Cooling. It has been proposed that adaptive heterothermy is used by many ungulates in arid areas to minimize water loss from evaporative cooling (i.e., sweating and panting). By allowing the body temperature to rise during the day, animals are able to store heat and release it at night when ambient temperature falls below the body temperature, thus reducing the need to dissipate heat during the day via evaporative cooling. Normally hydrated desert-adapted ungulates with access to free water typically maintain body temperature within a fairly narrow range by evaporative cooling (Taylor 1970*a*, *b*). While some species must maintain body temperatures within this narrow range regardless of their state of hydration, body temperatures of some fluctuate over a wider range when dehydrated (Taylor et al. 1969*a*; Finch 1972).

The larger range over which body temperature fluctuates in dehydrated versus hydrated animals is often attributed to adaptive heterothermy and its water-conserving function (Schmidt-Nielsen et al. 1957; Taylor 1970*a*, 1972; Schoen 1972; Taylor and Lyman 1972). However, Mitchell et al. (2002), in their review of the adaptive heterothermy, suggested that the rise in body temperature of ungulates observed in previous studies was largely an artifact of studying animals in captive conditions in which they were prevented from employing behavioral and other thermoregulatory mechanisms. Furthermore, in their studies of free-ranging wildebeest, springbok, impala, and oryx, Mitchell et al. (2002) failed to find evidence of adaptive heterothermy and concluded that increased magnitude of daily fluctuations in body temperature observed in dehydrated animals was actually dehydration-induced hyperthermia, not evidence of adaptive heterothermy. Dehydration-induced hyperthermia may be adaptive in conserving water because it results in a increase in the temperature at which animals switch from thermoregulation via convection and radiation to evaporative cooling (Mitchell et al. 2002).

Selective brain cooling via countercurrent heat exchange in the nasal passages is often associated with adaptive heterothermy and allows some ungulate species to survive body temperatures >42 ºC for long periods of time. The carotid rete is an area of the carotid artery divided into a series of small blood vessels just below the brain. It comes into contact with a network of small veins returning from the nasal passages where heat is transferred from the warmer arterial blood to the venous blood that has been cooled by the animal's respiration when passing through the nasal passages (Taylor 1969*a*; Louw and Seely 1984; Wilson 1989). Countercurrent heat exchange can result in blood entering the brain ≤ 3.9 ºC cooler than in the rest of the body (Taylor 1972).

The carotid rete is not present in all ungulates, but has been found in a variety of both arid and non-arid dwelling mammals (e.g., eland, elk). Some researchers have concluded that the carotid rete is an adaptation to reduce heat in blood going to the brain after exercise and consequently provides an advantage to animals inhabiting arid areas (Baker 1979). However, Mitchell et al. (2002) also questioned the role of selective brain cooling as a mechanism for maintaining the brain at lower temperature while body temperature is allowed to rise with adaptive heterothermy. They hypothesized that selective brain cooling is used in free-ranging animals under moderate heat loads to switch from evaporative to non-evaporative routes, and therefore has a thermoregulatory function unrelated to adaptive heterothermy (Kuhnen 1997; Mitchell et al.2002).

Metabolic Rate. Reduction in basal metabolic rate (BMR – metabolic rate of resting animal with body temperature in thermoneutral zone) can minimize metabolic heat gain and reduce water loss in ungulates; desert-adapted ungulates often have lower metabolic rates than do other ungulates (Macfarlane et al. 1971; Shkolnik et al. 1972; Wilson 1989; Louw 1993). The lower metabolic rates of desert-adapted ungulates (e.g., camel, Bedouin goat, eland, steenbok [Raphicerus campestris]) are associated with lower water turnover rates in these animals (Macfarlane and Howard 1972; Maloiy et al. 1979). Furthermore, dehydrated animals often have lower metabolic rates than when normally hydrated (Schmidt-Nielsen et al. 1967; Taylor 1969a; Finch and King 1982).

Diet and Water Balance. The amount of preformed water contained in the food of some ungulate species (e.g., oryx, Grant's gazelle, springbok) has been associated with free water requirements. At times preformed water provides a significant portion of the total water intake and affects the ability of some species to survive long periods without free water (Taylor 1968*a*, 1969*a*; Schmidt-Nielsen 1979; Zervanos and Kauffman 1981; Jhala et al. 1992). Dependence on free water sources and rates of consumption of forage are associated with the moisture content of forage (Jarman 1973). The lower moisture content of forage used by grazing versus browsing animals makes the former more dependent on availability of free water (Maloiy 1973*a*; Kay 1997).

Dehydration reduces the rate of forage intake (dry matter intake) in some ungulate species (e.g., white-tailed deer [Lautier et al. 1988], zebu cattle, domestic sheep, desert bighorn sheep [Turner 1973]) whereas others (e.g., arid adapted donkey [Maloiy 1970], dorcas gazelle [Mohamed et al. 1988], bushbuck, reedbuck, Uganda kob [Taylor and Maloiy 1967], Bedouin goat [Schoen 1969; Chosniak et al. 1988], and camel [Wilson 1989]) tend to maintain forge intake even when dehydrated. Increases in apparent dry matter digestibility have been documented in dehydrated ungulates, including Bedouin goats (Silanikove 1985), cattle (Thornton and Yates 1968), Thomson's and Grant's gazelles (Maloiy 1973b), and desert bighorn sheep (Turner 1973). The increase in apparent dry matter digestibility in dehydrated ungulates has been associated with slower rates of passage of digesta through the rumen, thus allowing more time for fermentation (Brosh et al. 1983, 1986; Choshniak et al. 1988).

Methods for Studying Water Physiology

A variety of methods is available for studying water physiology in mammals. Methods for studying water balance and water flux include desiccation and the use of labeled water to measure water volume and turnover rate in different body water compartments. There are different substances available to label water, depending on the particular body water compartment of interest. Titrated water is commonly used to measure total body water, inulin and sodium thiocyanate to measure extracellular water, and Evan's blue dye to measure blood plasma volume. Inulin is also used to measure glomerular filtration rate in studies of kidney function. Laboratory tools including centrifuges, osmometers, spectrometers, and autoanlyzers have been used to study aspects of blood and fluid chemistry and osmolality of body fluids. Methods for the study of the different routes of water loss include the use of metabolic chambers and metabolic masks to assess water lost via respiration, use of absorbent capsules to measure rates of cutaneous water loss, and collection of urine and feces to determine water loss.

Water Balance and Water Flux

Two methods have been used to estimate total body water (TBW): desiccation and labeled water. The desiccation method involves weighing an animal in the state of hydration of interest, killing the animal and drying the carcass to a constant mass, then estimating total body water by the difference in live versus dry mass. The second method involves the use of the indicator-dilution principle to estimate TBW or water volume in individual compartments (Lassiter and Gottschalk 1980*a*; Holleman et al. 1982; Guyton and Hall 1996). Total body water or the volume of an individual fluid compartment is determined by injecting a known volume and concentration of substance that will mix uniformly with the fluid of the compartment of interest, then, samples of the compartment fluid are taken after the introduced fluid equilibrates with the compartment fluid, and the concentration of the indicator substance is determined. The volume of the compartment can be determined by the following equation:

$$\text{volume B} = ([\text{volume A}]\times[\text{concentration A}])/\text{concentration B}$$

where volume B is the compartment volume, volume and concentration A are the volume and concentration of the indicator substance used, and concentration B is the concentration of the indicator substance in the fluid of the compartment (Guyton and Hall 1996).

However, because body fluids are constantly changing, modifications to the above equation and collection of serial samples of the compartment fluid are necessary (Lassiter and Gottschalk 1980*a*; Guyton and Hall 1996). The rate of the disappearance of the indicator substance in the body fluid is used to determine TBW flux rate. There are six assumptions in the use of titrated water to estimate total body water and water flux: (1) body water volume does not change during the measurement period; (2) water flux rates are constant during measurement period; (3) the isotope is not incorporated into body constituents other than water; (4) the isotope only leaves the body in the form of water; (5) concentration of isotope in water lost is equal to the concentration in body water; and (6) water in the environment does not enter the animal via the skin or lungs (Holleman et al. 1980; Nagy and Costa 1980). The effects of violating those assumptions and methods for minimizing related errors are described in Nagy and Costa (1980) and Nagy (1983). For example, most errors can be minimized or avoided by recognizing violations of assumptions and using appropriate equations to adjust for these violations; water flux rate estimates using the titrated water method are usually ±10% of actual flux rates (Nagy and Costa 1980).

In the past, a variety of substances has been used to estimate TBW (e.g., antipyrine, deuterated water, and titrated water), extracellular fluid volume (ECFV – e.g., inulin, sodium thiocyanate, bromide, sucrose, mannitol, radiosulfate), and blood plasma volume (e.g., radioiodinated human serum albumin, Evan's blue dye) (Lassiter and Gottschalk 1980*a*; Guyton and Hall 1996). Currently, the most common substances used are deuterated and titrated water to estimate TBW; inulin and sodium thiocyanate to estimate ECFV; and Evan's blue and radioiodinated human serum albumin to estimate blood plasma volume (Lassiter and Gottschalk 1980*a*; Guyton and Hall 1996). Intracellular fluid volume cannot be measured directly, but is estimated by the difference between total body water and extracellular fluid volume (Lassiter and Gottschalk 1980*a*; Guyton and Hall 1996). Radio-isotopically labeled water methods are not limited to the laboratory or captive animals and can be used on free-living animals in natural conditions under some circumstances (Nagy 1975, 1994). Animals must be captured and held briefly at least twice—once to administer the labeled water, collect baseline samples, and mark the animal so that it can be identified later, and at least once after the isotopically labeled water equilibrates (mixes uniformly) with the fluid of the compartment of interest. The equilibrium time for titrated water in ungulates varies from 5 – 6 hr in sheep and goats, 7 – 8 hr in cattle, and 8 – 12 hr in camels (Siebert and Macfarlane 1971; Macfarlane and Howard 1972; Holleman et al. 1982).

Blood Constituents

Hemocrit or Packed Cell Volume. Hemocrit or packed cell volume is determined by centrifugation. Whole blood is centrifuged in calibrated tubes to determine the total cell volume to total blood volume; calibrated centrifuge tubes can be used that allow the direct estimate of percent of cells (Lassiter and Gottschalk 1980*b*; Guyton and Hall 1996).

Blood Osmolality, Sodium, Potassium, and Urea Concentration. Blood osmolality is determined using an osmometer. Serum sodium (Na^+) and potassium (K^+) concentrations are determined using flame-photometry. Urea and phosphate concentrations are determined using an autoanlyzer using sample preparation techniques specific to the constituent of interest; preparation techniques are provided in Schalm et al. (2000).

Water Loss

Pulmonary Water Loss.Water lost during respiration can be measured by placing the animal in a sealed metabolic cage if animal is small enough or by fitting an animal with a metabolic mask. The relative humidity of both inspired and exhaled air are measured. The absolute water content of exhaled air is calculated from the relative humidity. Water content of expired air is measured either using a humidity sensor or by use of a drying agent (e.g., Drierite) to absorb water from exhaled air (Taylor 1969*b*; Borut et al. 1979; Schmidt-Nielsen et al. 1981*a*, *b*; Dmi'el and Robertshaw 1983).

Cutaneous Water Loss. Cutaneous water loss can be estimated by applying a desiccant capsule containing Drierite to a shaved area of the skin for a specific period of time; by weighing the capsule before and after application water content can be determined and cutaneous evaporation rate estimated (Musewe et al. 1976). However, differences in sweat gland density over different areas of the body and differences in surface area must be taken into consideration. Cutaneous water loss can also be calculated using total evaporative water loss estimated by the body mass lost by an animal during an experiment (Borut et al. 1979; Taylor et al. 1970*a*; Dmi'el and Robertshaw 1983). All mass lost during an experiment is assumed to be due to evaporative water loss; either the animal cannot urinate or defecate during the experiment or all urine and feces need to be collected to account for mass lost due to those routes (Borut et al. 1979; Taylor et al. 1970*a*; Dmi'el and Robertshaw 1983). Respiratory water loss is measured using the above method, and total cutaneous water loss is assumed to be the difference between the total evaporative water loss and the respiratory water loss (Borut et al. 1979; Taylor et al. 1970*a*; Dmi'el and Robertshaw 1983).

Fecal Moisture Content. Fecal moisture content is determined by weighing a fresh sample of feces. The sample is then dried at 50 ºC to a constant mass and reweighed. Moisture content is the difference between the fresh and dried mass (Woodall et al. 1999).

Glomerular Filtration Rate and Urine Osmolality. Glumerular filtration rate (GFR) is the amount of filtrate produced per minute by all nephrons in both kidneys and is associated with rates of urine production (Lassiter and Gottschalk 1980*a*; Guyton and Hall 1996). Inulin is commonly used as a marker to measure the GFR in animals (Lassiter and Gottschalk 1980*a*; Guyton and Hall 1996). Sterile inulin is administered to the animal intravenously, serial blood and urine samples are collected and the concentration of inulin is determined (Lassiter and Gottschalk 1980*a*). Because inulin is freely filterable in the glomerulus and it is neither reabsorbed nor secreted by the renal tubules, the amount excreted is equal to the amount filtered. Therefore, the glomerular filtration rate can be calculated using the following equation:

Glomerular filtration rate = $(U_x V)/P_x$,

where U_x is concentration of inulin in the urine, V is the rate of urine flow, and P_x is the inulin concentration of the plasma (Lassiter and Gottschalk 1980a).

Urine osmolality is measured using an osmometer (Maloiy 1973*a*).

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Annotated Biblography

The annotation for each citation is in most cases the original abstract or summary of the original publication taken verbatim with no changes. In some cases we found it necessary to include other information from the publication, not contained in the original abstract or summary or to change the format of the abstract.

Ungulate Mammals

Abdelatif, A. M. and M. M. M. Ahmed. 1994. Water restriction, thermoregulation, blood constituents and endocrine responses in Sudanese desert sheep. Journal of Arid Environments 26:171-180.

Water restriction, thermoregulation, blood constituents and endocrine responses were studied in 10 male Butana sheep. Watering regimes were changed from ad libitum to once every 24, 48, or 72 hours. Restricted access to water reduced the intake of water and food and decreased the morning and afternoon values of rectal temperature and respiration rate. Water restriction increased the packed cell volume of erythrocyte, plasma osmolality, free fatty acids and urea, and decreased glucose concentrations in the blood. During water restriction, thyroid stimulating hormone level increased in the morning, but decreased in the afternoon; thyroxine level decreased in the morning and afternoon. Cortisol level showed an overlapping pattern with that of the control group during the afternoon. Restriction of water intake by sheep resulted in adjustments in water and heat balance and induces moderate changes in blood metabolites and endocrine responses.

Aggery, E. K. 1982. Seasonal changes in water content and turnover in cattle, sheep, and goats grazing under humid tropical conditions in Ghana. Pages 133-142 *in* Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

The effect of seasonal changes on water content and water turnover of cattle, sheep, and goats at pasture under humid tropical conditions was studied. Measurement of total body water and water turnover was based on the tritium dilution technique. Total body water was significantly lower in the dry season than in the wet season. In all seasons water turnover was highest in cattle, followed by sheep, then goats. Changes in body mass, body water, body solids, and water turnover were associated with seasonal variations in nutrition. The indication was that the goat would be a more suitable animal for production under dry conditions than cattle and sheep.

Ali, K. E., H. M. Mousa, and J. D. Hume. 1982. Total body water and water economy in camels, desert goats and desert sheep during water restriction and deprivation. Yugoslavica Physiologica et Pharmacologica Acta 18:229-236.

The total body water of one-humped camels, Sudan desert goats, and desert sheep was measured using titrated water under conditions of ad libitum water intake, 50% reduction in water intake for 8 days, and complete water deprivation for 5 days. Water output in urine and feces was also determined. When the animals were offered water ad libitum, total body water was 700 ± 20 ml kg^{-1} body mass in sheep, 750 ± 56 ml kg^{-1} body mass in goats and 526 ± 30 ml kg^{-1} body mass in camels. Water restriction and deprivation caused no significant changes in these values. Urine volume was reduced by about 75% in sheep and goats and 40% in camels during water restriction and deprivation. Fecal water output decreased during water restriction by about 37% in sheep and 45% in goats and camels. These decreases were doubled during water deprivation.

Al-Toum, M. O. and A. M. Al-Johany. 2000. Water deprivation and its effect on some blood constituents in Idimi gazelle, *Gazella gazella*. Journal of Arid Environments 45:253-262.

Water deprivation and its effect on some blood constituents were studied in the Idmi Gazelle (*Gazella gazelle*) at the King Khalid Wildlife Research Centre, Thummamah, Saudi Arabia. Animals were housed in stables and deprived of water for 8 days in winter and 3 days in summer. Blood was collected and analyzed during 3 phases of experimentation; hydrated, dehydrated and rehydrated. The gazelle's dehydration led to an increase in many of blood parameters such as red blood cells, white blood cells, packed cell volume, amount of hemoglobin, serum Na^+ and Cl^-, blood urea nitrogen and serum osmolality. The gazelles seem to be well-adapted physiologically to live in harsh desert extremes. Possible implications obtained from the results would be useful in captive breeding of this species.

Anand, R. S., A. H. Parker, and H. R. Parker. 1966. Total body water and water turnover in sheep. American Journal of Veterinary Research 27:899-902.

Titrated water was used to measure the total body water and water turnover in sheep kept under controlled environmental conditions (22 ºC). The mean total body water as a percentage of body mass was 54.6 ± 1.8. The biological half-life was 5.4 ± 0.4 days. Smaller variations were observed between individual sheep than reported by previous workers. The daily loss of water was 72.7 ml kg^{-1} and the daily intake and urine production were 66.8 and 27.1 ml kg^{-1}, respectively. The daily intake of water was 92% of total daily loss of water. Urine production was responsible for only 32.2% of the total water loss and 40.6% of the daily intake of water.

Bailey, C. B. 1964. Effects of environmental temperature in feed digestion, water metabolism, body temperature, and certain blood characteristics of sheep. Canadian Journal of Animal Science 44:68-75.

The effects of environmental temperature in feed digestion, water metabolism, body temperature and certain blood characteristics of sheep were investigated. In each of 4 periods, domestic sheep were maintained at 20 ºC for 1 week, at -11 ºC for the following week, and at 20 ºC again for the third week. In one period, water intake was voluntary; in the other 3 periods the sheep received either 1,000, 2,000, or 3, 000 g water day^{-1} through rumen fistulas. The change from the warm to the cold occasioned no change in feed digestibility but when the sheep were returned to the warm, the apparent digestion of both dry matter and fiber increased. When water intake was voluntary, water consumption, urine water loss, and apparent insensible water loss were lower in the cold than in the warm temperatures. During the second week at 20 ºC, the apparent insensible water loss was higher than during the first week at 20 ºC. When water intake was controlled at three different levels, urine and fecal water losses tended to reflect the differences in water intake. Temperatures in the rectum and subcutaneous tissues exhibited a decrease when the sheep were transferred from warm to cold and a transient increase on return to the warm. When water intake was voluntary or 1,000 g day^{-1}, transfer of the sheep to the cold was accompanied by increases of packed cell volume and plasma sodium and phosphate and small increases of potassium and chloride.

Baker, M. A. and M. J. Nijland 1993. Selective brain cooling in goats: effects of exercise and dehydration. Journal of Physiology 471:679-692.

Measurements of brain and central blood temperature (T_{br} and T_{bl}), metabolic rate (MR) and respiratory evaporative heat loss (REHL) were made in trained goats walking on a treadmill at 4.8 km h^{-1} at treadmill inclines of 0, 5, 10, 15 and 20% when they were fully hydrated and at 0% when they had been deprived of water for 72 h. In hydrated goats, exercise MR increased progressively with increasing treadmill incline. Both T_{bl} and T_{br} rose during exercise, but T_{bl} always rose more than T_{br}, and selective brain cooling (SBC = T_{bl} - T_{br}) increased linearly with T_{bl}. Significant linear relationships were also present between REHL and T_{bl} and between SBC and REHL. Neither the slope of the regression relating SBC to T_{bl} nor the threshold T_{bl} for onset of SBC was affected by exercise intensity. Manual occlusion of the angularis oculi veins decreased SBC in a walking goat, while occlusion of the facial veins increased SBC. Dehydrated goats had higher levels of T_{bl}, T_{br} and SBC during exercise, but the relationship between SBC and T_{bl} was the same in hydrated and dehydrated animals. In dehydrated animals, REHL at a given T_{bl} was lower and SBC was thus maintained at reduced rates of REHL. It is concluded that SBC is a linear function of body core temperature in exercising goats and REHL appears to be a major factor underlying SBC in exercise. The maintenance of SBC in spite of reduced REHL in dehydrated animals could be a consequence of increased vascular resistance in the facial vein and increased flow of cool nasal venous blood into the cranial cavity.

Banerjee, S. and R. C. Bhattacharjee. 1963. Distribution of body water in the camel (*Camelus dromedarius*). American Journal of Physiology 204:1045-1047.

The distribution of body water in the different compartments were determined in adult male Indian camels with one hump. The average distributions were as follows: serum volume, 5.9% of body mass; blood volume, 8.3% of body weight; total body water (urea space), 68.7% of body mass; extracellular water (thiocyanate space), 23.3% of body mass; intracellular water, 45.5% of body mass; and interstitial water, 17.4% of body mass. The serum and blood volumes of the camel were higher than similar values in other ruminants. When these values were compared with similar values in man, it was observed that the camel had significantly higher serum volumes, total body water, and intracellular water volumes. The capacity of the camel to hold more water might help the animal in withstanding the deprivation of water for a prolonged period in comparison to other animals.

Barboza, P. S., J. E. Blake, and R. E. Haugerud. 1999. Rangifer bulls in rut: body composition and water kinetics. Scientific and Social Programme Abstracts-10th Arctic Ungulate Conference, University of Tromso, Tromso, Norway.

Rut is a metabolically demanding period for male ruminants. Bulls must fight, patrol harems and mark territories as well as maintain and repair their body tissues. Seven adult male (*Rangifer tarandus tarandus*) were studies in 2 herds with a total of 34 females. Bulls became aggressive to handlers in late August when the antler velvet was shed. Plasma testosterone was greater in early September (246 day; 2,128 nag dL^{-1}) than in either June (176 day; 12 nag dL^{-1}) or October (301 day; 83 nag dL^{-1}). Subordinate males lost mass between September and November in a similar pattern to the dominant harem males. Peak mass and the date of peak mass did not vary with status or age in males 2 yr and older ($P>0.05$). Two bulls died in September from infected wounds. Surviving animals did not recover mass in winter suggesting that both injury and low body reserves can cause mortality. Titrated water dilution space declined with body mass. High rates of water flux in August probably reflect intakes of both food and drinking water to support mass gains and losses to panting for thermoregulation. Low water fluxes at the end of the rut may indicate low intakes of food and renal conservation when snow is the only source of free water. Animals lost 35% of the ingesta-free mass in 77 d of rut. Lean mass and body protein were depleted by 23% whereas 78% of the fat reserve was expended. Daily losses of protein and fat were 77 g and 437 g respectively which corresponded to a loss of 19MJ day^{-1} of 63% of body energy during rut. The daily energy deficit was equivalent to 90% of the standard metabolic rate. Body reserves probably provide sufficient energy for basal metabolism but additional costs of activity and thermoregulation must be supported by food intake.

Benga, G. and T. Borza. 1995. Diffusional water permeability of mammalian red blood cells. Comparative Biochemistry and Physiology 112B:653-659.

A program of comparative nuclear magnetic resonance measurements of the membrane diffusional permeability for water and of the activation energy of this process in red blood cells from 21 mammalian species was conducted. On the basis of diffusional permeability for water these species could be divided into three groups. First, the red blood cells from humans, cow, sheep, and large kangaroos (*Macropus giganteus* and *M. rufus*) and diffusional permeability for water values around 5 x 10^{-3} cm s^{-1} at 25 ºC and 7 x 10^{-3} cm s^{-1} at 37 ºC. The red blood cells of other marsupial species, mouse, rat, guinea pig, and rabbit had diffusional permeability for water values roughly twice as high, whereas echidna red blood cells were half that of human red blood cells. The value of activation energy was in most cases correlated with the values of diffusional permeability for water values. An activation energy value of 26 kJ mol^{-1} was found for red blood cells from humans and species having similar diffusional permeability values. Low activation energy values (ranging from 15 to 22 kJ mol^{-1}) appeared to be associated with relatively high diffusional permeability values. The highest activation energy value (33 kJ mol^{-1}) was found in echidna red blood cells. This points to specialized channels for water diffusion incorporated in membrane proteins; a relatively high water permeability of red blood cell membrane could be due to a greater number of channel proteins. There are, however, situations where a very high water permeability of red blood cells is associated with a high value of activation energy as is the case of red blood cells from mouse, rat, and tree kangaroo. It was also found that diffusional permeability in different species was positively correlated to the red blood cell membrane phosphatidylcholine and negatively correlated to the sphingomyelin content. This suggests that in addition to the number of channel proteins, other factors are involved in the water permeability of the red blood cell membrane.

Ben Goumi, M., F. Riad, J. Giry, F. De La Farge, A. Safwate, M. Davicco, and J. Barlet. 1993. Hormonal control of water and sodium in plasma and urine of camels during hydration and dehydration. General and Comparative Endocrinology 89:378-386.

Eight dromedary camels were studied for 24 days under controlled conditions (3 days), and during water deprivation (14 days) and rehydration (7 days) in Tadla, Morocco during the summer. Blood samples were drawn every 6 hr. During dehydration, food intake gradually fell and was zero on the last day and animals lost about 30% of their body mass. However, most of this reduction in weight was attributed to water loss, since body mass of the animals returned to control values following rehydration. Dehydration was associated with a decreased in plasma volume (~ 42 ± 3%) and a concomitant rise in plasma Na concentration (from 1.2 ± 0.2 to 20.0 ± 5.2 ng $AL^{-1} ml^{-1} hr^{-1}$), without significantly changed plasma concentrations of aldosterone and atrial naturiuretic peptide. Dehydration was associated with increased urine osmolality (from 952 ± 515 to 1963 ± 498 mOsm kg^{-1} water), reduced urine production (from 4565 ± 2230 to 817 ± 178 ml day^{-1}), and increased Na excretion. Most of these parameters returned to control values during initial rehydration, except for plasma rennin activity, which remained elevated for 7 days, and diuresis, which rose to 12773 ± 6707 ml day^{-1} on Day 7 of rehydration.

Bianca, W., J. D. Findlay, and J. A. McLean. 1965. Responses of steers to water restriction. Research in Veterinary Science 6:38-55.

An investigation was made into the effects of dehydration on various metabolic and thermoregulatory functions of steers held in an environmental chamber in both temperate (15 ºC) and hot (40 ºC) environments. During 4 days of dehydration at 15 ºC decreases occurred in food intake, the excretion of feces and urine, evaporation, body weight, heat production, respiratory ventilation, plasma potassium, and in urinary potassium output. At the same time increases were found for hemocrit, plasma total solids, plasma sodium, plasma chloride and blood urea, and in the output of urinary sodium. During 2 days of dehydration at 40 ºC, qualitatively similar changes occurred in most of these variables. The rapid ingestion of large amounts of water at the end of each dehydration period caused dramatic but transient changes in many of the quantities investigated. Some of these changes were related to shivering, which followed drinking in the temperate, but not in the hot environment. The repayment of the water debt accumulated during dehydration occurred very rapidly, most of it within the first day of rehydration. The restoration to normal of the various physiological values deranged by dehydration required more than 1 day in most instances. There did not seem however, to be permanent changes nor any impairment of health due to the relatively short period of dehydration. The results are discussed in relation to mechanisms involved in water balance and temperature regulation.

Bianca, W. 1965. Reviews of the progress of dairy science. Section A: Physiology. Cattle in a hot environment. Journal of Dairy Research 32:291-345.

Reviews the physiology and mechanisms associated with heat production, evaporative cooling, evaporation from respiratory passages, water exchange, reproduction, milk production, feed intake and the influence of body size on cattle living in hot environments.

Bianca, W. 1970. Effects of dehydration, rehydration, and overhydration on the blood and urine of oxen. British Veterinary Journal 126:121-132.

Each of 4 oxen, kept in an environment of 20 ºC, was subjected to the following 3 treatments, deprivation of water for 3 days followed by rehydration by drinking, deprivation of water for 3 days followed by rehydration by infusion of water through a rumen cannula, and over-hydration brought about by infusion of water into the rumen of the normally hydrated animals. Dehydration for 3 days caused hemoconcentration, which was associated with a 34% increase in blood viscosity. The hemoconcentration observed was due, in the first place, to a loss of water from the plasma, but some water was also lost from the red cells, as evidenced by increases in mean corpuscular hemoglobin concentration and in red cell total solids. The osmotic fragility of the red cells, and urinary specific gravity were increased. Rehydration by drinking produced a cardiac acceleration and in most of the blood variables an overshoot, i.e. a sharp transient rise over the values already elevated as a result of dehydration. Since both these responses were absent in rehydration by infusion, it was thought that they were brought about by the stress of sudden drinking following a period of dehydration. After rehydration, osmotic fragility remained high for several hours. In 2 instances, rehydration by drinking led to intravascular hemolysis and resulting hemoglobinuria. Overhydration caused a marked diuresis and a slight hemoconcentration. There were no obvious signs of water intoxication, however instances of hemolysis and hemoglobinuria occurred.

Bohra, H. C. and P. K. Ghosh. 1977. Effect of restricted water intake during summer on the digestibility of cell-wall constituents, nitrogen retention and water excretion in Marwari sheep. Journal of Agricultural Science 89:605-608.

In May-June 1976, studies were made on the effect of 50% reduction in daily water intake during summer on food intake, digestibility coefficients of the cell-wall constituents (CWC), nitrogen retention and water excretion in urine and feces in the captive Marwari breed of sheep of the Rajasthan Desert, India. Animals were held in metabolic cages and feces were collected. The water-restricted animals consumed 54 and 42% less dry matter and digestible energy respectively than normally-watered animals. The digestibility coefficients of different CWC were apparently, though not significantly, higher in water-restricted animals. Throughout the study period, animals of both the groups, particularly the water-restricted group, remained in negative nitrogen balance. Moisture loss through the feces was about 22% less in the water-restricted group than in the control animals. The water-restricted animals lost 21.1% of body mass in 23 days and these animals, when allowed water ad libitum, were able to recover 71.5% of the lost body mass within 3 days.

Borut, A. R. Dmi'el, and A. Shkolnik. 1979. Heat balance of resting and walking goats: comparison of climatic chamber and exposure in the desert. Physiological Zoology 52:105-113.

This study compared heat-balance experiments carried out under standardized conditions in a climate chamber with those performed under natural conditions, using identical methodology and instrumentation. Heat production and partitioning of evaporative cooling were measured in the black Bedouin goat from the Sinai desert when the goats rested or walked on a treadmill in a climate chamber (26 ºC and 40 ºC, relative humidity 30%). These were measured in the same goats while they were fully exposed to desert conditions. Heat production of resting goats was 2 kcal/kg/hr at 26 ºC and morning experiments in the field and 2.5 kcal kg^{-1} hr^{-1} at 40 ºC and noon experiments. Heat production of goats walking at a speed of 2.60 – 2.95 km hr^{-1} was 4.1 – 4.9 kcal kg^{-1} hr^{-1} in both climatic chamber and field experiments. Under mild conditions, 26 ºC and morning, evaporation dissipated up to 50% of heat produced. At 40 ºC in climatic chamber, evaporation equaled heat production, but at noon in the desert it increased two-fold. Under these desert conditions both resting and walking goats had the same excess, 1.72 kcal^{-1} kg^{-1} hr, of evaporative heat loss over heat production. This represents the net heat load imposed by the desert environment; its magnitude approximately equals the goat's resting metabolism. In the climatic chamber the goats used mostly panting to dissipate heat. In the desert, however, the amounts of heat dissipated by sweating were twice as great as those lost through the respiratory system. These high rates of sweating (up to 143 g water^{-1} m$^{2-1}$ hr^{-1}) are attributed to the absorption of solar radiation, a factor that does not exist in the laboratory but is very prominent in the desert environment.

Brosh, A., B. Sneh, and A. Shkolnik. 1983. Effect of severe dehydration and rapid rehydration on the activity of the rumen microbial population of black Bedouin goats. Journal of Agricultural Science 100:413-421.

Drinking regimes of Bedouin goats affect their feeding behavior and the ruminal environmental conditions, as expressed by changes in osmotic pressure as well as in pH of the rumen content. The osmotic concentration of the rumen content of a goat drinking once daily was 330 mOsm kg^{-1} just before drinking. After water deprivation for 4 days, the osmotic concentration reached 360 mOsm^{-1} kg and, immediately after excessive drinking decreased to 82 mOsm^{-1} kg. After a short time, the osmotic concentration increased to 300 mOsm kg^{-1} and after 13 hr reached a peak of 440 mOsm kg^{-1}, mainly owing to the release of degradation products. The pH was also affected by food consumption. Just prior to drinking, the pH in the rumen of dehydrated goats was 6.9. It decreased to 6.0 after excessive drinking and feeding. Later it ranged between 6.4 and 7.1. Most of the microorganisms in the rumen are attached to the fiber fraction. No difference could be observed in direct bacterial counts in the fluid fraction between dehydrated and goats watered daily. However, the number of protozoa was reduced in dehydrated goats, especially after excessive drinking, as some species of protozoa seem to explode in a hyposmotic ambient. The fermentation capacity of the fiber fraction was higher than that of the fluid fraction, indicating also the presence of more microorganisms in the fiber. In addition, the osmotic changes occurring during the dehydration-rehydration cycles had no significant effect on fermentation capability of the rumen microorganisms. At a low osmotic concentration in a NaCl deficient ambient, there was some decrease in fermentation rate, but this could be nullified with the addition of NaCl, which is required for microbial activity. The decrease in fermentation rate is not due to its effect on the osmotic concentration. The microorganisms in the fiber fraction were found to be less affected by NaCl deficiency in the ambient medium.

Brosh, A., I. Choshniak, A. Tadmor, and A. Shkolnik. 1986. Infrequent drinking, digestive efficiency and particle size of digesta in black Bedouin goats. Journal of Agricultural Science 106:575-579.

When given access to water once every 4 days, black Bedouin goats that were fed dry Lucerne hay required, on average, only half the water and 60% of the gross energy they consumed when water was offered to them once daily. Digestibility of the feed in these goats increased by 4%. The outflow of fluid from the rumen slowed down during the water deprivation period. A flow rate of 1,080 ml kg$^{-0.75}$ day^{-1} was recorded during the 1st day of the period and only 350 ml kg$^{-0.75}$ day^{-1} during the last day. While being offered water once daily the outflow from the rumen amounted to 1,243 ml kg$^{-0.75}$ day^{-1}. Following the subjection of black Bedouin goats to infrequent drinking the mean retention time of the digesta in the rumen was extended by 33% and in the entire gastrointestinal tract by 43%. It is suggested that the slowing down of the ruminal flow that followed the subjection of the goats to infrequent drinking enabled the particulate matter to stay longer in the digestive tract despite their smaller size.

Bullard, R. W., D. B. Dill, and M. K. Yousef. 1970. Response of the burro to desert heat stress. Journal of Applied Physiology 29:159-167.

Two female burros were studied with regard to regulation of sweating and responses to dehydration and rehydration under the natural desert conditions of Boulder City, Nevada, in July. Sweat in the donkey appeared to be expelled in cycles of ≤ 2 min^{-1} that occur synchronously all over the body surface. The sweating rate was determined by both central and skin temperatures. Cooling the major portion of the skin area during sweating appeared to reduce the magnitude of cycles, but not the overall sweating rate until general body cooling had occurred. However, heat applied locally to the skin or sweat glands had a marked stimulating effect suggesting that the local temperature of the gland is important in its function and that reflex regulation of sweating, acting by way of peripheral thermal detectors, is less important. The most potent stimulating agent upon intradermal injection was epinephrine. Other autonomic agents were almost completely ineffective upon the rate of sweating. Moderate dehydration, amounting to 14% and 9% of body mass during desert exposures, did not greatly alter blood concentrations, performance, or temperature regulation. Rehydration was rapid and precise after this degree of dehydration.

Burke, M. G. 1988. Water economy of tropical feral goats. American Zoologist 28:181A.

The behavioral ecology and population dynamics of the feral goats of Aldabra Atoll, Seychelles, were studied for 20 months between 1976 and 1986. The semi arid climate and the availability of water influenced the behavior and the timing and rate of reproduction of the goats. The only source of fresh drinking was rain puddles, which the goats used readily. By the end of the six-month dry season, however, most such puddles had disappeared, and goats drank seawater from tidal pools and the lagoon. The goat's kidneys showed normal gross morphology; relative renal medullary thickness was within the range reported for other feral and domestic goats. The Aldabra goats conserved water by producing relatively dry feces with mean water content of only 36%, by remaining relatively inactive during the hottest part of the day, and by feeding primarily at dusk and dawn when air temperatures were cooler and forage had higher water content and occasional dew. Births occurred year round, but a distinct peak occurred at the beginning of the dry season. Reproductive rates were lower during dry years.

Cameron, R. D., III. 1972. Water metabolism by reindeer (*Rangifer tarandus*). Ph.D. dissertation, University of Alaska, Fairbanks, Alaska, USA. 109p.

The effects of climatic and nutritional variation on body fluid compartmentalization and turnover were investigated in female reindeer (*Rangifer tarandus*) using titrated water and sodium sulfate $^{-35}$S. An initial field study characterized these changes on a seasonal basis under natural grazing conditions. Between early winter and late spring body mass was either maintained or reduced, while total body water (percentage of body mass) increased, indicating losses of body solids. Water flux rates were higher in the late spring than during other seasons; lowest values were recorded in early winter. A laboratory study was subsequently undertaken to ascertain the differential influences of temperature and nutrition on water flux. At low temperatures (-5 to -20 ºC) water flux was linearly related to nitrogen intake, and a direct relationship was found between the excretion rates of fecal water and nitrogen. At higher temperatures (+10 ºC) water flux increased relative to the intake of nitrogen due to higher rates of insensible water loss and an increase in the ratio of fecal water to fecal nitrogen excretion. Urine volume varies directly with water flux, independent of temperature and nitrogen intake. Variations in the nutritional status and changes in water turnover are discussed in relation to climate and the quality and availability of feed, and with regard to mechanisms for the conservation of energy and nitrogen.

Cameron, R. D. III and J. R. Luick. 1972. Seasonal changes in total body water, extracellular fluid, and blood volume in grazing reindeer (*Rangifer tarandus*). Canadian Journal of Zoology 50: 107-116.

Seasonal changes in total body water, extracellular fluid, and blood volume in grazing reindeer (*Rangifer tarandus*) was studied in 1968 - 1969 at the University of Alaska, Reindeer Research Station near Cantwell, Alaska. The effects of climatic and nutritional changes on body fluid compartmentalization and turnover were investigated in grazing female reindeer. Total body water volume and turnover, extracellular fluid volume, and blood volume were estimated using titrated water, sodium sulfate $^{-35}$S, and sodium chromate $^{-51}$Cr, respectively. During winter and spring, body mass was either maintained or reduced while total body water (percentage of body mass) increased, resulting in appreciable losses of total body solids. In summer, large gains in body mass were accompanied by reduced total body water volumes resulting in substantial increases in body solids. An apparent fluid shift from the intravascular to the extracellular compartment during late spring suggested the occurrence of a starvation edema. Mean water flux rates (ml day^{-1} kg^{-1} body mass) were higher in late spring than during other seasons; lowest values were recorded in early winter. Seasonal variations in nutritional status as reflected by body composition and fluid compartmentalization, and changes in water turnover are discussed in relation to climate and the quality and availability of forage. The complicating influences of pregnancy and lactation are also considered.

Cameron, R. D., J. R. Luick, and R. G. White. 1982. Water turnover in reindeer. Pages 189-194 *in* Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

The nutritional and climatic effects on water turnover in reindeer are described. At low ambient temperatures (ca. -20 ºC) water turnover is related to protein and mineral intake, which is reflected in the relations of fecal and urinary water to nitrogen and ash excretion via these avenues. As ambient temperature increases, respiratory water, fecal water, and urine flow increase, resulting in an increase in water turnover.

Cameron, R. D. III, R. G. White, and J. R. Luick. 1976. Accuracy of the tritium water dilution method for determining water flux in reindeer (*Rangifer tarandus*). Canadian Journal of Zoology 54:857-862.

The accuracy of the tritium water dilution method in estimating water flux was evaluated in reindeer (*Rangifer tarandus*) under various conditions of temperature and diet. Two non-pregnant female reindeer were restrained in metabolism stalls, within controlled-environment chambers, at temperatures of +10, -5, and –20 ºC; varying amounts of a commercial pelleted ration (crude protein, 13%) or mixed lichens (crude protein, 3%) were offered, and water was provided ad libitum either as snow or in liquid form. Total body water volume, and water turnover rate were estimated using titrated water, and the daily outputs of and urine were measured for each of 12 different combinations of diet and temperature. Statistical analysis of the data showed that the tritium water dilution technique gives accurate determinations of total body water flux over a wide range of environmental and nutritional conditions.

Carlisle, D. B. and L. I. Ghobrial. 1968. Food and water requirements of the dorcas gazelle in the Sudan. Mammalia 32:570-576.

Food and water requirements of the dorcas gazelle were studied using field observations in the Sudan. The dorcas gazelle (*Gazella dorcas*) in the Sudan does not eat grass during the dry season but eat the leaves of *Acacia tortilis* to the complete or almost complete exclusion of other foods. *Acacia tortilis* retains its leaves throughout the year and in regions where rain has fallen during the last year the moisture content of the leaves is about 60%. Comparison of the water and caloric requirements of penned animals with analyses of *Acacia* leaves should be adequate to provide all the food and water requirements of the gazelle throughout the dry season without there being a need for the animals to drink.

Carlson, G. P., G. E. Rumbaugh, and D. Harrold. 1979. Physiologic alterations in the horse produced by food and water deprivation during periods of high environmental temperatures. American Journal of Veterinary Research 40:982-985.

Eight normal horses were held without access to food or water for 72 hr during a period of high environmental temperatures. During this period, the horses had an average weight loss of 51.6 kg (10.7% of body mass). Highly significant decreases in extracellular fluid volume (18.6 L) and plasma volume (5 L) were observed during this period as compared with baseline values. Plasma protein, sodium, chloride, and osmolality progressively increased in response to dehydration, whereas packed cell volume, plasma potassium, calcium, magnesium, and phosphate were not significantly altered. The dehydration and clinicopathologic alterations produced were similar to those observed in other species in which the principle problem was a water deficit. After the end of the experimental dehydration period, the horses replaced 62% of the weight loss during a 1-hour period with access to water only.

Choshniak, I. and A. Shkolnik. 1977. Rapid rehydration in the black Bedouin goats: red blood cell fragility and role of the rumen. Comparative Biochemistry and Physiology 56A:581-583.

The fragility of red blood cells and the role of the rumen during rapid rehydration in the Bedouin goat were studied. Following dehydration, goats regularly drink volumes of water amounting to 30 – 40% of their body mass. In vitro experiments showed that 50% hemolysis of the red blood cells of these goats occurred at a concentration of 110 mM NaCl. Blood plasma concentration dropped from 336.5 ± 6.9 mOsm kg^{-1} before drinking to only 303.7 ± 7.6, mOsm kg^{-1}, 6 hr afterwards. Changes in plasma volume were moderate. The rumen was shown to first retain the water imbibed, and to release in only gradually later on: within 5 hr following the drinking 18% of the ruminal fluid left in the rumen.

Choshniak, I., A. Brosh, and A. Shkolnik. 1988. Productivity of Bedouin goats: coping with shortages of water and adequate food. Pages 47-64 *in* Isotope aided studies on livestock productivity in Mediterranean and North African countries. International Atomic Energy Agency, Vienna, Austria.

The study was carried out under outdoor summer conditions on goats that were watered only once every 4 days and goats that were watered once daily. Under each of the watering regimes the goats were fed alfalfa hay (a high quality roughage), and Rhodes grass, and wheat straw, medium and low quality feed, respectively. In all trials except 1, the goats maintained constant body mass. The exception occurred when the goats were watered daily while on a diet of wheat straw. Infrequent drinking considerably hampered feed intake when the goats were fed high quality roughage. When wheat straw was fed the intake was low but was not affected by drinking. When goats were watered infrequently they gulped down volumes of water that often caused the osmolarity of the rumen fluid to drop from 360 mOsm kg^{-1} to 80 mOsm kg^{-1}. Over the entire range of osmotic concentration the bacterial populations in the goat's rumen maintained their viability. By reducing the fluid flow through the gut, infrequent drinking helped to extend the time the digesta were retained along the digestive tract. As a result, digestibility of the roughage was improved. Infrequent drinking was also found to reduce the animal's demand for metabolizable energy. It also improved the balance in the utilization of dietary protein while not interfering with the ability to recycle urea. Frequent watering of ruminants in the desert is likely to increase their demand for food, lower their gain in digestible energy, and increase their demand for digestible energy and make it more difficult for them to balance their energy budget. Improving feed quality for animals in the desert, when water availability declines, is also not advantageous. It may only increase the animal's needs for water, render them dependent on frequent drinking, and restrict their grazing area to the close vicinity of water sources.

Choshniak, I, C. Wittenberg, and D. Saham. 1987. Rehydrating Bedouin goats with saline: rumen and kidney function. Physiological Zoology 60:373-378.

Following a period of water deprivation, Bedouin goats became rehydrated by drinking 0.9% NaCl solution. During one continuous drinking bout, these goats ingested 3.26 ± 0.42 liters of saline and regained their initial body mass. The outflow from the rumen during the first hour after drinking saline amounted to 596 ± ml hr^{-1}, eight times the rate recorded during the time when goats became rehydrated when drinking water. Within an hour after they had drunk saline, urine flow exceeded the predrinking levels. Six hours following drinking it barely regained the rate recorded at the end of the dehydration period. The pattern of changes in the glomerular filtration rate and renal plasma flow was similar to that observed with urine flow. It is concluded that the rumen in the Bedouin goat "stores" water following rapid rehydration with water but does not function as an osmotic protective mechanism with the animals become rehydrated with saline. Presumably, the rate at which water leaves the rumen is inversely related to the hypotonicity of the rumen fluid.

Choshniak, I, C. Wittenberg, J. Rosenfeld, and A. Shkolnik. 1984. Rapid rehydration and kidney function in the black Bedouin goat. Physiological Zoology 57;573-579.

Black goats, tended by Bedouin tribesmen in the extreme deserts of the Middle East, drink only once every 2 – 4 days and imbibe amounts of water that often exceed 40% of their dehydrated body mass. The water that the goats drink copiously is first retained in the rumen and only gradually flows into the other body fluid compartments. Five hours after the drinking, 81% of the water imbibed was still stored in the spacious rumen of the goat. The kidney of the Bedouin goat responded to the voluminous drinking by a drop in the blood flow that was followed by a compatible drop in both the glomerular filtration rate and urine flow. The urine flow, even 4 hr following drinking, was below the rate recorded in the dehydrated animal. Urine Na^+ concentration that amounted to 80.3 mM in the dehydrated animal dropped to only 37.7 mM following the drinking. A drop (from 144 mM to 49 mM) was also simultaneously recorded in Cl^- concentration; K^+ and urea concentration, however, changed only slightly. It is suggested that the rumen in the goat serves as a water reservoir that helps maintain the osmotic stability of the body proper. The kidneys in these animals efficiently conserve the water imbibed as well as the body's Na^+ and Cl^-. Studies of sheep that assign similar roles to the rumen and kidneys indicate that the physiological mechanism described in the present study is generally shared by ruminants tended in a pastoral system.

Cloete, G. and O. B. Kok. 1986. Aspects of the water economy of steenbok (*Raphicerus campestris*) in the Namib Desert. Madoqua 14:375-387.

Behavioral and physiological aspects of the water economy of steenbok (*Raphicerus campestris*) in the Namib Desert were investigated. Field observations indicate that the antelope are normally independent of free water, their main water source being dietary. Daily dietary water intake of captive steenbok was determined as 342.5 ml, while water turnover rate was calculated as 135 ml day^{-1}. Urine analyses and kidney morphology do not suggest particular adaptations of renal function for desert conditions, while thermoregulatory behavior appears to play a major role as a water-conserving mechanism.

Coppock, D. L., J. E. Ellis, and D. M. Swift. 1988. Seasonal patterns of activity, travel and water intake for livestock in South Turkana, Kenya 14:319-331.

The nomads of Ngisonyoka Turkana exploit a harsh and seasonally variable environment using 5 livestock species in a dynamic management system. Season, species, and management influenced animal activity budgets during one annual cycle in 1981 - 1982. Relative to the long dry season, the brief wet season was a time of high resource abundance, increased water intake (cattle, goats, sheep), reduced travel (all species) and increased time available for feeding (cattle, goats, sheep, donkeys). Browsing camels generally showed the least seasonal change in activity budgets and water intake, while grass-dependent cattle exhibited the most change.

Degen, A. A. 1977*a*. Fat-tailed Awassi and German Mutton Merino sheep under semi-arid conditions I: Total body water, its distribution and water turnover. Journal of Agricultural Science 88:693-698.

The total body water, its distribution and water turnover were measured in native fat-tailed Awassi sheep and German Mutton Merino sheep under semi-arid conditions using titrated water. Total body water, extracellular fluid volume and plasma volume were measured during summer while sheep were grazed in natural pasture that remained as dried stem-cured hay and in the winter while they grazed lush natural pasture. No differences were found between breeds in any of the measurements in both seasons. Within both breeds, the percentage of titrated water space and extracellular fluid volume were larger in the summer whereas the percentage of plasma volume remained the same. Total body water and water turnover were measured in these breeds in 8 trials while the sheep grazed in native pasture in the autumn, winter, and spring, shrubs in the winter and legumes in the summer. Water and shade were freely and easily accessible throughout the grazing period. The total body water was found to be consistently lower in the Awassi, indicating a higher energy reserve. The water turnover in 24 hr kg^{-1} $wt^{0.82}$ was found to be higher in the German Mutton Merino in all trials; the differences ranged between 3 and 28%. However, in only 2 of 8 trials were the differences significant. Thus, water turnover was only slightly lower in the Awassi although this breed evolved under Middle Eastern arid and semi-arid regions.

Degen, A. A. 1977*b*. Fat-tailed Awassi and German Mutton Merino sheep under semi-arid conditions II: Total body water and water turnover during pregnancy and lactation. Journal of Agricultural Science 88:699-704.

The total body water and water turnover of fat-tailed Awassi females, a desert adapted breed, and German Mutton Merino females, a temperate environment breed, were measured during the 3rd, 4th, and 5th month of pregnancy and during the first month of lactation using titrated water. Measurements were taken under grazing conditions with unrestricted water in a semi-arid region. Both breeds of sheep lost weight during this period. The percentage of total body water increased, especially during the 5th month of pregnancy when the German Mutton Merino increased their total body water by 5.2% and the Awassi by 1.0%. It was concluded that the nutritive intake was not sufficient to supply the increased energy demands and that sheep were mobilizing body solids, the German Mutton Merino at a faster rate. The German Mutton Merino females turned over about 20% more water per kg $wt^{0.82}$ during pregnancy and lactation than did the Awassi ewes. There was little difference in water turnover between the control and pregnant sheep within their breed during gestation. During lactation the experimental Awassi increased their water turnover by 29% over the control Awassi and the experimental German Mutton Merino increased their water turnover by 26% over the control German Mutton Merino. In both breeds the increase in water turnover during lactation was smaller than that found in other lactating semi-arid ruminants and the increase in water turnover during pregnancy and lactation was smaller than that recommended by the Agricultural Research Council.

Degen, A. A. 1977*c*. Fat-tailed Awassi and German Mutton Merino sheep under semi-arid conditions III: body temperature and panting rate. Journal of Agricultural Science 89:399-405.

Rectal, external auditory meatus, and skin temperatures and panting rates were measured in native fat-tailed Awassi and imported German Mutton Merino sheep. The Awassi evolved under desert conditions, have a localized fat deposit, course carpet wool, long ears, and long spiral horns (males). In contrast, the German Mutton Merino evolved under temperate conditions, have well-distributed fat, medium fine wool, short straight ears and are polled. The study was carried out during the summer in the northern part of the Negev desert. The mean daily rectal temperature fluctuation was higher in the German Mutton Merino than in the Awassi (1.78 ºC vs. 1.08 ºC). The external auditory meatus temperature was lower than the rectal temperature by 1.5 ºC in the German Mutton Merino and by 1.7 ºC in the Awassi, indicating a cooler brain temperature. The maximum skin temperature was similar to the maximum rectal temperature in both breeds, thus sweating was of little importance. The panting rate of the German Mutton Merino increased five-fold (40.6 – 199.4 pants min^{-1}) whilst the rate of the Awassi increased four-fold (35.3 – 135.0 pants min^{-1}). There was no between breed difference in either the rectal temperature or panting rate until 25 - 30 ºC ambient temperature and it is thought that the higher rectal temperature of the German Mutton Merino at this ambient temperature might have triggered the higher panting rate. It seems that the German Mutton Merino use panting to a greater extent than the Awassi, whereas the Awassi dissipate heat through the skin more efficiently than the German Mutton Merino. It is concluded that both breeds are thermostable, much of the between breed difference in rectal temperature can be attributed to their anatomical differences.

Degen, A. A. and B. A. Young. 1981. Effect of air temperature and feed intake on live weight and water balance in sheep. Journal of Agricultural Science 96:493-496.

Environmental conditions and total feed intake influence the water intake of sheep. In general, high temperatures increase the requirements for water needed for evaporative cooling and high feed intakes necessitate more water for excretion of waste products. This study was designed to measure the partition of water output in sheep maintained at 4 air temperatures and offered 4 levels of a ration.

Degen, A. A. and M. Kam. 1991. Energy intake, nitrogen balance and water influx of Dorper sheep when consuming different diets. Journal of Arid Environments 21:363-369.

Dorper sheep are well adapted to arid areas and inhabit extreme deserts. We hypothesized that these sheep would have low energy and nitrogen requirements, allowing them to be raised in these areas. We measured energy intake, N requirement and water influx of Dorpers (40 kg body mass) that were offered either Lucerne hay (17.5% crude protein), Lucerne hay plus wheat straw or wheat straw (3.25% crude protein) and water ad libitum. Dry matter digestibility and apparent digestible energy as a percent of gross energy were 67.7% and 66.1%, respectively, for Lucerne hay, and 46.5% and 50.7%, respectively, for wheat straw. Dorpers gained body mass and were in positive N balance on Lucerne hay plus wheat straw and lost body mass and were in negative N balance on wheat straw. Metabolizable energy intake was 925 kJ kg^{-075}/day on Lucerne hay, 706 kJ kg$^{-0.75}$ day^{-1} on Lucerne hay plus straw, and 420 kJ kg$^{-0.75.}$day^{-1} on wheat straw. Apparent N digestibility of Dorper was 76.9%, and 68.1% and 24.3% for Lucerne hay, Lucerne hay plus wheat straw and wheat straw respectively, and their water influxes on these respective diets were 3.74 L day^{-1}, 3.17 L day^{-1}, and 1.68 L day^{-1}. Energy and N requirements of Dorpers were similar to many sheep breeds and greater than a number of desert sheep and desert herbivores. We concluded that Dorpers did not appear to have special physiological adaptations of low energy and nitrogen requirements.

Dill, D. B., M. K. Yousef, C. R. Cox, and R. G. Barton. 1980. Hunger vs. thirst in the burro (*Equus asinus*). Physiology and Behavior 24:975-978.

The burro can withstand deprivation of food and water for up to 48 hr even in summer heat. The relationships of hunger and thirst following periods of deprivation were studied. In 8 periods of deprivation maximum temperatures ranged from 35 to 45 ºC and estimated increase in osmotic pressure in 2 burros ranged up to 17%. Given free choice of hay and water at the end of deprivation they chose hay always when estimated increase in osmotic pressure was less than 10%. In 1 case the second 24-hour period included an 8-hour walk. In this case the estimated increase in osmotic pressure was 17% in both and both chose water first. Their ability to eat dry hay after long periods of dehydration is essential to their survival in hot deserts where they can graze for day before returning to a water source.

Dmi'el, R. and D. Robertshaw. 1983. The control of panting and sweating in the black Bedouin goat: a comparison of two modes of imposing a heat load. Physiological Zoology 56:404-411.

The black Bedouin goat uses both panting and sweating as modes of evaporative heat loss. The control of panting and cooling was studied by examining the body temperature distribution under heat loads which produced equivalent levels of evaporative heat loss, namely, solar radiation and high air temperature conditions, conducted in indoor and outdoor settings, respectively. Heat exposure induced by high air temperature resulted in a proportionally greater respiratory water loss than did outdoor exposure to solar radiation; the greater respiratory cooling was related to higher hypothalamic and arterial temperatures but lower skin temperatures. However, solar radiation resulted in a higher temperature of the skin under irradiated fur, and this was associated with a greater cutaneous moisture loss. Thus, the mode of evaporation was concluded to be appropriate to the thermal stimulus: higher nasal temperature resulted in a predominant panting response, and high skin temperature invoked greater sweating. The gradient between arterial and hypothalamic temperature was not necessarily correlated with panting, providing evidence that blood flow through the countercurrent heat exchanger, the carotid rete mirabile, was utilized only when hypothalamic temperature rose above a critical level.

Dmi'el, R. 1986. Selective sweat secretion and panting modulation in dehydrated goats. Journal of Thermal Biology 11:157-159.

Sweating from the trunk and the head, respiratory water loss, oxygen consumption and rectal temperature, were measured in daily watered and in dehydrated black Bedouin goats exposed to summer conditions in the desert. After 72h of water deprivation the goats lost 19.5% of their body mass. Although rectal temperatures and total evaporation were similar in both states of hydration, a 3-fold reduction in the sweating from the trunk, associated with a 26% decrease in metabolic rate, was found in the dehydrated goats. Concurrently, the rates of sweating from the head and the respiratory water loss were increased 2.9 and 2.3-fold, respectively. It is proposed that the selective sweat secretion and panting modulation enable a preferential brain cooling in the dehydrated goat.

El Hadi, H. M. and Y. M. Hassan. 1982. Seasonal changes in water metabolism of Sudan Desert sheep and goats. Pages 133-142 *in* Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

Seasonal changes that occur in body mass, body temperature, total body water, and water turnover were investigated in grazing sheep and goats using titrated water at different times of year to understand how different breeds adapt to the environmental conditions in Sudan. Sheep had lower body water content and turnover rates than goats. Goats maintained a lower body temperature under hot conditions than the sheep, possibly because of a lower food intake and maintenance requirement and a higher evaporative heat loss. It might be deduced from this that goats will survive better when food is in short supply provided sufficient water is available, and that sheep will grow relatively better when food is adequate. However, in the absence of comparative information on reproductive performance under these conditions it is not possible to make an unequivocal statement about the relative productivity of these types of small ruminants.

Etzion, Z., N. Meyerstein, and R. Yagil. 1984. Titrated water metabolism during dehydration and rehydration in the camel. Journal of Applied Physiology 56:217-220.

The metabolism of titrated water in the camel was compared in 2 10-day periods, 1 when water was readily available and the second during dehydration. There was a radically depressed metabolism after 2 days of dehydration. Two other experiments examined the absorption rate of drinking water. In 1 experiment drinking water was labeled with tritium, and in the second experiment dilution of tritium-labeled blood was examined. In both experiments there was a rapid uptake and dilution of the blood, which continued up to day after drinking. The results are in accord with other data showing changes in erythrocyte shape 4 hr after rapid rehydration. It is concluded that there is a rapid absorption of water in the dehydrating camel.

Etzion, Z. and R. Yagil. 1986. Renal function in camels (*Camelus dromedaries*) following rapid rehydration. Physiological Zoology 59:558-562.

The desert camel, like the goat, rapidly replaces lost water after being severely dehydrated. In contrast to the goat, however, the camel quickly absorbs water into its bloodstream, which allows for a rapid return to normal of its renal function. The glomerular filtration rate, renal plasma flow, and urine flow return to normal within 30 minutes of drinking. The urine becomes highly diluted in appearance as well. The changes in urea metabolism are probably associated with the decline in antidiuretic hormone concentrations. To prevent serious hemodilution, aldosterone secretion accounts for the slight drop in glomerular filtration rate and renal plasma flow 2 hr following drinking. The camel has thus adapted to the desert not only by being able to withstand severe dehydration but also by being able to rapidly restore body functions, especially renal function.

Farid, M. F. A. 1985. Long-term adaptation of sheep to low protein intake under simulated drought conditions. Journal of Arid Environments 8:79-83.

Barki sheep maintained on low protein diets or fed decreasing amounts of protein, were able to adapt by reducing urinary nitrogen excretion, and subsequent recycling of conserved nitrogen to the rumen, as reflected upon the more efficient utilization of the apparently digested nitrogen. After 50 - 60 days on the low protein diets, sheep activated positive nitrogen balance while receiving only 60% of their maintenance requirements. Similarly, gradually decreasing the level of protein intake enabled sheep to adapt and improve their state of nitrogen balance. The findings are discussed in the light of their value for the supplementary feeding and management of sheep on arid and semi-arid rangelands.

Farid, M. F. A., H. M. Abou-El Nasr, N. I. Hassan and F. Z. Swidan. 1989. Long-term adaptation of sheep to low protein roughage diets: effects of water deprivation and urea supplementation in the drinking water. Journal of Arid Environments 16:211-216.

Nine Barki x Merino crossbred rams were fed low protein roughage diets in 3 groups: daily watering, and intermittent watering every 3 days with and without urea supplements in the drinking water. The experiment lasted 63 days to investigate possible long-term adaptive responses. Live body masses was recorded every 2 weeks, and urine was collected for 3 consecutive days every 2 weeks. The experiment ended with a 10-day rehydration period. Daily dry matter intake was not affected by water deprivation or urea supplementation, and the amounts offered were apparently insufficient for maintenance in all groups. Nitrogen intake was significantly greater in the urea-supplemented group. All groups showed a loss of nitrogen in urine at the beginning of the experiment, 136 to 157% of total nitrogen intake. However rapid adaptation was observed and after 1 month urinary nitrogen excretion represented 57 to 75% of intake. The urea-supplemented group constantly excreted more nitrogen, but the trend of adaptation was similar in all 3 groups. All sheep lost weight that amounted to 2.1, 2.1, and 4.1% of their initial weight in the control and water-deprived with and without urea supplementation, respectively. On rehydration, the latter 2 groups restored or slightly exceeded their initial weight.

Finberg, J. P. M., R. Yagil, and G. M. Berlyne. 1978. Response of the rennin-aldosterone system in the camel to acute dehydration. Journal of Applied Physiology 44:926-930.

Plasma rennin activity, rennin substrate concentration, aldosterone concentration, and Cortisol levels were determined in 5 camels during dehydration (8 – 10 days of complete denial of water) and at timed intervals after rapid rehydration in cool spring and hot summer weather. Plasma sodium concentration increased from 138 ± 3.7 to 147 ± 2.5 (mean ± SE) meq L^{-1} during spring dehydration, and from 146 ±1.3 to 1.14 ± meq L^{-1} during dehydration in the summer. Plasma sodium concentration returned to control levels over the course of several hours following rapid rehydration. Only minor changes in plasma potassium concentration occurred. The hormonal changes were accentuated in the summer dehydration. Plasma rennin activity increased on dehydration, and returned to control levels over the course of several hours following rehydration. Aldosterone concentration increased slightly on dehydration but was markedly elevated 24 hr after rehydration. Rennin substrate concentration showed a slight increase following rehydration in the spring. Changes in cortisol were insignificant. The results are consistent with the role for angiotensin and aldosterone in enhancing sodium and water reabsorption from kidney and large intestine on dehydration in the camel.

Finch, V. A. 1972. Thermoregulation and heat balance of the East African eland and hartebeest. American Journal of Physiology 222:1374-1379.

Energy exchange between animals and their environment was assessed by estimating the total energy balance in the field under conditions of intense solar radiation in a thermoneutral temperature zone. Two representative species were chosen: the eland (*Taurotragus oryx*), which uses sweating primarily, and the hartebeest (*Alcelaphus buselaphus*), which uses panting primarily as a means of evaporative cooling. Results show that evaporative cooling in both species varies in relation to changes in skin temperature and not to changes in body temperature. Estimation of the heat balance showed that the eland absorbed 40% and the hartebeest 34% of the potential impinging radiation. Metabolic heat contributed to 10 - 12% to the total heat load. Reradiation from the fur surface liberated 69% in the eland and 80% in the hartebeest of the absorbed heat. Convection contributed 4 - 6% to the total heat dissipation at the fur surface. The eland eliminated 78% of the remaining absorbed and metabolic heat through sweating, 20% through respiratory cooling, and stored 2%. The hartebeest eliminated 33% of the remaining absorbed and metabolic heat through cutaneous evaporation, 61% through panting, and stored 6%. Conductance of heat through the fur of the hartebeest is 14% of that in the eland.

Finch, V. A. and J. M. King. 1982. Energy-conserving mechanisms as adaptations to under nutrition and water deprivation in the African zebu. Pages 167-178 *in* Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

In a study designed to simulate pastoral cattle management practices on marginal and rangelands in Kenya, the physiological adaptations for energy conservation were investigated in African Zebu cattle during a period of under nutrition and water deprivation. In experimental design, the food available to cattle was restricted to 50% of maintenance, watering reduced to every 2 days and distances walked increased from 8 to 16 km day^{-1}. Restricting food for nearly 3 months resulted in a 13 - 14% weight loss in cattle. A 2-day watering regime did not decrease food intake. Cattle that walked longer distances lost slightly more weight, but not significantly more. There was a significant overall reduction in water requirements. Slowing water turnover is seen as adaptive in a water-limited environment. Higher solar intensities increased water turnover somewhat, as did extending walking distances. The resting metabolic rate of cattle on restricted food and water was reduced 30% below that of well-fed and daily watered cattle. This reduction in metabolic requirements would result in conserving energy in dry seasons. Cattle became more thermolabile when offered smaller quantities of food. A heat debt was incurred at night and sweating rates were regulated at low levels during the day, resulting in heat storage. It is suggested that this is a mechanism by which energy is conserved through increasing thermogenesis to maintain body temperature within the normal range.

Gabor, T. M., E. C. Hellgren, and N. J. Silvy. 1997. Renal morphology of sympatric suiforms: implications for competition. Journal of Mammalogy 78:1089-1095.

The ability to conserve water in collared peccaries (*Dicotyles tajacu*) and feral hogs were assessed by comparing renal morphology in free-ranging populations living sympatrically in southern Texas in 1994 – 1995. Kidneys of collared peccaries had relatively larger and thicker medullae and presumably a greater capacity to concentrate urine than feral hogs. Renal indices of peccaries were similar to values predicted from allometric functions, whereas indices of hogs were smaller than predicted. Renal mass of hogs, when scaled by body mass$^{0.85}$ was larger than that of peccaries. Indices of renal function from this study were greater than values reported previously for these species. Geographic variation and adaptation during growth may play a role in renal morphology. Genetic constraints probably control large-scale differences, constraining feral hogs to being less suited to water-stressed environments. Results were consistent with predictions that peccaries should have a competitive advantage over hogs in xeric environments with minimal surface water because of ecophysiology. However, a suite of environmental, behavioral, and functional factors appears to control competitive interactions between native peccaries and introduced hogs.

Ghobrial, L. I. 1970. A comparative study of the integument of the camel, dorcas gazelle, and jerboa in relation to desert life. Journal of Zoology 160:509-521.

A comparative histological study of the integuments of the dorcas gazelle (*Gazella dorcas*), jerboa (*Jaculus jaculus*), and the camel was conducted. Tubular sweat glands are present in the skin of the dorcas gazelle and the camel but not in the jerboa. Hairs occur in groups in the skin of jerboa and camel but occur singly in the Dorcas gazelle where they are of two types; short under hairs and long covering hairs. Each hair follicle is associated with a sebaceous gland. Both the unkeratinized epidermis and its horny layer are comparatively thin in the jerboa and gazelle, and in dry air this may permit greater loss of water by transpiration than in the camel, which has a comparatively thick epidermis.

Ghobrial, L. T. 1970. The water relations of the desert antelope *Gazella dorcas.* Physiological Zoology 43:249-256.

Water turnover, routes of water loss, and water intake rates were studied in captive dorcas gazelle (*Gazella dorcas*). Daily free-water intake rates averaged 3.1% and 4.5% of body weight during winter and summer, respectively. Daily intake of preformed water averaged 0.2% and 0.15% of body mass during winter and summer, respectively. Daily urine output in winter averaged 2.1% of body mass and had solute concentrations of 1.4 osm L^{-1}. In summer, daily urine output averaged 1.4% of body mass and had solute concentrations of 1.2 osm L^{-1}. Average fecal production averaged 0.3% of body mass with water content of 52%. During summer, average fecal production averaged 0.17% of body mass with water content of 51%. Gazelles began to sweat at 25 ºC. Cutaneous water loss at 20 – 22 ºC was 2.8 – 5.6 g hr^{-1} m$^{2-1}$; at 23 – 25 ºC, was 28.2 – 56.4 g hr^{-1} m$^{2-1}$; at 26 – 30 ºC, was 81.8 – 87.4 g hr^{-1} m$^{2-1}$. Respiratory rate increased from 45 – 55 breaths min^{-1} at 28 ºC to 50 – 75 breaths min^{-1} at 29 ºC. Respiratory water loss was 0.15 – 0.35 mg min^{-1}. Total respiratory and cutaneous water loss was 6 – 12 g hr^{-1} at 32 – 35 ºC.

Ghobrial, L. I. 1974. Water relation and requirement of the Dorcas gazelle in the Sudan. Mammalia 38:88-107.

Thirty dorcas gazelle (*Gazella dorcas dorcas*) were studied for: the actual calories and water requirements in comparison to the calculated amount of moisture which would be gained from the preformed water in green acacia leaves, if the required calories were to be consumed; the tolerance of the gazelle to the absence of free water, and its physiological and behavioral adaptation for conservation of water and thermoregulation. Field studies on the distribution, habit, and habitat of the dorcas gazelle during the two dry seasons, the hot summer, and cold winter were carried out Sudan.

Ghobrial, L. I. 1976. Observations on the intake of sea water by the Dorcas gazelle. Mammalia 40:489-494.

Artificial sea water with varying salt concentrations were provided to dorcas gazelles (*Gazella dorcas*) without access to other water sources to determine the effect on food intake, urine output, body mass, and chloride concentration in urine. Gazelles did not voluntarily drink seawater even when deprived of fresh water. Water intake and food intake increased with decreasing salt concentrations of water; urine output increased and urine concentration decreased in association with decreases in salt concentration. Body mass decreased with increasing salt concentration.

Ghobrial, L. I. and J. L. Cloudsley-Thompson. 1966. Effect of deprivation of water on the dorcas gazelle. Nature 212:306.

The dorcas gazelle (*Gazella dorcas*) requires water or succulent food in order to maintain homeostasis in desert conditions. It loses weight steadily on a diet of dry millet without water. Feeding ceases when 14 – 17% of normal body mass has been lost and the animals appear weak and emaciated. This may take up to 12 days under winter conditions at Khartoum when the air temperature ranges between 10 and 30 ºC with a relative humidity varying from 20 to 40%; but, in summer, when air temperature fluctuates from 35 to 45 ºC, with relative humidity varying 10 to 30%, gazelles cannot survive for more than about 5 days without water. Two experimental animals died after 6 days water deprivation, during which they lost 24% of their original body mass. This contrasts with a loss of 30%, which can be tolerated without ill effects by the camel and about 12%, which can be withstood by man and most other animals. During dehydration, the blood urea of gazelles increases from 5 – 10 mg 100 ml^{-1} to 70 – 110 mg 100 ml^{-1} (in the animals that died it reached 225 mg 100 ml^{-1}). At the same time, the hemoglobin content of blood increases from 14 – 18 g 100 ml^{-1} to 20 – 29 g 100 ml^{-1}, the hemocrit from 40 – 55% to 55 – 59% and the plasma protein from 4.5 – 5.5 g 100 ml^{-1} to 5.5 – 7.0 g 100 ml^{-1}. These results, accompanied by an increase in electrolytes, indicate a decrease in extracellular water and a concentration of the contents of body fluids, even though urine production is reduced from about 200 – 700 ml to 30 – 80 ml day^{-1} and the amount of water lost with the feces is reduced by 50%.

Ghosh, P. K., M. S. Khan, and R. K. Abichandani. 1976. Effect of short-term water deprivation in summer on Marwari sheep. Journal of Agricultural Science 87:221-223.

Effect of 24 hr and 48 hr of water deprivation on glomerular filtration rate (GFR), and on blood and urine electrolyte levels in Marwari sheep of the Rajasthan Desert, India have been recorded. Body mass, urine volume, GFR, and erythrocyte sodium concentration in these animals registered considerable decreases due to dehydration. Both plasma sodium and urinary potassium concentrations remained unaffected. While plasma potassium was somewhat reduced, the potassium in red blood cells increased after 48 hr of water deprivation. The most remarkable response was in the concentration of urinary sodium, which rose to more than double the normal level.

Giddings, S. R. 1990. Water metabolism in the gemsbok (*Oryx gazella*). MS Thesis. University of Pretoria, Pretoria, South Africa.

Water metabolism in the gemsbok (*Oryx gazella*) was studied in the laboratory using titrated water and ^{51}Cr. The distribution of gemsbok is confined to the arid regions of Southern Africa, where surface water may be limited or saline in nature. Failure to obtain adequate water from the diet may lead to dehydration and/or imbibition of saline water. The goal of this study was to determine some of the effects of dehydration and the intake of saline water on the physiology of the gemsbok. Fewer significant changes in the variables measured were found between fresh and saline water acclimated animals, than between hydrated and dehydrated animals. It was concluded that the effects of dehydration were more stressful than those resulting from the imbibition of saline water. The regulation of plasma fluid volume and the intracellular fluid volume, at the expense of the interstitial fluid, was found to be an important determinant of survival in dehydrated animals. Similarly, the regulation of blood variables ensured the continued functioning of the circulatory system. Dehydration, and to a lesser extent, the imbibition of saline water, resulted in a non-significant decline in the body water pool. Water turnover also declined when saline water was imbibed, indicating that water-conserving mechanisms were operative. Renal function was significantly altered by dehydration, whereas imbibition of saline water had less effect. The trends recorded indicated that the kidney was responsible for the excretion of excess electrolytes and the conservation of water. Another important water conserving mechanism recorded in dehydrated animals involved the increased energy assimilation from food eaten. In addition fecal water loss was reduced in dehydrated gemsbok and to a lesser extent in gemsbok that had imbibed saline water.

Gotaas, G., E. Milne, P. Haggarty, and N. J. C. Tyler. 2000. Energy expenditure of free-living reindeer estimated by the doubly labeled water method. Rangifer 20:211-219.

The doubly labeled water (DLW) method was used to measure total energy expenditure (TEE) in 3 male reindeer (*Rangifier tarandus*) aged 22 months in winter (February) while the animals were living unrestricted at natural mountain pasture in northern Norway (69 20'N). The concentration of ^{2}H and ^{18}O were measured in water extracted from samples of collected form the animals 0.4 and 11.2 days after injection of isotopes. Calculated rates of water flux and CO_2 production were adjusted to compensate for estimated losses of ^{2}H in fecal solids and in methane produced by microbial fermentation of forage in the rumen. The mean specific TEE in the three animals was 3.057 W kg^{-1} (range 2.436 - 3.728 W kg^{-1}). This value is 64% higher than TEE measured by the DLW method in four captive, non-pregnant adult female reindeer in winter and probably mainly reflects higher levels of locomotor activity in the free-living animals. Previous estimates of TEE in free-living rangifier in winter based on factorial models range from 3.038 W kg^{-1} in female woodland caribou (*R. t. caribou*) to 1.813 W kg^{-1} in female Svalbard reindeer (*R. t. platyrhyncbus*). Thus, it seems that existing factorial models are unlikely to overestimate TEE in reindeer/caribou: they may, instead, be unduly conservative. While the present study serves as a general validation of the factorial approach, we suggest that the route to progress in the understanding of field energetics in wild ungulates is via application of the DLW method.

Haggarty, P. and R. E. Haugerud. 1999. Quantifying the free-living energy exchanges of Arctic ungulates with stable isotopes. Rangifer Report No 4:10. 10th Arctic Ungulate Conference, 9-12 August 1999, University of Tromso, Tromso, Norway (Abstract).

When natural diets meet an animal's requirement for energy, other essential nutrients will usually be supplied in amounts at least sufficient for survival. Knowledge of the energy requirements of free ranging species under typical conditions is important in assessing both their nutritional needs and their ecological relationships. The doubly labeled water (DLW) method is currently the most promising objective field of methodology for estimating free-living energy expenditure but expenditure is only equal to the energy requirement when an animal is in energy balance. Reproduction and seasonal cycles of fat deposition and utilization represent significant components of the energy budget of Artic ungulates but the information gained in the course of a typical DLW study may be used to estimate processes such as milk output and fat storage and mobilization in order to predict requirements from expenditure. The DLW method has been exhaustively validated under highly controlled conditions and the introduction of innovations such as fecal sampling for the estimation of body water isotopic enrichment, the availability of appropriate correction factors and stoichiometries for known sources of error, and the iterative calculation of unknown parameters, have produced a methodology suitable for use in species under truly free ranging conditions. The few studies carried out so far in Arctic ungulates indicate that previous predictions have generally underestimated the true level of expenditure, that there is considerable between animal variation in the level of expenditure and that this is largely determined by physical activity. The disadvantages of the DLW methodology are that it remains expensive and the isotope analysis is technically demanding. Furthermore, although DLW can provide and accurate value for free living energy expenditure, it is often important to have information on the individual components of expenditure, for example the relative contribution of physical activity and thermoregulatory thermogenesis, in order to interpret the values for overall expenditure. For these reasons the most valuable use of the DLW method in the field may be to validate factorial models and other approaches so that they may be used with confidence. Additional important information on the energy exchanges of free ranging animals may be obtained from the other stable isotope methodologies. In addition to the use of the isotopes ^2H and ^{18}O in the DLW method, natural variations in the abundance of ^{13}C and ^{15}N in the Arctic environment may be exploited to study diet selection in ungulates.

Haim, A. and J. D. Skinner. 1991. A comparative study of metabolic rates and thermoregulation of two African antelopes, the steenbok (*Raphicerus campestris*) and the blue duiker (*Duiker cephalopus*). Journal of Thermal Biology 16:145-148.

The steenbok, a small diurnal antelope is widely distributed in the southern African subregion even in extreme deserts. The blue duiker is limited in its distribution to forests on the eastern coast of the subregion. In 1986 – 1987, a comparative study on heat production and dissipation was carried out in the laboratory using captive animals from the zoo of Pretoria, South Africa in order to assess the ability of these 2 species to cope with dry habitats. Metabolic chambers were used to determine oxygen consumption and body temperatures were determined using thermocouples. Low metabolic rates, a high lower-critical point and high overall minimal thermal conductance as found in the steenbok when compared to the blue duiker seem to be important adaptations which help the steenbok to conserve water even when exposed to high ambient temperatures and, therefore, to inhabit extreme arid habitats.

Hassan, G. A., F. D. El-Nouty, M. H. Salem, M. G. Latif, and A. M. Badawy. 1988. Water requirements and metabolism of Egyptian sheep and goats as affected by breed, season, and physiological status. Pages 65-83 *in* Isotope aided studies on livestock productivity in Mediterranean and North African countries. International Atomic Energy Agency, Vienna, Austria.

Water requirements and metabolism and some physiological and blood characteristics were studied in dry non-pregnant Barki and Rahmani females and in Baldi goats during spring, summer, and winter seasons using titrated water methods. The Rahmani sheep showed greater thermal discomfort than the Barki during the summer season. Goats had higher overall mean total protein and albumin levels and lower packed cell volumes than sheep. In addition, goats showed the highest overall mean total body water and the lowest water turnover rate and water loss, followed by Barki, then by Rahmani sheep; such may also be the order of their tolerance to extreme environmental conditions. Pregnancy was associated with a significant increase in body mass and a decline in the packed cell volume and total serum protein, and these changes were greater in goats than sheep. They were accompanied by significant increases in total body water and water turnover rate. All these changes were more pronounced during late pregnancy than during mid-pregnancy, although the effect of stage of pregnancy on total body water did not occur in the Barki females. The pregnancy induced changes in total protein and water turnover rate were greater in spring, while those in total body water were greater in winter. The above parameters also showed similar changes during lactation (particularly during early lactation), but lactating animals showed a decrease instead of an increase in body mass. Goats showed greater reductions in body mass, packed cell volume, and water half-life and greater increases in water turnover rate than sheep during the spring season. Withdrawal of drinking water for 4 days caused a reduction in body mass, blood glucose, and plasma T_3 and T_4, and an increase in packed cell volume, total serum protein, and plasma osmolality. Plasma aldosterone increased slightly during dehydration but increased markedly during the rehydration period, particularly in the Rahmani sheep during the summer season. The above parameters changed similarly when the animals were starved for 4 days (feed but not water was withheld), but total serum protein showed a decrease instead of an increase. Changes during dehydration were more pronounced in summer, while those during starvation were greatest in winter.

Hazam, J. E. and P. R. Krausman. 1988. Measuring water consumption of desert mule deer. Journal of Wildlife Management 52:528-534.

The authors developed an accurate (≤1% error) to measure water consumption of large, free-ranging animals. The system was field tested in the

Picacho Mountains, Arizona in the summers of 1985 and 1986. The water consumption of desert mule deer (*Odocoileus hemionus crooki*) was recorded. Three collared males visited water sources 1.1 times day^{-1} over 10 days. Deer consumed from 1.52 to 6.0 L water catchment visit^{-1} (mean = 3.70, *n* = 54). Females drank more (mean = 4.16, *n* = 20) than males (mean = 3.55, *n* = 24) during late summer (*P* = 0.019).

Hecker, J. F., O. E. Budtz-olsen, and M. Ostwald. 1964. The rumen as a water store in sheep. Australian Journal of Agricultural Research 15:961-968.

The rumen fluid volume in sheep was measured by the method of phenol red dilution. Serial determinations made in 22 sheep deprived of food and water for up to 8 days showed that the greatest decrease in rumen fluid volume occurred during the first 2 – 3 days, the magnitude of the decrease depending on the initial volume. After the third day, the rate of loss of rumen fluid became slower as the rumen fluid volume became depleted. Sheep deprived of food only gave similar results to those of deprived of both food and water. This absorption of rumen fluid during the first 2 – 3 days of food and water deprivation may account for the expansion in plasma volume, which has been recorded on the third day. In a group of 8 sheep deprived of food and water for 4 days, the mean rumen volume loss for the period amounted to about half the body weight loss. These results support the view that in the sheep, the water balance of the body proper is kept virtually unaltered by fluid drawn from the alimentary tract during the first days of water deprivation. The animal does not become dehydrated, in the physiological sense, until the reserve is depleted. For this reason, the rumen may be regarded as a water “store” in sheep.

Hofmeyr, M. D., and G. N. Louw. 1987. Thermoregulation, pelage conductance and renal function in the desert-adapted springbok, *Antidorcas marsupialis*. Journal of Arid Environment 13:137-151.

The springbok (*Antidorcas marsupialis*), a gazelle of the open, arid plains of southern Africa, can survive under hot conditions without access to free water. The pelage of the springbok (4.4 ± 1.2 mm) is thinner than predicted from its body mass and has a high conductance (6.7 W m$^{2-1}$ K^{-1}), which increases rapidly with increasing wind speed. When prevented from thermoregulating behaviorally, it either gains or loses heat rapidly, resulting in either thermal panting and sweating or a strong shivering response, even at moderate ambient temperatures. The unusually thick pelage is thought to be an adaptation to facilitate heat loss during and after sprinting in this remarkably swift antelope. Under natural free-ranging conditions, the springbok maintains a fairly constant body temperature (37.5 – 41 ºC). It makes extensive use of orientation of the long axis of the body towards the solar beam, thereby reducing the profile area exposed to direct solar radiation and exploiting areas of the pelage, such as the white rump, with a high reflectance value (0.72). The kidney has a high relative medullary (5.3) and the theoretical potential for concentrating urine is high (2,700 - 3,000 mOsm kg^{-1}).

Hoppe, M. G., J. H. Green, J. Hardcastle, P. T. Sanford, and P. A. Sanford. 1975. The rumen as a reservoir during dehydration and rehydration in the camel. Journal of Physiology 254:76-77.

The rumen function during dehydration and rehydration in the camel was studied in covered stalls at temperatures ranging from 16 to 27 ºC and deprived of water for 20 days. The volume and outflow of the rumen were measured using polyethylene glycol. Food intake remained normal at 4 – 5 kg/day for 4 days, then declined to 0.3 kg day^{-1} after 10 days. Plasma osmolality increased from 315 to 340 mOsm L^{-1} and urine osmolality from about 1,500 to 2,400 mOsm L^{-1}. Initial rumen fluid volume was 14 – 30 L and rumen outflow was 51 – 69 L day^{-1}; these values declined to 10 – 14 L and 3 – 16 L day^{-1} after 17 days of dehydration. Camels were then allowed to drink their fill; after 12 min they drank 34 – 44 L. Rumen fluid volume increased and 22 hr later remained at about 42 L. Rumen osmolality declined to 60mOsm L^{-1} and 22 hr later it was 140 mOsm L^{-1}, half its normal value. Rumen polyethylene glycol concentrations increased indicating that absorption of water through the rumen wall exceeded dilution by inflowing saliva. Blood osmolality and hemocrit declined 1 hr after drinking. The results suggest that the water drunk by a dehydrated camel is retained in the rumen for 24 hr or longer allowing a gradual rehydration and adjustment of the body fluid compartments.

Holtenius, K. 1989. Water and electrolyte transport in the ruminant forestomach. Swedish University of Agricultural Science Report S-75007. Uppsala, Sweden.

The affects of food deprivation on the composition of blood plasma, rumen fluid, rumen absorptive function and how differently composed intraruminal fluid loads affect absorption of water and electrolytes from the rumen in fed and food-deprived animals were investigated in goats and sheep. Ruminal absorption of water was measured in water-deprived sheep during rehydration and omasal water absorption and fiber digestion were compared in normally fed and watered sheep, goats, and cattle. Water movements across the rumen epithelium were reduced by food-deprivation and plasma volume was decreased. Intraruminal load of volatile fatty acids increased blood flow to the ruminal subepithelium and stimulated Na absorption in food-deprived goats. Water diffusion across the epithelium was also increased, however net absorption of water was not large enough to restore plasma volume. In water-deprived sheep voluntary drinking was followed by immediate and substantial absorption of water from the rumen. A large portion of fluid (43%) leaving the reticulo-rumen through the omasal orifice was not retained in the omasal body of sheep and bypassed the omasum via the omasal sulcus or passed quickly through the omasum to the abomasum. Only 17% of the fluid bypassed the omasum in goats.

Hossaini-Hilali, J., S. Benlamlih, and K. Dahlborn. 1994. Effects of dehydration, rehydration, and hyperhydration in the lactating and non-lactating black Moroccan goat. Comparative Biochemistry and Physiology 109A:1017-1026.

The effects of water deprivation, rehydration and hyperhydration were investigated in 6 black Moroccan goats. Mean daily water intake was 46 ± 5 ml kg^{-1} in lactating and 36 ± 4 ml kg^{-1} in non-lactating black Moroccan goats, and milk production 21 ± 1 ml kg^{-1}. Mean urine excretion was 8 ± 2 ml kg^{-1} body mass in both groups, and the daily water losses via evaporation and were estimated at 23 ± 3 ml kg^{-1} during lactation and 28 ± 4 ml kg^{-1} during non-lactation. Forty-eight hours of water deprivation caused a body mass loss of 9% and 6% in lactating and non-lactating goats, respectively, and a drop of 28% in milk production with only slight decrease in food intake. After rehydration, the elevated plasma osmolality as well as Na and total protein concentrations returned to basal values within 2 – 3 hr, indicating a rapid absorption of the ingested water, but urine excretion did not increase. After hyperhydration (10% of body mass), 46% of the load was excreted by the kidneys within 6 hr. In conclusion, black Moroccan goats have a low water turnover, and they can retain water upon rehydration but not store excess water after hyperhydration.

Jarman, P. J. 1973. The free water intake of impala in relation to the water content of their food. East African Agricultural and Forestry Journal 38:343-351.

The weekly free water intake of 2 captive impala (*Aepyceros melampus*), living in semi-natural circumstances in paddocks in the Serengeti National Park, Tanzania, was measured over a period of 9 months. Over the same period various climatic factors were measured, and intermittently the water content of plants in the community from which the impala selected their food, was determined. It is shown that the daily intake of free water was primarily influenced by the water content of the food, and secondarily influenced by climatic factors as those affected the water content of vegetation. Data on water intake are compared with those obtained by other workers. Strategies which impala may use to minimize their need to drink are discussed, and it is shown that their pattern of food and habitat selection in the dry season confer advantages in water conservation.

Jessen, C. and G. Kuhnen. 1996. Seasonal variations of body temperature in goats living in an outdoor environment. Journal of Thermal Biology 21:197-204.

Blood and brain temperatures were measured continuously in three animals on 319, 248, and 127 days. Over a 30 C range of the 24-h mean of air temperature, the 24-h mean of body core temperature changed 0.5-C or less. The 24-h mean of body core temperature was, in the range between 38°C and 39 C. mainly determined by non-thermal factors. The 24-h amplitude of body core temperature was closely correlated with the 24-h amplitude of air temperature, and was small in winter and large in summer. The relationship between blood and brain temperatures was highly variable and did not reveal a consistent temperature effect within the range of the most frequently occurring body core temperatures.

Jhala, Y. V., R. H. Giles, Jr. and A. M. Bhagwat. 1992. Water in the ecophysiology in blackbuck. Journal of Arid Environments 22:261-269.

Blood and urine characteristics of water-deprived blackbuck (*Antelope cervicapra*) were studied in Velavadar National Park, India. Blackbuck maintained their blood volume during water deprivation for 3 days. The blackbuck produced highly concentrated urine (specific gravity 1.058) and with low (43.3%) moisture content. The minimum water requirements of the blackbuck were calculated to be 4.26 L 100 kg^{-1} day^{-1} at an average maximum shade temperature of 48 ºC. Observations on wild blackbuck indicate the importance of preformed water in their forage. Wild blackbuck are in a negative water balance in summer when ambient temperature is high and moisture content of forage is low and are thus not independent of drinking water in summer. A management technique of supplying drinking water based on moisture content of forage is suggested.

Kamal, T. H. 1982. Water turnover rate and total body water as affected by different physiological factors under Egyptian environmental conditions. Pages 143-154 *in* Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

The titrated water dilution technique was used to determine total body water and water turnover rate, which is assumed to be similar to water intake, in water buffalo (*Bubalus bubalis*), Red Danish cattle, fat-tailed Osemi sheep, and crossed Nubian-Bedouin goats and camels. There was a significant effect of species on total body water and water turnover rate. The combined data of buffalo, cattle, and sheep revealed a significant effect of pregnancy on total body water but not on water turnover rate. The combined data of buffalo and cattle showed significantly lower total body water and a higher water turnover rate in lactating animals than in females. In buffalo water turnover rate was on average 81% higher in summer grazing than in spring. It was also 118 and 20% higher in summer non-grazing, than in either spring or summer grazing, respectively. The differences between treatments in females, pregnant, and lactating, were significant, except between spring and summer grazing in females. The total body water on average was 12% higher in summer grazing than in spring. It was also 18 and 5% higher in summer non-grazing than in either spring or summer grazing, respectively. The differences between treatments in females, pregnant, and lactating, were significant except between summer grazing and summer non-grazing in lactating cows.

Kamal, T. hr and M. K. Shebaita. 1972. Natural and controlled hot climatic effects on blood volume and plasma total solids in Friesians and water buffaloes. Pages 103-110 *in* Isotope studies on the physiology of domestic animals. International Atomic Energy Agency, Vienna, Austria.

Blood, plasma, and red cell volumes in ml/kg body mass, hemocrit, circulating plasma solids in grams, and hemoglobin percentage were determined in winter (18.4 ºC, 43% relative humidity) and summer (29 ºC, 55% relative humidity) using titrated water in 12 Friesian cattle and 11 water buffaloes. These measurements were also made on 4 Friesians and 3 buffaloes exposed in the climatic chamber to cool (16 ºC, 50% relative humidity) and hot (32 ºC, 50% relative humidity) climates for 1 week each. ^{51}Cr-tagged red cell technique was used in determining red cell volume, which in turn was used with the hemocrit to deduce plasma and blood volumes. The animals were non-lactating females in the season experiment and females in the other experiments. Blood, plasma, and red cell volumes as well as the circulating plasma solids increased in Friesians from winter to summer. In buffaloes the vascular fluids increased insignificantly whereas the circulating plasma solids did not change. Hemoglobin decreased insignificantly in Friesians and significantly in buffaloes. In both species hemocrit did not change with season. The continuous exposure to high ambient temperature in the climatic chamber induced a greater heat stress. Beside the increase in vascular fluids, the hemoglobin and hemocrit decreased and the circulating plasma solids increased in both species. Sunlight and heat exposure caused hemoconcentration in Friesians and hemodilution in buffaloes. In Friesians blood and plasma volumes decreased and hemocrit increased whereas in buffaloes the opposite occurred. The circulating plasma solids increased in Friesians indicating tissue destruction. One Friesian female succumbed to sunstroke as post mortem examination revealed subcutaneous burns, brain membrane and spleen destruction, and intestinal hemorrhage. The data suggests that buffaloes are more heat tolerant than Friesians.

Kamal, T. H, O. Shehata, and I. M. Elbanna. 1972. Effect of heat and water restriction on water metabolism and body fluid compartments in farm animals. Pages 95-100 *in* Isotope studies on the physiology of domestic animals. International Atomic Energy Agency, Vienna, Austria.

Eight Ossimi male sheep, five Nubian male goats, 4 female Friesian cattle, and 4 male water buffaloes were maintained in the climatic chamber for 3 weeks at 18 ºC and 58% relative humidity, followed by 1 week outdoors, then by 3 weeks in the climatic chamber at 32 ºC and 36% relative humidity. Total body water and turnover rate were determine on the thirteenth day of each climatic condition, using titrated water. Extracellular fluid using thiosulphate was determined on the 13th and 20th day of each exposure period. Intracellular fluid was determined by difference. Feed and water were restricted for 12 hr daily during body water and water turnover rate determination; and during the other body fluids determination. Body fluid compartments were computed on dry body mass basis. At high temperature, total body water increased in buffaloes and sheep whereas in goats and Friesians it did not change. The values for goats, Friesians, sheep, and buffaloes were 1,290, 2,331, 1,239, and 1, 787 ml kg^{-1} dry body mass, respectively at 32 ºC. The water turnover rate increased with heat exposure in goats, sheep, Friesians, and buffaloes. The averages were 120, 181, 159, and 182 ml kg$^{0.82}$ daily respectively at 18 ºC, and 228, 321, 312, and 313 ml kg$^{0.82}$ daily, respectively at 32 ºC. The heat increased the extracellular fluid in sheep and Friesians, and increased it insignificantly in buffaloes and goats. At 18 ºC the averages for goats, Friesians, sheep, and buffaloes were 568, 452, 429, and 515-ml kg^{-1} dry body mass respectively, whereas at 32 ºC they were 603, 638, 688, and 879 ml kg^{-1} dry body mass daily respectively. At 32 ºC the intracellular fluid was significantly higher in sheep and buffaloes than at 18 ºC. The opposite was true in Friesians and goats. In spite of the fact that heat increased the water turnover rate in goats (90%) and Friesians (96%) more than in sheep (77%) and buffaloes (72%), the latter were more able to retain water in their bodies than the former in hot climates.

Kamau, J. M. 1988. Metabolism and evaporative heat loss in the dik-dik antelope (*Rhynchotragus kirki*). Comparative Biochemistry and Physiology 89A:567-574.

Metabolism and evaporative heat loss in 12 adult dik-dik antelope (*Rhynchotragus kirki*) were studied in a climatic chamber under laboratory conditions. The rate of oxygen consumption, respiratory frequency, evaporative water loss, heat balance, rectal and surface temperatures were determined at ambient temperatures ranging from 1 to 44 ºC. The thermal neutral zone was found to be between 24 and 35 ºC. Respiratory frequency ranged between 27 and 630 breaths min^{-1}. At ambient temperature of 44 ºC, 95% of heat produced by the dik-dik was lost via respiratory evaporation. Despite and increase in rectal temperatures, cutaneous evaporation did not increase. During panting, oxygen consumption increased in accordance with the expected Q_{10} effect, contrary to earlier findings. Measurements of circadian rhythm in oxygen consumption showed that the minimum (0.42 ml O_2 g^{-1} hr^{-1}) occurred at midnight while the maximum (0.78 ml O_2 g^{-1} hr^{-1}) occurred at midday. The 24 hr mean oxygen consumption was 0.61 ml O_2 g^{-1} hr^{-1}. These measurements suggest that in nature, determinants other than light may be responsible for triggering variations observed in oxygen consumption.

Kamau, J. M. and G. M. O. Maloiy. 1985. Thermoregulation and heat balance in the dik-dik antelope: a field and laboratory study. Comparative Biochemistry and Physiology 81A:335-340.

Experiments were conducted in the field to study the physiological responses of dik-dik (*Rhynchotragus kirki*) to direst solar radiation and shade. The results were compared to those obtained in the laboratory. The rate of metabolic heat production when animals were exposed either to the sun or the shade was identical. Dik-dik antelopes lost about 50% more heat evaporatively when exposed to the sun compared to the shade at an ambient temperature of 28 ºC in the field or 40 ºC in a climatic chamber. Heat storage in the laboratory at 40 ºC or at 28 ºC in the shade accounted for between 30 and 35% of the total heat production. The corresponding value in the sun was 55%. The net rate of heat gain under the sun was four times greater than under shade at 28 ºC or in the laboratory at 40 ºC. Behavioral mechanisms for avoidance of high insulation must constitute important adaptations that the dik-dik uses to avoid dehydration and dependence on drinking water in the natural environment.

Kay, R. N. B. 1997. Responses of African livestock and wild herbivores to drought. Journal of Arid Environments 37:683-694.

The ways in which herbivores regulate their energy and water balance under hot, dry conditions are briefly reviewed. Cattle account for about two-thirds of the biomass of domestic livestock in Africa, but their Eurasian origin means that their physiology and grazing behavior are not wholly adapted to the natural pastures and climate of Africa, especially when drought strikes. In general, most herbivores can withstand heat and water shortage quite well, provided conditions do not become extreme. However, malnutrition will inevitably develop as pasture productivity declines under drought and overgrazing. This will affect most seriously animals that cannot range far from water and that depend mainly on drought-susceptible grasses rather than on more resistant shrubs and trees.

Khan, M. S., P. K. Ghosh, and T. O. Sasidharan. 1978. Effect of acute water restriction on plasma proteins and on blood and urinary electrolytes in Barmer goats of the Rajasthan Desert. Journal of Agricultural Science 91:395-398.

The effect of 96 hr water deprivation on plasma proteins, blood and urinary electrolyte concentrations were studied in Barmer goats of the Rajasthan Desert. The total plasma proteins, particularly albumin, increased significantly by water deprivation. Plasma potassium concentrations remained unchanged. The urinary K/Na ratio increased considerably. There was a decrease in urinary sodium concentration after the fourth day of water deprivation.

Khan, M. S., T. O. Sasidharan, and P. K. Ghosh. 1979. Glomerular filtration rate and blood and urinary urea concentrations in Barmer goats of the Rajasthan Desert. Journal of Agricultural Science 93:247-248.

Glomerular filtration rate and blood and urinary urea concentrations in Barmer goats of the Rajasthan Desert were studied in goats receiving water ad libitum and goats with restricted access to water. Measurement of glomerular filtration rate and blood and urine urea concentrations was determined using metabolic cages. Water restricted animals did not show weight loss or animals with ad libitum water. Restricted water intake caused an increase in the urea-N concentration. There was no decrease in urinary urea-N concentration in water-restricted goats.

Glomerular filtration rate declined to 33% of its normal value in water restricted goats.

King, J. M. 1979. Game domestication for animal production in Kenya: field studies of the body water turnover of game and livestock. Journal of Agricultural Science 93:71-80.

Field studies were made of titrated water turnover, drinking water, and dietary water intake throughout the year, in 212 individuals of the following species: African buffalo (*Synerus caffer*), dromedary camel, zebu cow, eland (*Taruotragus oryx*), small East African goat, fringe-eared oryx (*Oryx beisa callotis*), and Dorper sheep. There were significant differences in the water consumed and water turnover between species and between seasons. Furthermore the species (or season) differences were also significantly different for each season (or species). The lowest turnover rates were found in oryx, then camel, sheep, goat, eland, cow, and buffalo, and then expressed in ml $L^{0.82}$ day^{-1}, which was the appropriate metabolic unit for these species. The restraints imposed by traditional African animal husbandry have drastically reduced the natural ability of eland to conserve body water but had much less effect on buffalo and oryx. The reason appears to be that eland is behaviorally adapted to a semi-arid environment, whereas a species like oryx is more physiologically adapted.

King, J. M., G. P. Kingaby, J. G. Colvin, and B. R. Heath. 1975. Seasonal variation in water turnover by oryx and eland on the Galana Game Ranch Research Project. East African Wildlife Journal 13:287-296.

Measurement of total body water and water turnover of oryx (*Oryx beisa*) and eland (*Taurotragus oryx*) were based on the single injection of dilution principal using titrated water. Under a daylight-grazing regime the water turnover varied from 24 to 98 ml kg^{-1} day^{-1} in oryx and 42 to 121 ml kg^{-1} day^{-1} in eland. This large seasonal variation was most highly correlated with heat load expressed as solar radiation or mean ambient temperature. Lack of correlation between water turnover and dry matter intake, and low correlation with dietary moisture may have been due to difficulties in measuring these parameters accurately. When preformed water was calculated by subtraction of drinking and metabolic water from total turnover, it was found to have a positive correlation with turnover rate and a negative correlation with water drunk. This high water turnover was not associated with high drinking requirements of other species. The relationship between climate, pasture, and water turnover, could be upset by changes in the activity of the animal from the normal day grazing pattern. The results obtained from the domestic game animals were used to explain how wild oryx and eland could exploit a hot, semi-arid environment without drinking. To achieve this, the wild animal must obtain most of its nutritional requirements between evening and morning, and its water requirements during the period of maximum relative humidity between midnight and dawn.

King, J. M., P. O. Nyamora, M. R. Stanley-Price, and B. R. Heath. 1978. Game domestication for animal production in Kenya: prediction of water intake from titrated water turnover. Journal of Agricultural Science 91:513-522.

Five male animals of each of the following species, zebu cattle, eland (*Taruotragus oryx*), small East African goat, fringe-eared oryx (*Oryx beisa callotis*), and Dorper sheep, were penned, and their water intake measured and metabolic water production estimated. The figures for water input were compared with simultaneous measurements of body water turnover by liquid scintillation counting of titrated water in plasma, following dioxane precipitation. It was found that the resultant regression was sufficiently linear with the intercept near zero to justify the use of a ratio to predict input from turnover. The titrated water turnover overestimated the water input by an amount approximately equal to the overestimate of body water pool by the titrated water space. Although there was a considerable amount of variation in individual ratios that could not be explained, there was no significant difference in the mean ratios between species.

King, J. M. and V. A. Finch. 1982. Value and limitations of using titrated water for predicting body composition and water intake in the African zebu. Pages 57-67 *in*

Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

The titrated water space gave a 10% overestimate of the total body water pool obtained by dissection and drying, using 12 Zebu steers. The decrease in percent body fat between a weight of 220 and 190 kg was significantly related to an increase in the percent body water pool. The percent body fat could be predicted from the percent titrated water space, but the approach was considered questionable, particularly outside the bounds of these trials. A comparison between water input from food and drink plus calculated metabolic water and titrated water turnover was made in 6 - 12 Zebu steers on 4 occasions, for 42 individual comparisons. There was a shortfall of 11% between input and turnover even after correction of the overestimate of the body water pool by tritium. The shortfall could be accounted for by respiratory water exchange, which was estimated to represent 10% of the total water input. Although the mean ratio of input: titrated water turnover was 0.96 ± 0.022, there were significant differences between individual ratios and experiments. The main reason for the difference was probably due to non-steady-state conditions during the periods of estimating water turnover. Errors in the prediction of total water input from titrated water turnover will be the rule rather than the exception for tropical herbivores in semi-arid areas where intermittent watering is practiced unless the experiment is very carefully designed.

Knox, K. L., J. G. Nagy, and R. D. Brown. 1969. Water turnover in mule deer. Journal of Wildlife Management 33:389-393.

Water turnover and kinetics were determined in 11 female mule deer (*Odocoileus hemionus*) ranging in weight from 18 to 42 kg using titrated water. The percent body water, turnover, half time, and flux of 9 deer maintained in non-confined captivity were 67%, 11% day^{-1}, 6.5 days, and 74 ml kg^{-1} day^{-1}, respectively. The values for the same parameters in 2 closely confined deer were: 70%, 31% day^{-1}, 2.3 days, and 216 ml kg^{-1} day^{-1}, respectively. Dry matter consumption was 65g kg$^{0.75}$ and water consumption was 140 g kg$^{0.75}$ in the non-confined deer. The data suggest that water kinetics in non-confined mule deer is not essentially different from other animals.

Kuhnen, G. 1997. Selective brain cooling reduces respiratory water loss during heat stress. Comparative Biochemistry and Physiology 118A:3:891-895.

Terrestrial mammals developed several mechanisms to reduce water loss to counteract water shortage. One avenue of water loss is the evaporative heat loss by sweating and panting, which increases with body temperature. Sweating and panting are activated by temperature signals of the body, whereby the brain is the most important site in generating temperature signals. Goats, like other artiodactyls, can cool their brains selectively below the temperature of the trunk core. The aim of the present study is to determine whether an inhibition of the selective brain cooling (SBC) mechanism will increase substantially the respiratory evaporative water loss during heat stress due to the higher brain temperature. The inhibition of SBC was performed by increasing brain temperature experimentally at the same rate as trunk temperature by means of extracorporeal heat exchangers. These experiments without SBC resulted in higher respiratory evaporative water loss compared to experiments with normal SBC. Eighteen experiments in two conscious goats had shown that at a trunk temperature of 40°C the respiratory water loss was reduced on average by 29 g/hr (0.7 l/day) due to the effect of SBC. This amount of water corresponds to about one third of the general water requirements. In conclusion, SBC substantially reduces the water loss in goats during heat stress and consequently improves survival chances during water shortage.

Lackey, M. N., E. B. Belknap, M. D. Salman, L. Tinguely, and L. W. Johnson. 1995. Urinary indices in llamas fed different diets. American Journal of Veterinary Research 56: 859-865. 1995.

Indices of renal function and damage were measured in 12 healthy male adult llamas (*Llama glama*) fed a diet of mixed alfalfa/grass hay (mixed hay) and water ad libitum. Using a collection bag fitted over the preputial area, urine samples were collected at 6, 12, and 24 hours. Serum samples were obtained concurrently to determine endogenous creatinine clearance (CL), total (TE) and fractional excretion (FE) of electrolytes (Na, K, Cl, P), electrolyte CL, urine and serum osmolality, urine enzyme activities (glutamyltransferase and N-acetyl - D-glucosaminidase) and urine protein concentration. Urine production was quantified. Three months later, 10 of the 12 llamas were fed a grass day diet and water ad libitum. Similar samples were obtained and similar measurements were made. Urine production was higher when the llamas were fed the mixed hay diet. Total urine volume for llamas fed mixed hay ranged from 628 to 1,760 ml day^{-1}, with a median of 1,307.5 ml day^{-1}, compared with a range of 620 to 1,380 ml day^{-1}, compared with a range of 620 to 1,380 ml day^{-1} and a median of 927.50 ml day^{-1} for llamas fed grass hay. Median urine osmolality was higher in llamas fed mixed hay (1,906 mOsm kg^{-1} of body mass, with a range of 1,163 to 2,044 mOsm kg^{-1}). Creatinine CL did not vary significantly over time for either diet. Median creatinine CL was higher for llamas fed mixed hay, compared with llamas fed grass hay 0.78 ml min^{-1} kg^{-1}, with a range of 0.20 to 1.83 ml min^{-1} kg^{-1} vs. 0.45 ml min^{-1} kg^{-1}, with a range of 0.13 to 3.17 ml min^{-1} kg^{-1}. Clearances for K and Cl varied significantly among the periods. However, median CL for Na and P did not vary over time for either diet. Overall values for these electrolytes in llamas fed mixed hay and grass hay diets were: NaCl 0.001 and 0.002 ml min^{-1} kg^{-1} and PCL, 0.0006 and 0.0004 ml min^{-1} kg^{-1}, respectively. The FE rates of K, Cl, and P did not vary significantly over time for either diet. Median respective FE for these electrolytes in the llamas fed mixed hay and grass hay include: FEk, 84.90 and 63.10%; FeCl, 0.85 and 1.30%; and PFe 0.10 and 0.10%. Fractional excretion of Na varied over time for both diets and could not be expresses accurately as an overall median. Median respective TE of electrolytes for llamas fed the mixed hay and grass hay diets were: TE Na, 0.007 and 0.03 mEq kg^{-1} hr^{-1}; TE Cl, 0.04 and 0.06 mEq kg^{-1} hr^{-1}; and TE P, 0.0002 and 0.00 mg kg^{-1} hr^{-1}; TE K varied significantly ($P<0.05$) over time. Urine N-acetyl-β-D-glucosaminidase activity was influenced by an interaction between diet and time. Median urine protein concentration was 26.0 mg dL^{-1}, with a range of 11.0 to 73.0 mg dL^{-1} for llamas fed mixed hay, and was 28.0 mg dL^{-1}, with a range of 16.0 to 124.0 mg dL^{-1} for llamas fed grass hay

Laden, F. S., L. Nehmadi and R. Yagil. 1987. Dehydration tolerance in Awassi fat-tailed sheep. Canadian Journal of Zoology 65:363-367.

Young Awassi sheep were subjected to 5-day periods of complete water restriction in metabolic cages. During water deprivation there were steady declines in food intake and faces and urine excretion. The blood hemocrit and urine and plasma osmolalities increased. There was a decline in blood and fecal water. As dehydration progressed, urinary excretion of osmotically active substances was greatly reduced. When drinking water was presented following 5 days of restriction it took 24 hr to replace water losses and for urine to be excreted. Fecal water did not return to normal within 24 hr. The Awassi sheep were capable of withstanding dehydration. The dehydrated sheep relied on fecal and renal water conservation to survive. Awassi sheep do not rapidly replenish water losses, nor do they rapidly reabsorb water, making their stay at water holes longer than goats.

Langman, V. A., G. M. O. Maloiy, K. Schmidt-Nielsen, and R. C. Schroter. 1978. Respiratory water and heat loss in camels subjected to dehydration. Journal of Physiology 278:P35.

Ambient air, rectal, and expired air temperatures and humidities under moderate heat load and dehydration were measured in 2 camels. Temperatures were measured using thermocouples and water content of expired air was measured with a dew point hygrometer attached to a heated face mask and air line. At night expired air tended towards ambient temperatures; during the day it tended towards rectal temperatures but was significantly lower. Expired air was always fully saturated. Camels recovered about 70 and 25% of the potential respiratory water loss during the night and day, respectively. Daytime respiratory heat loss was twice the rate at night. Heat and water exchange occurred within the turbinates of the nose as measured by temperature profiles.

Langman, V. A., G. M. O. Maloiy, K. Schmidt-Nielsen, and R. C. Schroter. 1979. Nasal heat exchange in the giraffe and other large mammals. Respiration Physiology 37:325-333.

The respiratory air of the giraffe (*Giraffa camelopardalis*) is exhaled at temperatures substantially below body core temperature. As a consequence, the water content of the exhaled air is reduced to levels below that in pulmonary air, resulting in substantial reductions in respiratory water loss. Measurements under outdoor conditions showed that at an ambient temperature of 24 ºC, the exhaled air was 7 ºC below body core temperature, and at ambient temperature of 17 ºC, the exhaled air was 13 ºC below body core temperature. The observations were extended to two additional species of wild (wildebeest [*Connochaetes taurinus*] and waterbuck [*Kobus ellipsiprumus*]) and four species of domestic ungulates (sheep, donkey, goat, and cow). All these animals exhaled air at temperatures below body core temperature. The average amount of water recovered due to cooling of the air during exhalation, calculated as percent of the water loss that would occur if air were exhaled at body core temperature, amounted to between 24 and 58%, the average value for the giraffe being 56%.

Lautier, J. K., T. V. Dailey and R. D. Brown. 1988. Effect of water restriction on feed intake of white-tailed deer. Journal of Wildlife Management, 52:602-606.

The effect of water restriction on feed intake of white-tailed deer was studied at Caesar Kleberg Wildlife Research Institute, Texas A&M University, Kingsville, Texas. Nine male white-tailed deer (*Odocoileus virginianus*) were held in pens and offered feed and water ad libitum for 3 - 4 days, and measured intake of both daily. We provided separate groups (3 x 3 balanced, simple crossover design) 33, 67, and 100% of ad libitum water intake for 4 days. Mean dry matter intake (DMI) (g $kg^{-0.75}$ body mass) for 3 - 4 days prerestriction was compared to each of the 4 days on restriction. Dry matter intake decreased ($P < 0.01$) for deer receiving 33% ad libitum water intake on days 3 and 4. One deer refused feed on day 4. There was a difference ($P< 0.05$) in mean DMI on day 3 between the group receiving 100% of ad libitum water and the group that received 33% of ad libitum water. Differences in DMI existed on day 4 among all 3 groups ($P<0.05$). The group receiving 33% of ad libitum water lost more weight than the other groups ($P < 0.05$). Because of lower than expected body water losses by the water-restricted animals, it appears that white-tailed deer possess some degree of physiological adaptation to dehydration. High daily maximum temperatures (36 ºC) may have exacerbated the effect of water restriction on DMI. Because of high temperatures and frequent summer droughts in southern Texas, the need for adequate water for white-tailed deer may be critical.

Longhurst, W. M., N. F. Baker, G. E. Connolly, and R. A. Fisk. 1970. Total body water and water turnover in sheep and deer. American Journal of Veterinary Research 31:673-677.

The total body water and body water turnover in Columbian black-tailed deer (*Odocoileus hemionus columbianus*) and domestic sheep were compared in winter and summer by testing with tritium oxide. There was a significant difference in water turnover in both species when data obtained in the winter were compared to those obtained in the summer. In addition, there was a significant difference in water turnover between the 2 species in winter and summer. Deer had a larger body water pool in relation to body mass than did sheep, but rate of body water turnover in deer was slower in winter and summer. The mean body water pools of sheep in winter and in summer were 53.3 and 46.0% of body mass. The water flux in sheep was 0.102 and 0.14 L/kg/day in winter and in summer, respectively. Comparable values in deer were 0.053 and 0.104 L kg^{-1} day^{-1}.

Macfarlane, W. V. 1965. Water metabolism in desert ruminants. Pages 191-199 *in* A. K. McIntyre and D. R. Curtis, editors, Studies in physiology. Springer-Verlag, New York, New York, USA.

Total body water, water turnover, and plasma volume were studied in camel, cattle, sheep, goats, and red kangaroos (*Marcopus rufus*) using thiocyanate and titrated water. Camels and cattle from hot arid regions had body water contents of 66 – 85% whereas cattle from cooler regions had body water contents of 68%. Plasma volume of animals from arid regions was approximately one third that of animals from cooler areas. Water turnover rates were also higher in animals from arid areas than in those from cooler regions. Interspecific and individual differences in these parameters are also discussed.

Macfarlane, W. V. and B. Howard. 1972. Comparative water and energy economy of wild and domestic mammals. Symposia of the Zoological Society of London 31:261-296.

Over 99% by number of the molecules present in a ruminant are water. Measurement of titrated water turnover provides ecophysiological information on the water metabolism of breeds, species or genera, compared in the field while exposed to the same environment. The powerful effects of solar radiation on water demand in the desert are integrated with those of air temperature and food supply by this approach. Water turnover is influenced by age, environmental temperature, food supply, density, lactation, and behavior. Yet the intrinsic rate at which each species uses water brings about the same rank order of water turnover among those species in different environments. This rank order for water turnover is closely correlated with the metabolic rate or oxygen turnover, which is high in some desert animals with high water turnover (eland [*Taurotragus oryx*], cattle, reindeer [*Rangifer tarandus*]), and low in other (camel, goat, oryx [*Oryx beisa*], musk ox [*Ovibos moschatus*]) which economize water. Other correlated variables are the rates of pulmocutaneous evaporation, and movement of water from gut to blood, which are rapid in animals with high rates of oxygen and water metabolism, low in others. Low rates of movement of water and energy through animals allow them longer survival in, and better adaptation to the desert. Sensitivity to vasopressin is high in desert mammals with low water turnover and low in those with high water demands. The recent distribution of mammals in arid areas shows anomalies of ecophysiology that could be explained if the functional evolution of some mammals took place in non-arid regions, followed by migration into the desert without modification of their functions. Others, evolved in the desert, remain there when high-rate animals perish.

Macfarlane, W. V., B. Howard, and B. D. Siebert. 1967. Water metabolism of merino and Leicester sheep grazing saltbush. Australian Journal of Agricultural Research 18:947-958.

Water metabolism of merino and Leicester sheep grazing saltbush were studied using titrated water. During late summer, Border Leicester wethers running with Merinos on a pure *Atriplex nummularia* stand turned over 10.6 to 17.5 L (mean = 13.7 L) of water daily, and diluted the sodium and potassium ingested to less than 1000 mOsm/L in the urine. Leicesters used 46% more water than Merinos as L day^{-1}, and 71% more as ml kg$^{0.82}$ day^{-1}. The two breeds produced similar urine concentrations. The sheep showed a wide variation in response and their individual water turnovers while feeding on *A. nummularia* and *A. vesicaria* ranged from 120 to 833 ml kg$^{0.82}$ day^{-1}. This suggests differences in functional types of adjustment to saltbush associations. On a *Danthonia* community Leicesters again turned over more water than Merinos but only about half as much water was required as on saltbush. Merinos grazing on *A. vesicaria* over 2 years maintained good condition with half the water intake of Merinos on *A. nummularia*, although the 2 species of saltbush had similar sodium and potassium contents. Total body water increased with water turnover rate on saltbush. Plasma sodium concentration was inversely related to water turnover, extracellular volume, and total body water on saltbush pastures. The content of extracellular sodium was, however, greatest in the sheep with the least sodium in the diet.

Macfarlane, W. V., B. Howard, and B. F. Good. 1974. Tracers in field measurements of water, milk, and thyroxine metabolism of tropical ruminants. Pages 1-23 *in* Tracer Techniques in Tropical Animal Production. International Atomic Energy Agency, Vienna, Austria.

Productive animals in the tropics may need to be adapted to hot-wet, or to alternating hot-wet and hot-dry environments. In both climates water is important for metabolism and for cooling. Isotopes are useful in measuring content and the turnover rate of water. Water content (^3H_2O) gives field information on body solids, fat, and protein content in relation to pasture and metabolic drain (as in starvation or lactation). Water turnover is closely linked with energy turnover. There is, among domestic stock, a hierarchy of turnover rates: a) high water turnover is found in tropical mammals such as buffalo, Banteng, cattle, eland (*Taurotragus oryx*), and pig; b) there are intermediate rates of water use in sheep, goats, and wildebeest (*Connocaetes taurinus*); c) low rates of energy and water turnover occur in dry-country animals like the camel or oryx (*Oryx beisa*). ^3H_2O turnover relates to food intake and as more water is taken more food is eaten. But the rank order of animals for water turnover remains similar in different conditions, with different food supplies. Production of wool or milk is associated with proportional water turnover, and has a genetic basis. Water turnover of lambs or calves is a direct function of milk intake and ^3H_2O yields both body solids increments, not necessarily associated with thermodynamic efficiency. Because metabolic rate is high in animals with high water turnover, it seemed likely that thyroxine would be related to those functions. Plasma bound iodine is (^{131} I or ^{125}I) very different in concentration in different genera and unrelated to rate functions. In the field, ruminant plasma bound iodine is high in summer, low in winter. Thyroxine secretion rate is low in large genera and high in small genera of ruminants. Secretin is higher in winter than summer. It is influenced greatly by food intake, rising with increasing food turnover and water turnover. Thyroxine seems to moderate intrinsic metabolic rates rather than set the rate of metabolism.

Macfarlane, W. V., B. Howard, and G. M. O. Maloiy. 1972. Titrated water in field studies of ruminant metabolism in Africa. Pages 83-93 *in* Isotope studies on the physiology of domestic animals, International Atomic Energy Agency, Vienna, Austria.

Titrated water was used to measure turnover of adult ruminants in Kenya. In the suckling young, water turnover by titrated water is a direct measure of milk intake. A hierarchy of ruminant ecophysiology of water and energy was measured in a number of environments in Kenya with groups of species grazing together. In the equatorial desert of Northern Frontier District, the rank order for titrated water turnover was: Boran cattle (347 mg kg$^{0.82}$ day^{-1}), twice the rate of Ogaden sheep (197 mg kg$^{0.82}$ day^{-1}), with Somali goats (185 mg kg$^{0.82}$ day^{-1}) and dromedaries (192 mg kg$^{0.82}$ day^{-1}) at the lowest turnover rates. On the hot-wet equatorial pastures, the rank order of sheep was Karakul, with the greatest turnover, then Merino, and Dorper sheep the lowest. Upland equatorial grasslands at Athi River, Boran cattle (224 mg kg$^{0.82}$ day^{-1}) grazed with eland (*Taurotragus oryx*) (213 mg kg$^{0.82}$ day^{-1}) and had almost identical rates of water use. Wildebeest (*Connocaetes taurinus*) (137 mg kg$^{0.82}$ day^{-1}) and hartebeest (*Alcelaphus buselaphus*) (116 mg kg$^{0.82}$ day^{-1}) turned over at half the rate of eland in the same environment. Thus eland appear to be cattle-like antelope, whereas the wildebeest and hartebeest were more like sheep in their rate of water use. The oryx (*Oryx beisa*) (70 mg kg$^{0.82}$ day^{-1}) is like a camel in turnover rate. In equatorial temperate upland pastures at Muguga, identical twin cattle agreed within 2% in the water turnover rates of twin pairs of cattle grazing together. Domestic cattle *s* types of twin used 16-38% more water than Zebu cattle. The identical twin functions indicate a close genetic control of the rate of water use on a given food type. Domestic species grazing the lush grasses showed a rank order of water like that found in the Northern Frontier District. Domestic cattle used more water (338 mg kg$^{0.82}$ day^{-1}) than Zebu cattle (284 mg kg$^{0.82}$ day^{-1}). The rate of use by cattle was twice that of Mosai sheep (195 mg kg$^{0.82}$ day^{-1}). Somali goats (137 mg kg$^{0.82}$ day^{-1}) used the least water in this environment. The Somali donkey (314 mg kg$^{0.82}$ day^{-1}) had a water use rate between those of the cattle species. Therefore similar hierarchies were maintained in different environments.

Macfarlane, W. V., B. Howard, and R. J. H. Morris. 1966. Water metabolism of merino sheep shorn during summer. Australian Journal of Agricultural Research 17:219-225.

Ten merino wethers in the dry subtropical region of "Gilruth Plains", Queensland, Australia were shorn in November during a period of sunshine with maximum temperatures between 36 and 38 ºC. The content, distribution, and turnover of water were estimated using titrated water before and after shearing. There was no significant change in total body water but the thiocyanate space increased by 12%, the plasma volume by 17%, and the plasma proteins were diluted by 17% after shearing. Water turnover rose from 81.5 to 159ml kg^{-1} day^{-1}. There was a correlation (r = 0.68) between the increase in respiratory rate that took place when the sheep were standing in the sun and the increase in water turnover during the same period. An average increment of 1,550 kcal day^{-1} in heat load from insulation occurred as a result of the removal of fleece during exposure to summer sun. The greater water turnover from evaporative cooling was associated with increased extracellular fluid space.

Macfarlane, W. V., B. Howard, H. Haines, P. J. Kennedy, and C. M. Sharpe. 1971. Hierarchy of water and energy turnover of desert mammals. Nature 234:483-484.

The uninhibited intake of food and water by cattle, sheep, goats, camel, eland (*Taurotragus oryx*), buffalo (*Bubalus bubalis*), wildebeest (*Connochaetes gnou*), kongoni (*Alcelaphus buselaphus*), oryx (*Oryx beisa*), moose (*Alces alces*), reindeer (*Rangifer tarandus*), and musk oxen (*Ovibos moschatus*) were measured. Buffalo had the highest water turnover, then cattle. In summer, the highest water turnover rates occurred in cattle, followed by sheep, then goats, and camels the least. Of the antelope, eland and zebu cattle were approximately equal in water turnover, while kongoni and wildebeest are comparable with sheep, at half the rate of eland, and an oryx used water at a lower rate than camels. Of the arctic species, reindeer had water turnover rates as high as cattle, the moose was slightly lower than reindeer, but twice that of sheep and goats, while the musk oxen had water turn over rates as low as camels. The metabolic rate of bovids follow the same rank order as water turnover.

Macfarlane, W. V. and B. D. Siebert. 1967. Hydration and dehydration of desert camels. Australian Journal of Experimental Biology 45:29 (abstract).

During winter, water turnover of camels is low, at 37 to 40 ml kg^{-1} day^{-1}, and this rises during the summer to 70 to 90 ml kg^{-1} day^{-1}. Because of the fat deposit in the hump, the body water content rarely rises above 75% of body mass. Without water in the summer, the camel loses weight at 2% day^{-1} and persists in functional order for 10 to 15 days. During slow dehydration the packed cell volume does not change, although the extracellular and plasma volume decreases by 15 to 20%. At more rapid rates of dehydration (2.5% day^{-1}) greater extracellular loss occurs, but there is deferential sparing of plasma volume and a high plasma albumin concentration is retained, while gut and cell water is drawn upon. Urine flow reaches 1 - 2 ml/min and vasopressin (0.1 mμ kg^{-1}) increases potassium and water excretion. Glomerular filtration falls to one-quarter normal the normal rate and urine reaches 3.1 osm L^{-1}. Fecal water is reduced to 40% of fecal weight. On rehydration the camel takes in 54% to 66% of the weight lost within 20 min. There is a reduction in urine flow to 0.2 ml min^{-1} and reduction in sodium and potassium excretion. Packed cell volume increases for some hours then decreases, the slow titrated water uptake from the gut does not reach equilibrium for nearly 18 hours. After one day urine flow as electrolytes are removed from the plasma to the gut. At these higher rates of urine flow, the camel responds to 1 μU kg^{-1} vasopressin by reduction in urine flow.

Macfarlane, W. V, C. H. S. Doling, and B. Howard. 1966. Distribution and turnover of water in Merino sheep selected for high wool production. Australian Journal of Agricultural Research 17:491-502.

Estimates of the distribution of body water and the rate of water turnover were made on Merino females in southwestern Queensland, Australia during January and November. January measurements were made while pasture conditions were lush green following good rains and November measurements were made when pastures were dry following several months with low rainfall. Females were selected from a flock that had been selectively bred from high wool production and from a control flock where all animals were allowed to breed. Plasma volume, extracellular volume, total body water, plasma protein, and water turnover per day were estimated. Body fluid compartments, as ml/kg body mass, were greater during the wet than during the dry period. Plasma volumes were significantly greater in January than in November by 10.3% for the selected females and 18.2% for control females. Estimates of extracellular volume showed a similar difference between months (15.4% for selected females and 17.4% for control females). January measurements of total body water exceeded November observations by 9.6% in selected females and 11.2% in control females. The values for plasma volume, extracellular volume, and total body water did not differ between selected females and control females. The daily turnover rate of water in ml kg^{-1} body mass was greater in January than in November by 30% for selected sheep and 51.1% for control sheep.

Macfarlane, W. V., R. J. H. Morris and B. Howard. 1958. Heat and water in tropical Merino sheep. Australian Journal of Agricultural Research 9:217-228.

The relation between environment and the water intake and output of young Merino sheep living in hot dry tropics was studied for 3 years in Julia Creek, Australia. Long (3 cm) wool insulates sheep from hot summer temperatures. The respiratory rates of sheep shorn of wool during the summer were more than twice those of unshorn sheep standing in the sun. Evaporative cooling, by panting, increases water demand, and in summer sheep drank an average of 12 times as much water as in winter, when they drank 7.3 ml kg^{-1} day^{-1}. Water intake was closely related to respiratory rate. Urine output was lower in summer than in winter.

Macfarlane, W. V., R. J. H. Morris, B. Howard, J. McDonald and O. E. Budtz-Olsen. 1961. Water and electrolyte changes in tropical Merino sheep exposed to dehydration during summer. Australian Journal of Agricultural Research 12:889-912.

During 3 summers field studies were made of Merino wethers deprived of water while exposed to sun and to maximum air temperatures ranging from 29 – 42 ºC at Julia Creek, Australia. Evaporative cooling determined the rate and extent of water and electrolyte changes and produced a different pattern each year. Control of body temperature failed when 31% of body mass was lost by the end of 10 days without water. In hotter weather 5 days without water caused a 25% loss of body mass and in some sheep irreversible circulatory failure. In the course of dehydration, after initial increase, the plasma and extracellular volume decreased up to 45% while concentrations of hemoglobin and plasma protein increased by 60%. In the plasma, potassium and sodium concentration increased less than that of hemoglobin. When 25% or more of weight was lost plasma urea concentration rose to 136 mg 100 ml^{-1}. Plasma osmolarity in some sheep reached 490 mOsm L^{-1} after 10 days. Urine volume fell after 2 days without water, and in a hot season less than 100 ml day^{-1} was passed on the fourth or subsequent days. Concentrations increased over the first 4 – 5 days, reaching a maximum of 3.8 mOsm L^{-1}, then declined. Between half and two-thirds of the osmolarity was accountable to sodium and potassium salts. In rapid dehydration, more sodium was excreted than potassium. There was reduced sodium excretion when water was ingested after dehydration. Renal function studies in females indicated that filtration, renal plasma flow, and glucose reabsorption was reduced to half after 5 days without water in the heat. The chance of survival in dehydration appears to be increased by low rates of water loss in the first 3 days, together with high sodium and low potassium excretion. A full rumen, containing water up to 13% of body mass, could provide all the extracellular fluid loss. More than half of the weight loss appears, however, to come from intracellular sources. Extracellular fluid was drawn upon to a greater extent when the rate of dehydration was rapid, than in the cooler periods of slow weight loss. Survival in the sun without water depends on insulation, water conservation, water reserves in rumen and extracellular fluid, the ability to adjust electrolyte concentrations, and the ability to maintain circulation with lowered plasma volume.

Macfarlane, W. V., R. J. H. Morris, B. Howard and O. E. Budtz-Olsen. 1959. Extracellular fluid distribution in tropical Marino sheep. Australian Journal of Agricultural Research 10:269-286.

Merino females and wethers maturing from 12 to 53 months of age were studied for 3.5 years at Julia Creek, Australia during summer and winter. Measurements were made of plasma volume and extracellular volume, plasma proteins, hemoglobin, hemocrit, and plasma electrolytes via blood extractions. The range of normal values for these parameters in healthy sheep varied widely. Large changes took place in the fluid volumes during the period of investigation; the changes appeared to be independent of seasons but to a great extent determined by nutrition. Poorly nourished sheep as a whole had increased extracellular fluid space, and the space shrank again on improved pasture. Age and sex did not influence the fluid volumes. Lactation was associated with an increase in fluid spaces, and year feeding with a decrease. Non-tropical sheep introduced from 30º S latitude during winter had similar fluid volumes to the tropical sheep when investigated 2 months after their arrival. Tropical Merinos at any age or season had larger plasma volumes than sheep kept in laboratory pens in Brisbane or in Melbourne, Australia.

Maloiy, G. M. O. 1970. Water economy of the Somali donkey. American Journal of Physiology 219:1522-1527.

Water balance, food intake, volume, and concentration of urine and changes in body mass were examined in the 7 Somali donkeys subjected to heat stress and dehydration while held in metabolic cages. The effects of an ambient temperature of 22 ºC or changes between 22 and 40 ºC at 12-hr intervals and a level of dehydration causing 15% loss of body mass at each of these temperatures on food intake and digestion were investigated. Dehydration at each environmental temperature depressed food intake and increased apparent digestibility of dry matter, but a periodic heat load without dehydration had no effect on either parameter. The animal's appetite failed altogether when 20 – 22% of its initial body mass had been lost. Fecal and evaporative routes were the main avenues of water loss in all experimental conditions. Evaporative water loss was reduced by 65 and 52%, respectively, when animals were dehydrated at 22 and 40 ºC. The donkey can survive a loss of water corresponding to 30% of its original body mass even at ambient temperature of 40 ºC, and can drink in 2 – 5 min enough water (24 – 30 L) to restore its deficit. Even when water was freely available, urine volume was low (0.7 – 1.2 L day^{-1}). The donkey's kidney was not able to excrete a highly concentrated urine; 1,440 – 1,545 mOsm kg^{-1} water was the maximum osmolality, with urea contributing 300 – 410 mM. When the donkey was offered various concentrations of NaCl solution as its sole source of drinking water, the maximum level accepted by the animal was 0.75 – 1.00% NaCl.

Maloiy, G. M. O. 1971. Temperature regulation in the Somali donkey (*Equus asinus*). Comparative Biochemistry and Physiology 39A:403-412.

In controlled laboratory experiments the metabolic rate, body temperature, respiratory, sweat, and heart rates were measured in adult Somali donkeys. At high ambient temperatures (40 – 50 ºC) the sweating rate rose to 145 g water m$^{2-1}$ hr^{-1} and the respiratory rate to approximately 130 min^{-1}. In cool conditions (10 ºC) the metabolic rate rose to approximately 5 ml oxygen kg^{-1} min^{-1} from a value in thermal neutrality (22 – 32 ºC) of 4 ml kg^{-1} min^{-1}. Between ambient temperatures of 5 and 50 ºC the rectal temperature ranged from 35 to 39 $^{-1}$C.

Maloiy, G. M. O. 1972. Renal salt and water excretion in the camel (*Camelus dromedarius*). Symposia of the Zoological Society of London 31:243-259.

A study of the glomerular filtration rate and renal sale and water excretion was studied in the camel under a variety of controlled experimental conditions. Changes in urine flow and concentration and insulin clearance during dehydration and salt loading were measured. Slow dehydration at 0.8% day^{-1} weight loss, involving a gradual reduction in daily water intake until body mass decreased by 20 - 22%, caused a 57% decrease in urine flow and a 30% reduction in the glomerular filtration rate. Salt loading increased glomerular filtration rate and urine flow by about 52 and 103%, respectively. In dehydrated and in salt loaded camels, respectively 99.8% and 99.2% of the water filtered at the glomerulus was reabsorbed. The observed changes in urine flow appeared to be brought about by alteration in glomerular filtration rate and renal tubular water reabsorption. Urine and plasma osmolality increased during salt loading and dehydration as did the osmolal U/P ratio and the concentration s of both urinary and plasma electrolytes and urea. The most concentrated urine excreted by the camel was 3,200 mOsm kg^{-1} with urea contributing 900 – 1,400 mOsm L^{-1}. The overall water expenditure of the camel was investigated in normally hydrated and dehydrated animals exposed to two ambient temperatures in a climatic chamber. The donkey in the same environment consumed and excreted more water and urine, respectively than the camel. The response of the camel to drinking NaCl solutions of various concentrations as it's only source of drinking water was also investigated and it was concluded that the 1-humped camel could drink 3.5 - 5.5% NaCl solutions that were more concentrated than sea water.

Maloiy, G. M. O. 1973a. The water metabolism of a small East African antelope: the dik-dik. Proceedings of the Royal Society of London 184:167-178.

In controlled laboratory experiments, rectal temperature, cutaneous moisture evaporation, and respiratory rate were studied in the dik-dik (*Rhynchotragus kirkii*). The water balance of the dik-dik was investigated when the antelope were either fully hydrated or dehydrated at the environmental temperature of 22 ºC or at temperatures alternating between 22 ºC and 40 ºC at 12 hr intervals. Fecal, urinary, and evaporative water losses were all reduced by varying degrees during dehydration at 22 ºC and 22 to 40 - ºC. The highest urine osmolality recorded was 4,318 ± 105 mOsm kg^{-1} water that occurred when the antelopes were severely dehydrated. At air temperatures (40 to 45 ºC) cutaneous evaporation measured with a non-ventilated sweat capsule was 19 g water m$^{2-1}$ hr^{-1} and the respiratory rate over 360 min^{-1}. Thus the respiratory tract seems to be the major avenue for dissipating excess heat in dik-dik exposed to thermal stress. Injection of adrenaline, intravenously, stimulated sweat discharges similar to those observed in the small gazelles, sheep, and goats. The low-water exchange and an efficient kidney helps explain the ability of this small antelope to inhabit hot arid areas.

Maloiy, G. M. O. 1973b. Water metabolism of East African ruminants in arid and semi-arid regions. Journal of Animal Breeding and Genetics 90:219-228.

This paper reviews some aspects of the water metabolism of ruminants in East Africa, with special attention to the importance of water in limiting animal production and management in hot arid or semi-arid regions. Topics related to thermal and metabolic adaptations of some East African Bovidae to heat and aridity including water requirements, water turnover rates, effects of water restriction and heat loads on food intake, and water economy are reviewed in sheep, goats, camels, Thomson's gazelle (*Gazella thomsonii*), impala (*Aepyceros melampus*), Grant's gazelle (*Gazella granti*), Hartebeest (*Alcelaphus buselaphus*), oryx (*Oryx besia*), wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus defassa*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), Zebu steer, and Hereford steer.

Maloiy, G. M. O., B. M. Rugangazi, and E. T. Clemens. 1988. Physiology of the dik-dik antelope. Comparative Biochemistry and Physiology 91A: 1-8.

The overall life history and physiology of the dik-dik antelope (*Rhynchotragus kirkii*) are reviewed. Aspects of the digestive physiology, physiological aspects of water metabolism, behavioral adaptations for thermoregulation, and reproduction are discussed.

Maloiy, G.M.O., B. M. Rugangazi, and E. T. Clemens. 2000. Nitrogen metabolism and renal function in the dik-dik antelope (*Rhynchotragus kirkii*). Small Ruminant Research 37:243-248.

Nitrogen metabolism and kidney function of the dik-dik antelope (*Rhynchotragus kirkii*) were studied under a range of controlled, experimental conditions and diets. Dik-dik antelope remained in nitrogen balance even when fed a diet low in protein and high in fiber. When fed a diet high in protein (20%) and water ad libitum, 55.3% of the urea altered by the kidney was reabsorbed. Limiting water intake increased urea reabsorption to 77.2%. The U/P urea concentrations were maintained at similar ratios on all diets, as well as during dehydration and solute loading. Minimum endogenous nitrogen excreted was 74 mg kg $^{0.75}$ day^{-1}. Dehydration (water deprivation) and solute loading (intraruminal infusion of 0.25 M NaCl) had varying effects on nitrogen metabolism. It is concluded that the metabolic nitrogen economy of the dik-dik antelope is qualitatively similar to that of other domestic and wild ruminants.

Maloiy, G. M. O. and C. D. H. Boarer. 1971. Response of the Somali donkey to dehydration: hematological changes. American Journal of Physiology 221:37-41.

The effects of dehydration and rehydration on blood plasma osmolality, sodium, chloride, and hemoglobin concentration, packed cell volume (PCV), red blood cells (RBC), and plasma proteins in Somali donkeys and Zebu steer were studied under varying temperature regimes (22 – 40 C) and under ad libitum and water restriction in the laboratory. Blood collection and titrated water methods were used. Increases in plasma osmolality, sodium, chloride, hemoglobin concentration, PCV, RBC, and plasma proteins were observed in dehydrated animals. Neither dehydration nor rehydration had any observable effect on mean cell hemoglobin, which remained at 22 pg (10^{-12} g) and 16 pg for the donkey and the Zebu steer, respectively, under all experimental conditions. In the donkey, decreases in mean cell volume and in intracellular and extracellular water were observed. Plasma volume was also reduced from a mean control value of 9.6 to 6.2 L. Most of the blood parameters were restored to their normal values within day after rehydration.

Maloiy, G. M. O. and C. R. Taylor. 1971. Water requirements of African goats and haired-sheep. Journal of Agricultural Science 77:203-208.

A number of species of desert-dwelling ungulates (e.g., Grant's gazelle and oryx) can apparently survive desert conditions without drinking. We were interested in finding out whether goats and sheep herded in the arid Northern Frontier Region of Kenya utilized the same physiological strategies for reducing water requirements as the wild ungulates. Using simulated desert conditions (12 hr day^{-1} at 22 ºC alternating with 12 hr day^{-1} at 40 ºC) in metabolic cages we found that both goats and sheep used water amounting to 8% of their body mass per day when water was available ad libitum; and this was reduced to about 4% of body mass when water intake was restricted. Evaporation was the major avenue of water loss under all experimental conditions. It was reduced from over 6% of body mass per day to about 3% in the simulated desert by restricting water intake. Restricting water intake had no effect on the temperature regulation of goats and sheep as had been observed in the wild desert-dwelling ungulates. It would appear that African goats and haired-sheep lack physiological mechanisms and are not free to utilize the behavioral mechanisms involved in freeing wild desert-dwelling ungulates for their dependence on drinking water.

Maloiy, G. M. O., C. R. Taylor and E. T. Clemens. 1978. A comparison of gastrointestinal water content and osmolality in East African herbivores during hydration and dehydration. Journal of Agricultural Science 91:249-254.

Gastrointestinal water content and osmolality were determined in camel, sheep, goats, Zebu, Hereford cattle and donkeys during hydration and dehydration by removing the intestinal tract. The digesta water in the foregut was similar for all hydrated animals, whereas the water content of the distal colon showed more variation with animals that produce in the form of pellets had lower colon water content. During dehydration only goats showed a reduction in foregut water content. During dehydration, donkeys were able to reduce the water content in the distal colon by 10%, followed by camels with a reduction of 6.8%, sheep, Zebu, and Hereford cattle exhibited reductions of 3 – 4%. Osmotic concentrations were higher in dehydrated animals than in hydrated animals.

Maloiy, G. M. O. and D. Hopcraft. 1971. Thermoregulation and water relations of two East African antelopes: the hartebeest and impala. Comparative Biochemistry and Physiology 38A: 525-534.

In controlled laboratory experiments rectal temperature, cutaneous moisture evaporation and breathing rate were studied in the hartebeest (*Alcelaphus buselaphus*) and impala antelope (*Aepyceros melampus*). At the high air temperatures (40 - 50 ºC), the sweating rate rose to 60 g water $m^{2-1}hr^{-1}$ and the respiratory rate to over 200 min^{-1} in both species. The water balance of the 2 species was investigated when the antelope were either fully hydrated or dehydrated at the environmental temperatures of 22 ºC or alteration between 22 and 40 ºC at 12-hr intervals. The total body water was estimated in 2 hartebeest antelope that were allowed to graze freely on the dry pastures of the Athi River Plains.

Maloiy, G. M. O. and E. T. Clemens. 1980. Colonic absorption and secretion of electrolytes as seen in five species of East African herbivorous mammals. Comparative Biochemistry and Physiology 67A:21-25.

Colonic absorption and secretion of electrolytes was studied in camels, zebu cattle, sheep, goats, and donkeys. The camel, sheep, goat, and donkey were equally efficient in recovering fluids from colonic contents, zebu cattle were least efficient. Compared to other species, Zebu cattle demonstrated a reduced sodium and water absorption, and net chloride secretion. Volatile fatty acid absorption was most evident in the colon of zebu cattle and the donkey. With the exception of the potassium flux, the camel, sheep, and goat demonstrated similar patterns of colonic electrolyte movement.

Maloiy, G. M. O., R. N. B. Kay, and E. D. Goodall. 1970. Digestion and nitrogen metabolism in sheep and red deer given large or small amounts of water and protein. British Journal of Nutrition 24:843-855.

The interaction between nitrogen and water intake was studied in 2 female sheep and 2 red deer (*Cervus elaphus*). They were given pelleted diets, at maintenance level, containing equal amounts. Nearly three-quarters of the nitrogen of the high-nitrogen rations but less than half of that of the low-nitrogen rations was excreted in the urine. Restriction of water intake reduced urinary nitrogen excretion by only about 1 g daily, mainly as a result of decreases in the excretion of urea and ammonia, but did not affect excretion of nitrogen in the feces. The urinary excretions of creatinine, creatine, hippuric acid, uric acid, and allantoin were also examined. The excretion of creatinine was not related to either nitrogen or water intake. The excretion of uric acid and of allantoin was greater in sheep than in the deer. The concentrations of urea in the plasma and of ammonia in the rumen fluid were measured before and after feeding. The plasma urea value was related to dietary nitrogen intake and was higher on the low-water than on the high-water regime. The rumen ammonia value also was related to the nitrogen intake but, while it generally increased after feeding when the high-nitrogen diet was given, it fell almost to zero 2 hr after feeding when the low-nitrogen diet was given. The sheep digested dry matter, cellulose, and nitrogen a little more fully than the deer. The high-water regime slightly increased the digestibility of dry matter and cellulose but did not affect the digestibility of nitrogen.

Maloiy, G. M. O., W. V. Macfarlane, and A. Shkolnik. 1979. Mammalian herbivores. Pages 185-209 *in* G. M. O Maloiy, editor. Comparative physiology of osmoregulation in animals. Volume 2. Academic Press, London, United Kingdom.

This review covers osmoregulation in mammalian herbivores and includes discussion of diffusion, secretion, and cell osmoregulation. Water balance, electrolyte balance, milk and osmotic balance, and mineral deficiency are reviewed as they pertain to maintenance of water balance by mammalian herbivores.

Maltz, E. and A. Shkolnik. 1980. Milk production in the desert: lactation and water economy in the black Bedouin goat. Physiological Zoology 53:12-18.

The black Bedouin goats that are herded in the extreme deserts of the Middle East are of small body size (16 - 26 kg). Even when lactating they drink only once every 2 days and can therefore graze far away from the widely spaced watering points. The water economy of the lactating Bedouin goats was studied under laboratory conditions (30 ºC, 30% relative humidity). Maximum milk yield was 61 - 87 g kg^{-1} day^{-1}; the volume of water consumed by lactating goats (158 ml kg^{-1} day^{-1}) was 3X the volume consumed before gestation. The rate of water turnover of the lactating goats (210 ml water kg^{-1} day^{-1}) was double that as nonlactating females. The ability of the goats to withstand 2 days of water deprivation without the milk yield being affected is attributed to very high body water content, amounting to 77 - 85% of the body mass. Following dehydration, when given free access to water, the goats at once replenish their entire water loss. Blood plasma volume was 9% of body mass in fully hydrated goats. During dehydration the blood plasma volume decreased in proportion to the decrease in total body fluids. Repeated periods of water deprivation had no effect on the ability to resume full milk production.

Maltz, E., N. Silanikove, and A. Shkolnik. 1981. Renal performance in relation to water and nitrogen metabolism in Bedouin goats during lactation. Comparative Biochemistry and Physiology 70A:145-147.

Renal performance in relation to water and nitrogen metabolism in Bedouin goats during lactation were studied in the laboratory under conditions of 25 ºC and 61% relative humidity. Water turnover rates were determined using titrated water and urea kinetics were assessed using ^{14}C labeled urea. Black Bedouin goats at 4 – 5 months post partum produce daily in the laboratory 50 g milk kg^{-1} body mass. Similar yields were recorded at mid-summer in goats herded in the desert where food is meager, low in protein and water is scarce. Urine concentration in lactating goats was higher than in goats before gestation but urine urea concentration was only a third that in non-lactating goats. The increase in urine volume in the lactating goats was less pronounced than the increase in drinking and water turnover rates or in food consumption. Daily renal absorption of urea in lactating goats amounted to 588 mmol compared to only 361 mmol in non-lactating goats. Urea entry rate in lactating goats was 65% higher than in non-lactating goats, 748.6 mmol urea were recycled daily in lactating goats compared to only 227 mmol in non-lactating goats. The role of the kidney plays in economizing both water and nitrogen metabolism in goats lactating in the desert is assessed and discussed.

Maltz, E, K. Olsson, S. M. Glick, F. Fyhrquist, and N. Silanikove. 1984. Homeostatic responses to water deprivation or hemorrhage in lactating and non-lactating Bedouin goats. Comparative Biochemistry and Physiology, 77A:79-84.

Three lactating and 3 non-lactating black Bedouin goats were subjected to 4 days of water deprivation or to hemorrhage, at the research zoo of Tel Aviv University. Four days of water deprivation caused body mass losses of 32 and 23% and plasma volume losses of 30 and 34% in lactating and non-lactating goats, respectively. Plasma osmolality increased 17 and 15% in lactating and non-lactating goats. Plasma arginine vasopressin concentration rose from about 5 pg ml^{-1} to a mean of 36 pg ml^{-1}. Plasma rennin activity increased from about 0.7 ng ml^{-1} hr^{-1} to a mean of 3.45 ng ml^{-1} hr^{-1} in lactating and to 3.15 ng ml^{-1} hr^{-1} in non-lactating goats. At 4.5 hr post-rehydration plasma osmolality and plasma vasopressin concentration were back to normal in non-lactating, but still elevated in lactating goats. Plasma rennin activity increased after rehydration. Rapid blood volume loss of 21 - 28% increased plasma vasopressin concentration to 16 - 35 pg/ml in non-lactating, but still elevated in lactating goats. Plasma rennin activity increased after rehydration. Rapid blood volume loss of 21 - 28% increased plasma vasopressin concentration to 16

- 35 pg ml^{-1} in non-lactating and to 70 or > 500 pg ml^{-1} in lactating goats. It is concluded that black Bedouin goats are well adapted to endure severe dehydration and rapid rehydration, but that they (especially lactating animals) react strongly to rapid volume depletion.

Mitchell, D., S. K. Maloney, C. Jessen, H. P. Laburn, P. R. Kamerman, G. Mitchell, and A. Fuller. 2002. Adaptive heterothermy and selective brain cooling in arid-zone mammals. Comparative Biochemistry and Physiology 131B:571-85.

Adaptive heterothermy and selective brain cooling are regarded as important thermal adaptations of large arid-zone mammals. Adaptive heterothermy, a process that reduces evaporation by storing body heat, ought to be enhanced by ambient heat load and by water deficit, but most mammals studied fail to show at least one of those attributes. Selective brain cooling, the reduction of brain temperature below arterial blood temperature, is most evident in artiodactyls, which possess a carotid rete, and traditionally has been considered to protect the brain during hyperthermia. The development of miniature ambulatory data loggers for recording body temperature allows the temperatures of free-living wild mammals to be measured in their natural habitats. All the African ungulates studied so far, in their natural habitats, do not exhibit adaptive heterothermy. They have low-amplitude nychthemeral rhythms of temperature, with mean body temperature over the night exceeding that over the day. Those with carotid retes (black wildebeest [*Connocaetes taurinus*], springbok [*Antidorcas marsupialis*], eland [*Taurotragus oryx*]) employ selective brain cooling but zebra, without a rete, do not. None of the rete ungulates, however, seems to employ selective brain cooling to prevent the brain overheating during exertional hyperthermia. Rather, they use it at rest, under moderate heat load, we believe in order to switch body heat loss from evaporative to non-evaporative routes.

Mittal, S. B. 1980. Dairy development and seasonal variation in the quality of milk in the arid zone of western Rajasthan. Pages 381-387 *in* H. S. Mann, editor, Arid zone research and development. Scientific Publishers, Jodhpur, India.

An investigation of the seasonal effect on the fat and non-fat solids contents of milk in western Rajasthan. It was found that the fat and non-fat solids contents tended to decline during summer and gradually increased through the monsoon season. The contents were maximum in the winter. It was concluded that the combined effect of environmental temperature, humidity, and feed seems to be the cause for the variation in the milk fat and non-fat solids contents.

Mohammed A. and A. Al-hozab. 2004. Effect of water deprivation and season on feed intake, body weight and thermoregulation in Awassi and Najdi sheep breeds in Saudi Arabia. Journal of Arid Environments 59:71-84.

Studies were conducted to compare responses to water deprivation in two local sheep breeds of Saudi Arabia, Awassi and Najdi, during different seasons. During water deprivation, body weight was significantly reduced by 11% during winter in both breeds, while it decreased 13.3% and 15.3% in Awassi and Najdi sheep in spring, and the corresponding values with reduction for summer were 18% and 21.5%. The decline in feed intake as a result of dehydration was highest in summer (96.5%) followed by spring (75%) and winter (62%) in both breeds. Water deprivation reduced respiration rate during winter and spring, and increased rectal temperature during spring and summer. Sweating rate was reduced in water-deprived sheep during summer and Awassi breed maintained lower sweating activity. Both breeds were able to consume a volume of water within 15 min following rehydration, which was amounting to 18.9%, 13.8% and 9.8% of their dehydrated body weights in summer, spring and winter, respectively. The lower rate of body weight loss and the maintenance of lower sweating activity during dehydration of Awassi indicated better ability of water conservation compared to Najdi breed. It was concluded that Awassi sheep possess better capability of withstanding water deprivation than Najdi sheep particularly when it was coupled with higher environmental temperature.

Mohamed, S. M., B. H. Ali and T. Hassan. 1988. Some effects of water deprivation on dorcas gazelle (*Gazella dorcas*) in the Sudan. Comparative Biochemistry and Physiology 90A:225-228.

The effects of water deprivation on dorcas gazelle (*Gazella dorcas*) were studied in captive animals at the Khartoum Zoo, Sudan in May 1986. Animals were held in unshaded cages and the effects of dehydration for 10 days and subsequent rehydration for 2 days on some physiological and biochemical parameters were studied in the Dorcas gazelle. At the end of the 10 days of dehydration, feed intake and body mass were decreased by 42 and 29% of the control values, respectively. Rehydration restored most of the loss in feed intake and body mass. Dehydration decreased the water content in the feces of the gazelles by 41%. Rehydration restored 36% of the lost fecal water. Urine volume in dehydrated animals decreased by 66%, an effect that was readily reversed by rehydration. Blood hemoglobin of dehydrated gazelles decreased by 22% but this effect was not reversed by rehydration for 2 days. Dehydration for 10 days decreased the concentration of serum glucose by 34% and increased that of urea and albumin by 34 and 18%, respectively. Rehydration for 2 days reversed these effects completely. The serum concentrations of sodium, potassium and chloride were increased by dehydration by 23, 44, and 18% respectively. After 2 days of rehydration the values returned to normal. No change in the heart rate, pulse or temperature was found during the dehydration period. The gazelles survived the 10 days of dehydration, although they tended to be drowsy, weak and emaciated during the last 2 days of dehydration. The animals appeared normal after rehydration.

More, T. and K. L. Sahni. 1978. Effect of long term water deprivation on body weight and water intake of breeding ewes under semi-arid conditions. Journal of Agricultural Science 90:435-439.

Thirty-nine adult female sheep of identical body size and age were randomly taken from the Chokla breed. They were divided into four groups, which were allowed water once in 24, 48, 72, and 96 hr. Seven females from each of the first, third, and fourth groups were mated for the first time in spring and for a second time in winter, so that they lambed in the monsoon and summer season, respectively. All the females were maintained on uncultivated pasture. Watering once in 72 and 96 hr cause body mass loss up to 26% compared with those watered daily. The females which failed to maintain pregnancy lost more than 30% of their body mass due to watering only once in 96 hr and there were about 43 and 100% lambing in the first and second breeding cycle of the same females. The remaining groups displayed 100% lambing. The water intake increased significantly in the third month of pregnancy in the group allowed water daily and water consumption was found to be about 13% of body weight, whereas the values for those watered once in 72 and 96 hr were 9 and 8%, respectively. The water-deprived animals were able to drink up to 32% of their body mass within 2 – 3 min. It is concluded that breeding females could be watered once in 72 hr without any loss of lambing during summer.

More, T. and K. L. Sahni. 1979. Effect of long-term intermittent watering on some blood and urine attributes of pregnant sheep under semi-arid conditions. Indian Journal of Animal Sciences 49:549-553.

Blood and urine attributes were examined in breeding ewes maintained under different watering regimes of once in 24 (control), 72, and 96 hr over a period of 1 year. Water deprivation significantly caused a progressive hemoconcentration and reduction in extracellular fluid space in all the groups of animals in both the stages of pregnancy during summer. An increase in extracellular fluid space on 130th day of pregnancy was significant and its level was higher in daily watered sheep during hot season than in winter. Watering intermittently increased plasma urea-nitrogen, non-esterified fatty acids, plasma bicarbonate and sodium, and changes were more pronounced during summer. Urinary osmolarity, specific gravity, and conductivity on 130th day of gestation showed increase with the water deprivation. There was also a reduction in urine K/Na ratio due to dehydration. It is concluded that breeding ewes could be given water once in 72 hours during summer without any serious clinical changes in the blood and urine.

More, T. and K. L. Sahni. 1980. Effect of water deprivation on blood and urine components of lactating sheep under semi-arid conditions. Indian Journal of Animal Science 50:411-416.

Effect of water deprivation was studied in 21 Chokla sheep using blood and urine samples. Sheep were provided with water ad libitum once in 24, 72, and 96 hr (group 1, 2, and 3, respectively). First and second lambing in these animals took place in July and May, respectively. Animals were sampled on the 30th and 60th days post-lambing for blood analysis. Extracellular fluid values were maintained on low levels in group 3 on 30th and 60th days after first lambing. It declined significantly on the 60th day of lactation in all groups. There was a higher level of extracellular space in group 2 during the second breeding cycle. Plasma-free fatty acids and urea nitrogen increased significantly with dehydration. However, there was no evidence of hemoconcentration either in hemocrit or hemoglobin levels, which were lower in all the females on the 30th day of lactation than the 60th day. Data on plasma sodium, potassium, and bicarbonate inconsistently responded during watering treatment. The deprivation of water caused significant increases in urine osmolarity and conductivity. There was also a rise in urine sodium concentration and thereby reduction in the potassium/sodium ratio. The present study showed lactating Chokla females were able to tolerate dehydration for 3 to 4 days during the rains and mid-summer of semi-arid area.

Morris, R. J. H., B. Howard, and W. V. Macfarlane. 1962. Interaction of nutrition and air temperature with water metabolism of merino wethers shorn in winter. Australian Journal of Agricultural Research 13:330-334.

Field observations were made on Peppin merino wethers at 6 and 9 per 0.4 ha throughout the year on improved pasture in Canberra, Australia. Estimations of water distribution with the use of tritium, thiocyanate, and T1824 indicated that stocking rate in autumn had little effect on body composition or water intake. Before shearing in July, however, the 9-per-0.4 ha sheep had lost 16% more weight than those at 6-per-0.4 ha, although body water distribution was similar in the two groups. After shearing, both groups shivered continuously for three weeks. The 6-per-0.4 ha animals had lower rectal and higher skin temperatures than the 9-per-0.4 ha sheep. Skin and rectal temperatures were reciprocal to wind velocity. Both groups lost over 3 kg weight (5.9 and 8.4% of body mass) in 2 weeks, but in the 9-per-acre sheep, body water increased by 8.7% while in the 6-per-0.4 ha group 4.4% of body water was lost. The 9-per-0.4 ha sheep lost 30.7% of tissue solids, compared with 7.5% in the better-fed animals. It is likely that cellular water content increased in the 9-per-0.4 ha animals. An increase in density of stocking from 6 to 9-per-0.4 ha costs three times as much tissue and fat during the cold period, while this loss of solids was partly obscured by replacement of tissues with water.

Murray, D. M. 1966. A comparison of cutaneous evaporation rates in cattle exposed to heat in a climate laboratory and in the field. Journal of Agricultural Science 66:175-179.

The cutaneous evaporation rates of 3 animals of different genotype have been determined under artificial heating in the laboratory and during exposure to field conditions. Cutaneous evaporation rates were measured from the back-thoracic region using a ventilated capsule technique. In both climate-laboratory studies and field observations cutaneous evaporation showed little relationship with rectal temperature, respiratory rate, or skin temperature. Basal cutaneous evaporation rates in the unheated chamber at 10 a.m. were found to be 40% lower in animals which were housed overnight than in those which entered the chamber following exposure to early morning sunlight. Only minor differences in cutaneous evaporation rates of the 3 animals were observed during either hot-room or field studies, despite their variation in genotype and sweat gland density. Under field conditions, cutaneous evaporation rates were almost twice those obtained during climate-controlled laboratory exposures, although the animals had lower rectal temperatures, respiratory rates, and skin temperatures throughout the field observations. Changes in moisture loss from the skin in animals exposed to field conditions closely followed fluctuations in direct solar radiation. It is suggested than the sweat glands of cattle may be stimulated to a greater extent by direct solar radiation in the field than by artificial heat such as that encountered during climate-laboratory exposures.

Musewe, V. O., G. M. O. Maloiy, and J. K. Kanja. 1976. Evaporative water loss in two small African antelopes: the dik-dik and the suni. Comparative Biochemistry and Physiology 53C:17-18.

In a temperature controlled chamber in the laboratory at the University of Nairobi, Kenya, Africa, experiments on the pulmocutaneous water loss, respiratory rate, rectal and skin temperatures of the dik-dik (*Rhynchotragus kirkii*) and the suni (*Nesotragus moschatus*) were measured before and during exposure to heat stress. Body temperature was assessed using thermocouples and cutaneous evaporation was determined by placing a desiccant capsule on a shaved area of skin. During exposure to thermal stress ($T_a > 40$ ºC) increases were noted in all measured parameters except sweating rate in both species. In both dik-dik and the suni antelopes, sweating did not appear to be an important avenue of evaporative heat loss during heat exposure. Intradermal injections of adrenaline and noradrenaline stimulated sweating while injections of acetylcholine, carbachol, prolactin, oxytocin and isoprenaline had negligible effects on sweating.

Nagy, K. A and M. H. Knight. 1994. Energy, water, and food use by springbok antelope (*Antidorcas marsupialis*) in the Kalahari Desert. Journal of Mammalogy 75:860-872.

Field-metabolic rates and water-influx rates (both measured via doubly-labeled water) and diet composition (rumen contents, plant sample analyses) were measured in free-ranging male springbok antelope (*Antidorcas marsupialis*) during 3 seasons in 1986 and 1987 at Kalahari Gemsbok National Park, South Africa and Gemsbok National Park, Botswana. Results from springbok that did not drink water during the hot, dry season indicate that they can achieve water balance without drinking if they can obtain plant food containing at least 67% water. Springbok may accomplish this by selecting flowers, seeds, and leaves of shrubs (mainly *Acacia mellifera* and *A. hebeciada*) before dawn, when these foods are most succulent. Springbok ate mostly grass during the hot seasons if drinking water was available, but, in the cold, dry season, their selection of succulent shrub leaves mainly (*A. mellifera*) apparently made them independent of drinking water. During the rut, males had high energy and water requirements and lost weight because they did not eat enough food to maintain balance. During most of the year, springbok used water and energy at comparatively low rates, in common with other desert adapted mammals. Their water-economy index was also low, indicating a conservative water metabolism. We estimated that an adult male springbok consumes ca. 504 kg (dry matter) of food year^{-1} and that the population of springbok consumed ca 76% of the annual grass productivity within the important dry riverbed habitats. Competition with other large grazers, and particularly with those restricted to foraging in close proximity to drinking water, probably existed during dry years of this study.

Nicholson, M. J. 1987. The effect of drinking frequency on some aspects of the productivity of zebu cattle. Journal of Agricultural Science 108:119-128.

A 28-month trial was carried out under extensive grazing conditions to examine the effects of giving water to Boran cattle once daily, once every 2 days, and once every 3 days, with cattle having ad libitum access to water serving as the control. In the dry season, the mass and condition of lactating cows given water every 3 days declined more rapidly than that of cows given water daily. Calving rates and birth weights were unaffected by treatments although when compared with cows given water ad libitum, birth weights were depressed by 2.5 kg in all treatments. Thirty steers showed no treatment differences in 28-month weights despite a depression in dry matter intake in the dry season by animals given water every 3 days. In contrast, 210-day weaning weights were significantly depressed by 9 kg when cattle drank water every 2 days and 14 kg when they drank every 3 days compared with calves given water daily. Total water consumed was depressed in all classes of stock by 5 – 10% under the 2-day regime and by 25 – 34% under the 3-day regime when compared to cattle given water daily. The results show that giving water every 3 days can be carried out indefinitely with all classes of stock with only minor effects on cattle productivity under the climatic conditions in which the trial was held. The management implications of giving water every 2 to 3 days to cattle under extensive, pastoralist and ranching conditions are discussed.

Nolan, J. V., J. B. Liang, N. Abdullah, H. Kudo, H. Ismail, Y. W. Ho and S. Jalaludin. 1995. Food intake, nutrient utilization and water turnover in the lesser mouse-deer (*Tragulus javanicus*) given lundai (*Sapium baccatum*). Comparative Biochemistry and Physiology 111A:177-182.

Voluntary food intake, digestibility and water turnover were determined in adult Malaysian lesser mouse-deer (*Tragulus javinicus*) given unlimited access to lundai foliage (*Sapium baccatum*). Daily dry matter (DM) intake was 42.4 g kg^{-1} metabolic live mass ($M^{0.73}$) or 3.7% M. Digestible energy intake was 853 kJ day^{-1} (571 kJ metabolizable energy $M^{0.73}$), calculated to be used with 79% efficiency. Apparent digestibility (%) of organic matter was 83.8, crude fiber 63.7, acid detergent fiber 60.5, neutral detergent fiber 72.1 and crude protein 65.0. Urinary excretion of the purine derivative, allantoin, was 0.05 mg g^{-1} digestible DM intake suggesting rumen microbial yield efficiency may be lower than in other ruminant species. Total water intake was 182 ml $M^{0.82}$, consistent with a very lean carcass. Turnover of body water was 17% day^{-1}. The mouse-deer produced relatively dry, well-defined fecal pellets.

Olsson, K., S. Benlamlih, K. Dahlborn, and F. Fyhrquist. 1982. Effects of water deprivation and hyperhydration in pregnant and lactating goats. Acta Physiologica Scandinavica 115:361-367.

The response to 30 hr water deprivation was studied in 7 goats during the last month of pregnancy and during lactation with anestrus as the control period. Plasma osmolality and plasma Na concentration increased by about 4% in pregnant and lactating goats and by about 2% in anestral goats. Plasma arginine vassopressin concentration rose by about 7 pg ml^{-1} in pregnant and lactating goats, but by about 3 pg ml^{-1} during anestrus. Plasma rennin activity was elevated in pregnant animals, but dehydration caused only a minor further rise. Total plasma protein concentration was low in pregnant goats and did not increased during water deprivation, but it did so in lactating animals, but remained unchanged during anestrus. Effective renal plasma flow fell by 20% in lactating animals, but no consistent effect of the dehydration was seen during pregnancy and anestrus. Urine flow decreased by about 75% during pregnancy, 55% during lactation and 65% during anestrus with the highest urine osmolality observed during anestrus. Milk production was only slightly reduced, but the milk osmolality increased in parallel with that of the blood plasma. When allowed to drink at the end of the water deprivation period, pregnant goats immediately drank 2.5 ± 0.5 L, lactating goats 3.3 ± 0.9 L and anestral goats 1.1 ± 0.3 L. When hyperhydrated, pregnant goats excreted the excessive water more readily and showed less response to exogenous AVP than lactating and anestral animals. In conclusion, pregnant and lactating goats are obviously more susceptible to a shortage of water supply than anestral animals but can easily excrete an excess of water.

Osman, H. E. and B. Fadlalla. 1974. The effect of level of water intake on some aspects of digestion and nitrogen metabolism of the desert sheep of the Sudan. Journal of Agricultural Science 82:61-69.

Five successive trials were conducted using 8 adult rams (Sudan desert sheep) to study the effect of restriction of water intake on some aspects of digestion and nitrogen metabolism. The feeds used in this study were berseem hay (*Medicago sativa*), lubia hay (*Dolichos lablab*), maize hay (*Zea mais*), a concentrate mixture, and dry desert grasses (hummra---a mixture of *Dactyloctenium aegyptium*, *Schoenefeldia gracilis*, *Eragrostis* *pilosa*, *Aristida funiculate*, and *Aristida* spp.). Restriction of water did not affect the digestibility coefficients of organic matter, crude protein, and crude fiber significantly. The digestibility coefficient of ether extract was significantly reduced whereas that of nitrogen-free extract was slightly higher when water was restricted. The concentrations of ammonia and volatile fatty acids in the rumen and of urea in the blood were recorded before and 3 hr after feeding. Increases in the rumen ammonia and blood urea nitrogen concentration were reduced by water restriction except when hummra was fed. Restriction of water intake also slightly increased the *in vitro* rate of fermentation of rumen contents which is taken as a measure of microbial activity in the rumen, and the retention of nitrogen. These results are interpreted as indications of more efficient nitrogen utilization under conditions of water restriction. There were no significant effects of the treatments on changes in the concentration of volatile fatty acids. The significance of these findings in relation to the management of desert sheep in arid parts of Sudan is discussed with special reference to the effect of the level of dry-matter intake on nitrogen balance.

Parker, K. L. 1988. Effects of heat, cold, and rain on coastal black-tailed deer. Canadian Journal of Zoology 66: 2475-2483.

Effects of heat, cold, and rain on costal black-tailed deer (*Odocoileus hemionus columbianus*) we recorded in a metabolic chamber at dry air temperatures between –20 and 32 ºC. For animals in summer pelage, respiratory rates, body core temperatures, and skin temperatures increased curvilinearly with increasing air temperature; thermally critical air temperatures occurred above 27 ºC and below 10 ºC. In winter body temperatures were lower in adults than in fawns, skin temperatures were highly variable, and respiratory rates increased at lower air temperatures than in summer; metabolic expenditures associated with thermoregulation increased at temperatures above freezing. During summer trials in the rain, body and skin temperatures at air temperatures greater than 12 ºC; at 10 ºC, energy expenditures after 5 hr of rainfall were greater than during heat or cold stress. For animals in winter pelage, changes in body temperature, skin temperature, and hair depth showed no consistent trends with duration of rainfall; only fawns increased metabolism at temperatures just above freezing (2 – 3 ºC) in the rain. Data from this study suggest that rainfall may pose major energetic constraints for black-tailed deer in summer pelage. Managerial provisions for thermal cover should place highest emphasis on summer habitats.

Parker, K. L. and C. T. Robbins. 1984. Thermoregulation in mule deer and elk. Canadian Journal of Zoology 62: 1409-1422.

Thermoregulatory responses of mule deer (*Odocoileus hemionus hemionus*) and elk (*Cervus elaphus nelsoni*) were analyzed for air temperatures outdoors between 2 and 34 ºC in summer and -38 and +24 ºC in winter. Body temperatures differed between species, seasons, and ages. Surface skin temperatures varied with air temperature, incident radiation, and seasonal pelage. Respiratory rate and water loss increased exponentially while exhaled air temperatures varied sigmoidally as air temperature increased. Expired air volume increased logarithmically with increasing respiratory rate. Cutaneous evaporation (g m^{-1} hr^{-1}) in summer was significantly greater in elk than in mule deer, which used panting as the primary means of heat dissipation in hot environments. Nonevaporative respiratory heat loss varied parabolically as a function of air temperature in both species. Thermally critical environments for mule deer occurred at operative temperatures of less than -20 ºC and greater than 5 ºC in winter and greater than 25 ºC in summer. Energy expenditures increased for elk at operative temperatures below -20 ºC and above +20 ºC in winter, with metabolic rates decreasing between 10 and -20 ºC. Maximum thermal resistances for mule deer and elk in winter were 1,400 and 2,000 s m^{-1}, respectively, compared with 600 and 400 s m^{-1} in summer.

Parker, K. L., M. P. Gillingham, T.A. Hanley and C. T. Robbins. 1993. Seasonal patterns in body mass, body composition, and water transfer rates of free-ranging and captive black-tailed deer. Canadian Journal of Zoology 71:1397-1404.

Body mass, body composition, and water turnover rates were determined over a continuous 2-year period in 9 free-ranging Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on Channel Island, Wrangell, Alaska and 8 captive deer between 1988 and 1990 using titrated water. Body masses showed a cyclic pattern, declined 14 - 31% between October and March, and were best described by a 5-parameter, biologically based regression model. The amount of mass lost by black-tailed deer over winter depended on the peak body mass attained during fall. During winter, animals used 70-82% of their body fat and 10 - 15% of protein reserves. Body fat was preferentially mobilized at rates 2.3 - 11.6 times higher than protein. Because of the higher energy content of fat, fat accounted for 83 – 92% of the catabolized energy. Water transfer rates varied seasonally with average summer values approximately four times those of winter; lactating deer had significantly higher rates of water transfer than nonlactating animals. Seasonal changes in all of the above parameters for wild deer were greater than those for eight deer of the same age in captivity

Rosenmann, M. and P. Morrison. 1963. Physiological response to heat and dehydration in the guanaco. Physiological Zoology 36:45-51.

The response to heat and dehydration was studied in the guanaco (*Lama guanicoe*) using captive animals (1 M and 1 F) in a climate-controlled room at the Santiago Zoo, Santiago, Chile. The guanaco regulated its body temperature with little variation at ambient temperatures up to 45 ºC for 6 hr at 15% relative humidity and following severe dehydration for 24 hr. The resting heart rate did not change from the normal range during heat stress even in the severely dehydrated animal. Hemoconcentration, determined via blood extractions, occurred following dehydration in proportion to the weight change of the body as a whole. The normal guanaco did not increase its respiratory rate, however, the dehydrated animal showed substantial hypernoea.

Rubsamen, K., R. Heller, H. Lawrenz, and W.V. Engelhardt. 1979. Water and energy metabolism in the rock hyrax (*Procavia habessinica*). Journal of Comparative Physiology 131B:303-309.

The influence of ambient temperature and water supply on water metabolism and O_2-consumption was measured in rock hyraxes (*Procavia habessinica*) in the laboratory using titrated water. With ad libitum food and water (control), water turnover rates of hyraxes were significantly lower than the general eutherian mean; water turnover rates were 61.4, 44.1, and 55.1 ml kg$^{-0.82}$ day^{-1} at 20, 27, and 35 ºC, respectively. When greens were fed ad libitum and no drinking water was given, water turnover rate at 20 ºC was two-fold higher, but at 27 and 35 ºC was similar to that in control experiments. Water turnover rates were significantly reduced when no drinking water and only 25 g greens/day were offered (25.8, 22.0, and 29.3 ml kg$^{-0.82}$ day^{-1} at 20, 27, and 35 ºC, respectively). Highest urine osmolality (3,200 mOsm kg^{-1}) was recorded at 35 ºC. Oxygen consumption under control conditions was 43% below that predicted on the basis of body mass for most eutherian mammals. The thermoneutral zone ranged from 27 to 35 ºC, and the basal metabolic rate was 165 kJ kg$^{-0.75}$ hr^{-1}.

Rubsamen, K. and S. Kettembeil. 1980. Effect of water restriction on oxygen uptake, evaporative water loss and body temperature of the rock hyrax. Journal of Comparative Physiology 138B:315-320.

Evaporative water loss, O_2 consumption and body temperature were measured using titrated water in 3 rock hyraxes (*Procavia habessinica*) under control and restricted water intake conditions, in the laboratory in Stuttgart, Germany. Water turnover rate was 61 ± 6 ml kg$^{-0.82}$ day^{-1} during control experiments and 37 ± 6 ml kg$^{-0.82}$ day^{-1} during water restriction. Water restriction reduced O_2 consumption below ambient temperatures (T_a) of 28 and above 33 ºC; there was no effect within the thermoneutral zone. Between 12 and 27 ºC total evaporative heat loss decreased from 0.41 ± 0.05 W kg^{-1} during control experiments during control experiments to 0.34 ± 0.04 W kg^{-1} during water restriction. Between 39 and 41 ºC evaporative heat loss increased to 1.61 W kg^{-1} during ad libitum and 0.72 W kg^{-1} during restricted water availability. During control experiments body temperature ranged between 37 and 40 ºC as T_a was changed between 12 and 38 ºC. During water restriction the animals became hypothermic below and hyperthermic above a T_a of 27 ºC.

Rubsamen, K. and W. V. Engelhardt. 1975. Water metabolism in the llama. Comparative Biochemistry and Physiology 52A:595-598.

Water metabolism of llamas (*Llama llamae*) and goats under conditions of ad libitum feeding (control) and under restricted food and water intake was measured using titrated water, in Stuttgart, Germany. Water turnover rates at control feeding were 62.1 ± 8.8 ml $kg^{-0.82}$ day^{-1} in llamas and 59.0 ± 10.9 ml $kg^{-0.82}$ day^{-1} in goats. Values decreased with reduced food intake to 46.9 ± 7.3 ml $kg^{-0.82}$ day^{-1} and 41.1 ± 8.0 ml $kg^{-0.82}$ day^{-1}. Under condition of reduced water intake, goats reduced food intake more than llamas.

Rubenstein, D. I. 1989. Life history and social organization in arid adapted ungulates. Journal of Arid Environments 17:145-156.

The life history and social organization of ungulate species adapted to arid environments is reviewed. The review includes coverage of the theories of life history, mating system evolution, and ecological features of arid environments. The author then makes broad and detailed interspecific and intraspecific comparisons of life history and social organization of ungulates inhabiting arid environments.

Rungangazi, B. M. and G. M. O. Maloiy. 1987. Salt excretion and saline drinking in the dik-dik antelope (*Rhynchotragus kirkii*). Comparative Biochemistry and Physiology 88A:331-336.

The ability of the dik-dik antelope *(Rhynchotragus kirkii*) to survive while drinking saline solutions was tested in controlled laboratory experiments by providing drinking water containing up to 0.5 M NaCl. Fluid intake increased from 230.5 ml day^{-1} when fresh water was offered to a maximum of 373.9 ml day^{-1} when 0.3 M NaCl solution was offered. At concentrations higher than 0.3 M animals lost weight, were anorexic, and developed diarrhea. It is concluded that the dik-dik antelope will probably tolerate drinking water containing 0.24 M NaCl.

Russel, A. J. F., J. Z. Foot, and D.M. McFarlane. 1982. Use of titrated water for estimating body composition in grazing females. Pages 45-56 *in* Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

Titrated water was used to estimate total body water, body composition, and water turnover of non-pregnant, pregnant, non-lactating, and lactating grazing sheep. Body composition was estimated from equilibrated and extrapolated values of titrated water space. These methods both overestimated the total body water measured directly. Body fat could be predicted satisfactorily from titrated water space within the physiological states of females (i.e., lactating, pregnant), although for lactating females the error of prediction is greater. It appears inadvisable at this stage to use equations derived from all classes of females to estimate body fat in females of any 1 physiological state. Water turnover varied, with the physiological state being highest for lactating females.

Schmidt-Nielsen, K. 1959. The physiology of the camel. Scientific American 200:140-151.

Reviews the overall physiology of the camel in relation to thermoregulation and water balance, particular adaptations that allow the camel to tolerate dehydration in a hot arid environment. Physiological mechanisms discussed include total body water, routes of water loss, nitrogen metabolism, and adaptive heterothermy.

Schmidt-Nielsen, K., B. Schmidt-Nielsen, S. Jarnum, and T. R. Houpt. 1956. Water balance of the camel. American Journal of Physiology 185:185-194.

Camels were exposed to prolonged periods of water deprivation during winter, spring, and summer under laboratory conditions in the Sahara Desert. Determinations were made of weight changes, water and food intake, urine flow and concentrations, and plasma concentrations. It was found that the camel can tolerate a loss of water corresponding to 30% of its body mass even when exposed to the severe desert heat. Other mammals dehydrated in a hot environment may die from circulatory failure when the water loss involves 12% of the body mass. Unlike many other mammals the camel des not lose its appetite when deprived of water but continues to eat normally until the desiccation becomes very severe. It has low urine output (0.5 – 1 L day^{-1} when kept on a diet of dates and hay), a low water content in the, and, when dehydrated in the summer, a very low evaporative water loss. When offered water the camel drinks in 10 minutes enough water for complete rehydration. The longest period that a camel was kept on dry food without drinking water in the hot summer was 17 days. This camel was not working and it had its protective fur, which decreased the heat gain from the environment. It is concluded that the ability of the camel to withstand prolonged dehydration is due to a tolerance to an extremely high degree of desiccation of the body and low overall water expenditure. Particularly effective as a water conserving mechanism is the low evaporative water loss during dehydration in the summer.

Schmidt-Nielsen, K. and B. Schmidt-Nielsen, S. Jarnum and T. R. Houpt. 1957. Body temperature of the camel and its relation to water economy. American Journal of Physiology 188: 103-112.

Body temperature of the camel and its relation to water economy were studied at Beni Abbes, Algeria. The rectal temperatures of normal healthy camels at rest may vary from about 34 ºC to more than 40 ºC. Diurnal variations in the winter are usually in the order of 2 ºC. In summer the diurnal variations in the camel deprived of drinking water may exceed 6 ºC, but in animals with free access to water the variations are similar to those found in the winter. The variations in temperature are of great significance in water conservation in 2 ways. The increase in body temperature means that heat is stored in the body instead of being dissipated by evaporation of water. The high body temperature means that heat gain from the hot environment is reduced because the temperature gradient is reduced. The effect of the increased body temperature on heat gain from the environment has been calculated from data on water expenditure. These calculations show that under the given conditions the variations in body temperature effect considerable economy of water expenditure. The evaporative heat regulation in the camel seems to rest exclusively on evaporation from the skin surface (sweating), and there is no apparent increase in respiratory rate or panting connected with heat regulation. The evaporation from isolated skin areas increased linearly with increased heat load. The critical temperature at which the increase sets in is around 35 ºC. The fur of the camel is an efficient barrier against the heat gain from the environment.

Schmidt-Nielsen, K. and B. Schmidt-Nielsen, T.R. Houpt, and S. Jarnum. 1956. The question of water storage in the stomach of the camel. Mammalia 20:1-15.

The paper discusses evidence that the camel stores water in its stomach. The evidence presented does not support the water storage hypothesis. The water storage function is generally ascribed to a special sac-like structures in the camel's rumen. The contents of these sacs usually is more solid than the general rumen contents. The sacs have a glandular structure. The fluid present is similar to digestive fluids, particularly saliva. It has no particular resemblance to drinking water, neither in appearance nor in chemical composition. The camel usually drinks an amount of water sufficient to restore the water content of the body. In these experiments, water was not ingested in excess of that needed to restore the normal composition of the body. After large amounts of water had been ingested the fluid in the rumen attained its usual composition in about 2 days. The rumen of the camel, like that of other ruminants, contains a large amount of fluid.

Schmidt-Nielsen, K., E. C. Crawford, A. E. Newsome, K. S. Rawson, and H. T. Hammel. 1967. Metabolic rate of camels: effect of body temperature and dehydration. American Journal of Physiology 212:341-346.

The effect of body temperature and hydration state on metabolic rate were studied in captive camels in Alice Springs, Australia. The metabolic rate increased with increasing body temperature as expressed by a mean Q_{10} of 2.06. The metabolic rate decreased with increasing dehydration, reaching about 77% of the original value at 77% of the initial hydrated body rate. The rate of respiration increased with rising body temperature with a mean Q_{10} of 10.86. The rate of respiration was decreased to 64% of the initial value when dehydration had reduced the body mass to 77% of the initial weight.

Schmidt-Nielsen, K., E. C. Crawford, and H. T. Hammel. 1981a. Respiratory water loss in camels. Proceedings of the Royal Society of London B 211:291-303.

Rates of oxygen consumption and respiratory water loss were studied in captive camels that were exposed to desert heat and water deprivation at Alice Springs, Australia. Body temperatures were measured using thermocouples and oxygen consumption was determined using a facemask. We found that changes in body temperature are accompanied by considerable changes in respiratory water loss. Body temperature fluctuations are greatest in dehydrated camels (up to 70 ºC), and in these the respiratory water loss might vary from about 0.06 to 1.2 g min^{-1}. The respiratory frequency varied from about 4 to 28 min^{-1}, while the metabolic rate varied by less than two-fold. The lowest values for respiratory water loss can be explained by the exhalation of air at temperatures far below body temperature, and, in addition, removal of water vapor for the exhaled air, resulting in exhalation of air at less than 100% relative humidity.

Schmidt-Nielsen, K., R. C. Schroter, A. Shkolnik. 1981b. Desaturation of exhaled air in camels. Proceedings of the Royal Society London. B 211:305-319.

We have found that camels can reduce the water loss due to evaporation from the respiratory tract by decreasing the temperature of the exhaled air and by removal of water vapor from this air, resulting in the exhalation of air at less than 100% relative humidity. 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% relative humidity. 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 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 vapor 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.

Schoen, A. 1968. Studies on the water balance of the East African goat. East African Agriculture and Forestry Journal 34:256-262.

The water balance of East African goats has been determined under normal conditions and under heat stress and water restriction. Water balance was calculated using the measurements of the amount of water drank, water content of food, water lost in feces and urine, and estimates of metabolic water. Water loss through urine, feces, and cutaneous evaporation decreased in goats under water restriction. Goats under water restriction increased urine osmolarity and allowed small increases in body temperature. Goats also maintained high food intake rates during water restriction.

Schoen, A. 1969. Water conservation and the structure of the kidneys in tropical bovids. Journal of Physiology 204:143-144.

Water balance and the response to dehydration in relation to kidney structure was studied in the bushbuck (*Tragelaphus scriptus*) from moist bushland, the Uganda kob (*Adenota kob*) from dry savannah, and the dik-dik (*Rhyncotragus kirkii*) from semi-desert habitats. It was found that when animals were dehydrated to 85% of normal body mass, the urine output fell from 99.1 ± 8.4 to 69.7 ± 2.0 ml $kg^{0.73}$ day^{-1} in the bushbuck, from 46.4 ± 3.7 to 27.2 ± 1.5 ml $kg^{0.73}$ day^{-1} in the kob, and from 10.9 ± 0.77 to 1.3 ± 0.04 ml $kg^{0.73}$ day^{-1} in the dik-dik. Urine osmolalities rose from 936 ± 52 to 1,369 ± 52 mOsm L^{-1} in the bushbuck, from 1,109 ± 16 to 1,594 ± 11 mOsm L^{-1} in the kob, and from 2,235 ± 138 to 4,762 ± 62 mOsm L^{-1} in the dik-dik. Kidney measurements from 6 individuals from each species showed that the medullae occupied a mean of 31% in the bushbuck, 38% in the kob, and 47% in the dik-dik; these differences were significant. If the relative medullary volume is a measure of the total length of the loop of Henlé, it may then be concluded that the urine concentrating capacity available is related to the aridity of the species' habitat.

Schoen, A. 1971. The effect of heat stress and water deprivation on the environmental physiology of bushbuck, reedbuck, and Uganda kob. East African Agricultural and Forestry Journal 37:1-7.

Water balance, feed intake, urine osmolarity, and sodium and potassium levels in the urine were studied in the bushbuck (*Tragelaphus scriptus dama*), reedbuck (*Redunca redunca wardi*), and Uganda kob (*Adenota kob thomasi*). Animals were studied in a climate controlled laboratory under normal, heat stress, and dehydrated to levels at which their body mass was 85% of normal. Under heat stress all animals were able to maintain feed intake rates of normal levels. The bushbuck and kob showed good evaporative heat loss responses, and the reedbuck a poor response to heat stress. When dehydrated the urine electrolyte concentration increased by about 50% and fecal water loss were reduced by about 5% in the bushbuck, 27% in the reedbuck, and 38% in the kob. Potassium was the predominant cation excreted in the urine under all conditions.

Schoen, A. 1972. Studies on the environmental physiology of a semi-desert antelope, the dik-dik. East African Agricultural and Forestry Journal 40:325-330.

The water balance of the dik-dik (*Rhyncotragus kirkii*) was determined under normal and heat stress conditions and when the animal was dehydrated at a level at which its body weight was stabilized at about 85% of normal. The rectal temperature, respiration rate, urine osmolarity, and sodium and potassium level in urine was measured. The heat tolerance of the dik-dik was due mainly to a substantial heat storage capacity, the body temperature fluctuating over a range of 6 ºC above normal when under heat stress. The dik-dik also demonstrated a very fast, shallow panting rate under heat stress, which reached nearly 400 cycles min^{-1}, 12 times the normal rate. When dehydrated and without an imposed heat load, the dik-dik made large economies in all water loss compartments, the urine could be concentrated to nearly 5,000 mOsm L^{-1}, and evaporative water losses were reduced to about 60% of normal. Under heat stress or when dehydrated, fecal water losses were reduced from over 70 g 100 g^{-1} to around 55 g 100 g^{-1} of dry fecal matter.

Shkolnik, A., A. Borut, and J. Choshniak. 1972. Water economy of the Bedouin goat. Symposia of the Zoological Society of London 31:229-242.

The water economy of 5 Sinai Bedouin goats (body mass 11 – 22 kg) was studied in a hot room at a temperature of 30 ºC, 30% relative humidity, with and without drinking water. Two black goats representing the breed commonly known as "mountain goat" were studied under the same experimental conditions for the purpose of comparison. Mountain goats are common all over Israel and thrive in the deserts of its eastern and southern regions. After two weeks of water deprivation, on a diet of dry hay and barley only, the Sinai goats lost about 30% of their body mass, but did not lose appetite. At the end of the first week under the same conditions, the mountain goats lost about 25% of body mass and consumed no more food. Both breeds maintained body water content during the water deprivation period within levels normal to ruminants, and their drinking capacity, at the termination of the water deprivation period, was very high: 23 - 26% of the body mass in mountain goats and 30 - 40% in Sinai goats. When normally watered the water content in all body compartments was high in both breeds. The total water content amounted to 75 - 78% of body mass and the blood plasma to 6 - 8%. The Sinai goats, however, were more efficient in preserving water. The following features found in the Sinai goat may contribute to its efficient water economy: low metabolic rate, 30% lower than the value predicted according to body mass; smaller evaporative water loss during water deprivation (541 mg water kg^{-1} hr^{-1} compared with 710 mg in the mountain goat); dry with only 40% water content and urine output per kg less than half that found in the mountain goat. The daily caloric value of the food consumed per day by the Sinai goat was a third of the intake per day by a mountain goat and the daily amount of water consumed by a Sinai goat was one fourth to one sixth the amount needed by a mountain goat although there is only a factor of two differences between the weights of the breeds.

Shkolnik, A, E. Maltz, and S. Gordin. 1980. Desert conditions and goat milk production. Journal of Dairy Science 63:1749-1754.

The influence of desert conditions on milk production was studied in the Black Bedouin goat. When goats were watered only once every 2 – 4 days foraging rates increased. During water deprivation, goats lost 25 – 30 % of body mass from reductions in total body water and blood plasma volume. However, goats maintained relatively high milk production rates. Daily yields of over 2 kg have been reported for animals weighing 15 to 25 kg. Milk composition is similar to that of other goat breeds. Milk production efficiencies have exceeded 33% of energy consumed. Adaptation of the small Black Bedouin goat breed to arid desert conditions is also discussed.

Siebert, B. D. and W. V. Macfarlane. 1971. Water turnover and renal function of dromedaries in the desert. Physiological Zoology 44:225-240.

Water turnover and renal function of camels was studied using titrated water. The body water content of camels was similar to that of other ruminants; it was 8 – 23% greater in the summer than winter. Water turnover in summer was twice that observed in winter and was higher in lactating than in nonlactating animals. Urine flow of hydrated camels in summer decreases rapidly with water restriction. Water absorption in the reticulorumen is absorbed slowly and is not readily excreted by the kidney. During dehydration, potassium is excreted while sodium tends to be retained in the extracellular fluid and is used later to restore fluid volume. Glomerular filtration rate in dehydrated camels decreases to 33% of the rate in hydrated camels resulting in very low urine flow rates of 0.5 – 1.5 ml min^{-1} are reached with urine concentrations of 2,000 – 2,500 mOsm L^{-1}.

Siebert, B. D. and W. V. Macfarlane. 1975. Dehydration in desert cattle and camels. Physiological Zoology 48:36-48.

The effect of dehydration on body fluids, water turnover rates, fluid volumes, blood parameters, water metabolism, and hemolysis of red blood cells was studied in cattle and camels. Titrated water, blood extraction, collection of urine and feces were used in this study. The body mass of cattle decline more (6.1% vs. 2.1%) than camels when both species were dehydrated. Cattle lost twice as much fluid from plasma than camels. Urine flow of dehydrated camels was lower and less variable than dehydrated cattle. Dehydrated cattle also had higher fecal moisture contents than dehydrated cattle.

Silanikove, N. 1985. Effect of dehydration on feed intake and dry matter digestibility in desert (Black Bedouin) and non-desert (Swiss Saanen) goats fed on Lucerne hay. Comparative Biochemistry and Physiology 80A:449-452.

The effect of dehydration on feed intake and dry matter digestibility in Black Bedouin and Swiss Saanen goats fed on Lucerne hay were studied during mid-summer in a captive herd in the research zoo at Tel-Aviv University, Israel. Food consumption decreased with the lengthening of the period of dehydration in both breeds in a similar manner. However, the Saanen goats reduced their dry matter intake and consequently their water intake much more than Bedouin goats. The apparent dry matter digestibility increased significantly in both breeds during dehydration, the response being larger in the Saanen goats. Bedouin goats were capable of maintaining during 3 days of dehydration a level of consumption, which is well above their maintenance requirements while the Saanen goats consumed only the amount of feed, which is needed to satisfy their maintenance requirements.

Singh, N. P., T. More, and K. L. Sahni. 1976. Effect of water deprivation on feed intake, nutrient digestibility, and nitrogen retention in sheep. Journal of Agricultural Science 86:431-433.

This paper describes the effect of water deprivation on nutrient digestibility and nitrogen retention in sheep. Thirty-six female sheep were divided into 3 groups, a group watered every 24 hr, a group watered every 48 hr, and a group watered every 72 hr. Maximum and minimum temperatures ranged between 21 and 24.8 C. The water and dry matter intake was 5.5 and 2.6% of body mass in the daily watered group, 5.5 and 2.1% in the group watered every 48 hr, and 4.8 and 2.2% in the group watered every 72 hr. Dry matter intake was significantly reduced when females were watered every 48 and 72 hr than in sheep watered every 24 hr. However, there was no difference in dry matter intake between groups watered 48 hr and 72 hr. Digestibility of dry matter, crude protein, ether extract, and crude fiber was highest in the group watered every 48 hr. Nitrogen intake was 22.1, 20.1, and 20.4 g animal^{-1} day^{-1} for the 24, 48, and 72 hr groups, respectively. The animals in the three groups lost 24.2, 20.4, and 26.3% of the total nitrogen intake through the feces and 29.1, 23.5, 27.1% through the urine.

Skadhauge, E., E. Clemens and G. M. O. Maloiy. 1980. The effect of dehydration on electrolyte concentrations and water content along the large intestine of a small ruminant: the dik-dik antelope. Journal of Comparative Physiology 135B:165-173.

The concentrations of Na, K, and Cl and the water content in the large intestine and rectum of an East African ruminant, the dik-dik antelope (*Rhynchotragus kirkii*) was investigated in hydrated and dehydrated animals. Intestinal contents were removed at 6 sites along the large intestine and rectum, and the water fraction and the amount of Na, K, and Cl were measured per g dry matter. An impermeant water marker showed that the dry matter amount was nearly constant along the lower gut. Local electrolyte absorption rates were determined in the terminal colon using a dialysis bag method. Approximately 4/5 of the absorption of NaCl and water took place in the upper large intestine. Throughout the lower gut the Na concentration of the absorbate was close to that of plasma. The Na and Cl concentrations of the digesta decreased while the K concentration rose, but K was still absorbed. Dehydration resulted in a reduction of 35% of the water lost per gram of dry matter. The water content was reduced from the start of the large intestine (by 13%), but the fractional absorption of salt and water in the large intestine and rectum was not significantly changed. The local electrolyte absorption rates and the electrical potential difference were slightly reduced. The Na and K concentrations of the absorbate remained nearly constant. The water saving during dehydration thus seems to proceed without specific adjustments of the transport parameters of the lower gut. The concentrations of Na and Cl in approached those, which in dialysis bag experiments, result in zero absorption of NaCl and water in the lower gut at different flow rates of dry matter.

Skatan, J. E. and O. Holand. 1989. Water turnover during winter in roe deer. International Union Game Biologists 19:191 (Abstract).

Water transfer rate was studied in 9 captive roe deer (*Capreolus capreolus*) by tritium water dilution technique. Six roe deer were feed 4 different diets: marrow stem kale, commercial livestock feed, fresh bilberry stems, and grains of oat, through sequential periods. Marrow stem kale diet gave the highest water transfer rates (259 ml $kg^{-0.8}$ body mass day^{-1}) and oats the lowest (68 ml $kg^{-0.8}$ body mass day^{-1}). In three roe deer fed the commercial livestock feed only, the water transfer rate and dry matter intake decreased from October to December. Ambient temperature was <0 ºC. From December to February the dry matter intake continued to decrease for this group, but the water transfer rate remained at the same level. Ambient temperatures in this period were >0 ºC. This might indicate that the water transfer rate depends both on ambient temperature and seasonal variations in food intake.

Smith, B. S. and A. R. Sykes. 1974. The effect of route of dosing and method of estimation of titrated water space on the determination of total body water and the prediction of body fat in sheep. Journal of Agricultural Science 82:105-112.

Eight mature female sheep were offered a ration that maintained body mass constant during a 20-week period. During the final 10 weeks a comparison was made in each animal of the pattern of equilibration and urinary losses of titrated water during 8 hr after dosing by four different routes. These were intravenous, intraperitoneal, intraruminal, and a combination of the intraperitoneal and intraruminal routes. Titrated water spaces were calculated from (a) the 8-hr plasma specific activity and (b) by extrapolation to zero time of the plasma specific activities during the 7 days after injection. At the end of the experiment the fat and water contents of the bodies of the sheep were determined directly. Complete equilibration of titrated water between plasma and rumen water was not achieved in all animals 8 hr after intravenous or intraperitoneal injection but was when the rumen was primed by the combination of intraperitoneal and intraruminal dosing. After intraruminal dosing equilibration was not achieved in any animal within 8 hr of dosing. Urinary losses of marker were lower after intraruminal dosing but otherwise averaged 4 – 5% of the dose L^{-1} urine. This was equivalent to 0.3 – 6.7% of the dose for individual sheep. Errors resulting from incomplete equilibration and urinary loss of marker did not influence the efficiency of prediction of total body water from titrated water space. The multiple correlation coefficient relating body fat with empty body weight and its water content was very high ($r = 0.99$). Errors introduced into this relationship by the inclusion of gut water in the prediction equations were apparently of a similar magnitude to those resulting from the errors in the estimation of titrated water space. The extrapolation method for the determination of titrated water space was shown to have the same accuracy as equilibration techniques under these controlled dietary conditions.

Sneddon, J. C., J. Van der Walt and G. Mitchell. 1991. Water homeostasis in desert-dwelling horse. Journal of Applied Physiology 71:112-117.

This study set out to investigate tolerance of the body water pool to short-term water deprivation in horses and, in particular, to assess whether feral horses from the Namib Desert showed tolerance to dehydration superior to Transvaal. Hydration status was compared in 6 feral horses from the Namib Desert and 6 Boerperd farm horses under conditions of normal hydration and after 72 hr of dehydration. Under normal hydration, the 2 groups did not differ significantly in water intake, plasma sodium and potassium concentrations, plasma osmolality, hemocrit, total plasma protein, body water content, or water turnover. The Namib horses were significantly smaller and turned over 5 L less water pre day than the Boerperd during normal hydration and turned over 4 L less during dehydration. Increases in plasma sodium concentration after 72 hr dehydration were greater in the Namib horses. It was concluded that horses can easily tolerate water deprivation that results in 12% reduction in body mass. The feral horses of the Namib Desert were not significantly different per unit mass from domestic horses with regard to indexes of total body water content under conditions of normal hydration and after 72 hr of dehydration. Their smaller size and, hence, lower water turnover might be mechanisms they use for survival in the Namib Desert.

Sneddon, J. C., J. Van der Walt and G. Mitchell. 1993. Effect of dehydration on the volumes of body fluid compartments in horses. Journal of Arid Environments 24:397-408.

Maintenance of plasma volume during dehydration is essential for survival in mammals. Supplemental fluid may be drawn from the interstitial, intracellular and transcellular (primarily gastrointestinal) compartments. We have studied the changes in the volumes of these compartments in arid-adapted (Namib) and in subtropical farm horses from the Transvaal (Boerperd) in response to dehydration, in order to identify mechanisms which protect plasma volume in these horses. As a fraction of total fluid loss, 6% was lost from the plasma, 27% from the interstitial space, and 67% from the combined intracellular/transcellular space. The Namib horses showed a tendency to lose, as a fraction of total fluid loss, more fluid from the interstitial space (29%) and less from the transcellular space. The Namib horses showed a tendency to lose, as a fraction of total fluid loss, more fluid from the interstitial space (29%) and less from the transcellular space (65%) than the Boerperd (21% and 73% respectively). The Namib horses absorbed intestinal fluid more rapidly than the Boerperds, as indexed by a larger difference in tritium content of the body water pool, between the dehydrated and rehydrated states, over the same period of rehydration. This difference was not significant ($P<0.115$). We conclude that hoses maintain their plasma volume effectively, as do arid-adapted species such as donkeys, camels, desert sheep and goats during acute dehydration, and that Namib horses tended to be more competent in this respect than Boerperd.

Soldatova, N. V. and A. V. Grazhdankin. 1989. Evaporative water losses in goitred gazelle (*Gazella subgutturosa*). Zoologicheskii Zhurnal 68:102-109. (In Russian with English summary).

Coat water-vapor conductance in goitred gazelle is similar to that one whose skin does not have sweat glands. In young goitred gazelles cutaneous evaporation intensity is 12.1 g m^{2-1} hr^{-1} on the back surface and 8.6 g m^{2-1} hr^{-1} on the abdomen. In adult females these parameters are 10.0 and 11.5 g $m^{2-1}hr^{-1}$ accordingly. Age differences in the cutaneous conductance are probably related to a different wool structure. With the air temperature up to 36 ºC and skin temperature up to 39.5 ºC cutaneous water evaporation goes mainly through diffusion and with higher temperatures, evaporation through sweat glands dramatically increases the water loss. No age differences were found in the intensity of pulmonary evaporation. With a moderate heat load young goitred gazelles lose about 25% of their metabolic thermoproducts through the evaporation diffusion and with an elevated heat load and panting about 45%. The share of pulmonary evaporation in the total evaporative water loss is 25 - 50%. Experimental findings indicate that goitred gazelles have two forms of adaptation bridging mechanisms of thermoregulation and water balance regulation. One of them allows gazelles to prevent an excessive dehydration with a moderate heat load, the other provides and effective use of the evaporative water loss for body cooling with elevation of ambient temperature.

Soppela, P., M. Nieminen, and S. Saarela. 1992. Water intake and its thermal energy cost in reindeer fed lichen or various protein rations during winter. Acta Physiologica Scandinavica 145:65-73.

Captive reindeer were fed four different rations which supplied equal energy but varying amount of crude protein: lichen (3%), mixed hay plus lichens (10%) and 2 feed concentrations with medium (12%) of high (18%) protein content. Kinetics of total body water were measured with titrated water from February to March 1985, and thermal energy cost of daily water intake was estimated. Biological half-time of water was shorter, and daily water intake significantly higher on the hay plus lichens diet and on the medium- or high-protein concentrates diet than on the lichen diet during March 1985. Similar differences were found between reindeer on medium-protein concentrate and on lichens at the end of the corresponding feeding period during April 1986. Daily water inflow was positively correlated with a dietary supply of digestible crude protein (r = 0.916). Thermal energy costs of daily water intake were highest 1.9 MJ 3.7 L^{-1} in reindeer on high-protein concentrate during March 1985, and 2.0

MJ 3.9 L^{-1} in reindeer on medium-protein concentrate during April 1986. The reindeer fed on lichens had minimal and nearly twice as small thermal energy cost of daily water intake (mean 1.1 MJ 2.1 L^{-1}) as on either of the concentrates. Our results show that even a moderate feed protein ration can significantly increase free water intake and its thermal energy cost in reindeer as compared to dominant natural feed (lichens) during winter. Careful protein supplementation is recommended to support body condition with a concomitant addition of easily soluble carbohydrates to compensate for increased thermal costs of water intake.

Springell, P. H. 1968. Water content and water turnover in beef cattle. Australian Journal of Agricultural Research 19:129-144.

Twenty-four steers, comprising British (Hereford and Hereford X Shorthorn), Zebu (Africander), and Zebu cross (British X Brahman or Africander) breeds, were either maintained on pasture, or yarded and fed diets of a low and a high nutritional value. Titrated water was injected into the animals on 5 occasions at intervals of 3 months. The body water content and the water turnover rate were calculated, and some of the sources of variation defined. Observed differences in the water content are attributable to nutritional factors rather than to breed differences. The mean body water content ranged from 615 to 809 ml kg^{-1} fasting body mass, where higher values were associated with a poor diet. The mean half-life of titrated water was lower in summer (as low as 58 hr) than in winter (up to 128 hr) in grazing and well-fed yarded steers. On a poor diet, however, the half-life in yarded cattle remained high and almost constant throughout the year, dropping to below 100 hr on only a single occasion. Occasionally the half-life was breed dependent, but generally no significant differences between breeds could be found. While mean turnover rates of up to 7.1 ml kg^{-1} hr^{-1} were found in better–fed cattle in summer, the value in poorly fed animals was almost constant throughout the year at about 3.3 ml kg^{-1} hr^{-1}. There was, however, a winter minimum in the well-fed yarded and grazing groups. The turnover rate was influenced by breed only to a limited extent. The results are interpreted in light of their possible significance in the adaptation to a tropical environment, and in relation to their value in predicting body composition.

Syrjala, L., J. Salonen, and M. Valtonen. 1980. Water and energy intake and nitrogen utilization in reindeer. Pages 252-261 *in* Reimers, E., E. Garre, and Skjenneberg, editors, Proceedings of the Second International Reindeer/Caribou Symposium, Roros Norway.

The influence of energy intake on nitrogen utilization and water requirements in reindeer (*Rangifer tarandus*) was studied over 4 winters between 1974 and 1977. Five digestibility and nitrogen balance trials were carried out, in digestibility cages where all feces and urine were collected, using a Latin Square design at air temperature of 10 ºC. Six different rations were offered with mean crude protein concentration ranging from 3.3 to 15.3%. The average crude protein, metabolizable energy, and total water intakes per day were 97 ± 38 g, 2.2 ± 0.5 Mcal, and 3,160 ± 1,040 g (mean ± SD), respectively. Protein utilization was strongly limited by the insufficient energy intake. Total water intake was highly positively correlated to the crude protein intake (CPI) ($r = 0.787$, $P < 0.001$) and urine excretion of nitrogen ($r = 0.758$, $P < 0.001$). On a negative nitrogen balance the water intake still increased slightly with extra nitrogen excretion. Urine nitrogen concentration on the different rations remained almost constant, but the urine volume was significantly correlated with total urine nitrogen. Total water required by reindeer can be calculated from the equation TWI = 21.5 x CPI + 1,080.

Taneja, G. C. 1973. Water economy in sheep. Pages 95 – 132 *in* H.F. Maryland, editor Proceedings of water-animal relations. Twin Falls, Idaho.

A series of experiments were conducted to find out the ill effects of prolonged water deprivation and to work out a watering schedule, which should save water expenditure and at the same time should not affect the animal’s health adversely. Sheep deprived of water for 5 days during summer lost and average of 25% of body weight, rectal temperature rose, respiratory rate decreased 20%, and plasma volume decreased 22%. Ill effects were not observed in sheep when at least 75% of normal water intake was maintained. In desert areas where *Prosopis spicigera* were in abundance, sheep drew much of their water supply by eating the pods of these trees, which contained 68% water during summer. In these experiments, sheep eating these pods lived without water for 12 days and did not show any loss in body mass. When sheep were deprived of water for 3 days there was a 50% reduction in plasma volume. It seems therefore, sheep does not have any mechanism of retaining the circulatory fluid during dehydration.

Taylor, C. R. 1968a. Hygroscopic food: A source of water for desert antelopes. Nature 219: 181-182.

Observations of diet selection of the oryx (*Oryx besia*) and Grant's gazelle (*Gazella granti*) and measurements of ambient temperature and relative humidity (RH) were recorded in 1965 on the El Barta Plains in the Northern Frontier Province, Kenya. Plants eaten by oryx and Grant's gazelle were collected throughout the day. The diet of oryx and Grant's gazelle consisted primarily of *Disperma* sp. *Disperma* sp. samples were collected and dried until a constant weight was obtained, they were then placed in 3 environments: 17 ºC, 85% RH; 23 ºC, 39% RH; and 40 ºC, 17% RH and the samples were weighed hourly to determine weight gain from absorption of moisture from air. Leaves in the 17 ºC environment equilibrated after 10 hr with 42% water content, leaves in the 23 ºC equilibrated after 2 hr with 39% water, and leaves in the 40 ºC environment equilibrated after 2 hr with 2% water. By adjusting their foraging times and feeding at night and the early morning, oryx and Grant's gazelle would be able to obtain more preformed water from the same plants than if they fed at midday.

Taylor, C. R. 1968b. The minimum water requirements of some East African bovids. Symposium of the Zoological Society of London 21:195-206.

Several of the wild East African bovids are reported to be capable of surviving in arid regions without drinking. Minimum amounts of water required by eland (*Taurotragus oryx*), oryx (*Oryx besia*), and Grant's gazelle (*Gazella granti*), whose ranges include the hot arid sub-Sahara, are compared with the amounts required by buffalo (*Syncerus caffer*), wildebeest (*Connocaetes taurinus*), and Thomson's gazelle (*Gazella thomsonii*), whose ranges are limited by water availability. Frequent droughts have provided a severe selection pressure for frugal use of water during the relatively short period in which zebu cattle have been resident in East Africa. Thus the water requirements of these animals provide a yardstick for evaluation the rate at which water conserving mechanisms evolve, while the water requirements of the temperate Hereford steer as a baseline against which to judge the efficiency of these mechanisms in other species. Studies were carried out in a climate-controlled room with an intermittent heat load, enabling one to evaluate adaptations for dealing with both heat and aridity. Oryx, Grant's gazelle, Thomson's gazelle, and zebu cattle are found to be specialized for conserving water and can maintain a constant weight on a total water input of approximately 2% of their body mass day^{-1} (in an environment of 22 ºC). Hereford steers require more than twice this amount of water. Zebu cattle are more specialized physiologically for coping with arid conditions than the eland, wildebeest, or buffalo. The eland, however, is able to gain independence of surface water by behavioral and physiological means other than conservation of water. In contrast, the Thompson's gazelle, which requires extremely small amounts of water, is unable to inhabit the hot arid regions of East Africa for reasons yet to be explained. The development of water sparing mechanisms is only one aspect of the complex of adaptations that determines the limits of a species' range.

Taylor, C. R. 1969a. The eland and the oryx. Scientific American 220:88-95.

The thermoregulation and water balance were studied in the eland (*Taurotragus oryx*) and the oryx (*Oryx biesa*) in a controlled environment with 12 hr of 40 ºC and 12 hr of 22 ºC. The oryx and eland were provided ad libitum water and rectal temperatures were measured. Both species allowed their body temperatures to rise (7 ºC in the eland and 6 ºC in the oryx) before beginning to use evaporative cooling. Both species were then dehydrated until their weighed 85% of their original weight, then exposed to the same conditions. The eland maintained a body temperature lower than ambient temperature whereas the oryx's body temperature regularly rose above ambient temperatures. The mechanism involving counter current heat exchange that allows these animals to allow increases in body temperature while maintaining brain temperatures lower than those of the body. The metabolic rates of hydrated and dehydrated eland and oryx were also determined. Both species decreased their metabolic rates when dehydrated, the oryx more than the eland. It was also found that both species were able to reduce pulmonary water loss at night by extracting more oxygen from each breath and breathed more slowly. The feeding habits and diet are also discussed relative to plant moisture content.

Taylor, C. R. 1969b. Metabolism, respiratory changes and water balance of an antelope, the eland. American Journal of Physiology 217:317-320.

The eland (*Taurotragus oryx*) and African zebu steer were used to assess oxygen consumption, respiratory volume, and respiratory water loss in a controlled laboratory setting in Muguga, Kenya. In experiments at 14 ºC, a temperature often encountered at night, the oxygen consumption of the eland was 19% higher than at 22 ºC. Ventilation volume, however, was unchanged. Furthermore, respiratory evaporation was less, since body temperature and therefore the amount of water contained in the saturated expired air decreased. The African zebu steer also increased its oxygen consumption at 14 ºC (by 28%), but its body temperature was more constant and ventilation volume and respiratory water loss increased.

Taylor, C. R. 1970a. Dehydration and heat: effects on temperature regulation of East African ungulates. American Journal Physiology 219:1136-1139.

This study investigated the effects of dehydration on rectal temperature and evaporative cooling at air temperatures up to 50 ºC in both desert and nondesert species. Six species of East African ungulates, Grant's gazelle (*Gazella granti*), Thomson's gazelle (*G. tompsonii*), oryx (*Oryx beisa*), wildebeest (*Connocaetes taurinus*), zebu steer, and African buffalo (*Syncerus caffer*), were selected on the basis of size, habitat, and whether they sweated or panted to dissipate excess heat. In all species dehydration caused an increase in the air temperature at which animals would begin to sweat or pant. Steady-state rectal temperatures were higher and rates of panting or sweating were lower in dehydrated than in hydrated animals. The magnitude of these effects was greater in desert than in nondesert species. At 45 ºC air temperature, rectal temperature of the 2 desert species, Grant's gazelle and oryx, exceeded air temperature by between 0.5 and 2 ºC, and rectal temperature of 46.5 ºC could be maintained for 6 hr without observable ill effects.

Taylor, C. R. 1970b. Strategies of temperature regulation: effects on evaporation in East African ungulates. American Journal Physiology 219:1131-1135.

This study investigated the effects of physiological adaptations for temperature regulation on water loss in 8 species of African ungulates, 3 desert-dwelling species, Grant's gazelle (*Gazella granti*), eland (*Taurotragus oryx*), and oryx (*Oryx beisa*), and 3 species that do not inhabit arid regions, Thomson's gazelle (*G. thomsonii*), wildebeest (*Connocaetes taurinus*), and African buffalo (*Syncerus caffer*), and 2 species of domestic ungulates, zebu steer, and Hereford steer. All species were subjected to simulated desert conditions (12 hr at 40 ºC) alternating with 12 hr at 22 ºC in the laboratory. Water loss was assessed via a total water balance method where the total intake of free water, preformed water, and estimates of metabolic water was assessed versus the amount lost in feces and urine. Under these temperature regimes with both ad libitum access to water and water restriction 2 strategies were found in desert-dwelling species to reduce water loss during periods of water restriction. Large ungulates, such as the eland have low body temperatures in the morning and slowly increase throughout the day; this mechanism reduces the need to increase water loss for temperature regulation. Conversely, small ungulates, such as Grant's gazelle, allow their body temperatures to quickly rise above ambient temperatures eliminating the need to pant or sweat to reduce heat loads. Intermediate size ungulates use a combination of these 2 strategies.

Taylor, C.R.. 1972. The desert gazelle: A paradox resolved. Symposia of the Zoological Society of London 31:215-227.

Water physiology of Grant's (*Gazella granti*) and Thomson's gazelle (*G. thomsonii*) were studied in metabolic cages. The range of the Grant's gazelle however, extends into the hot, arid regions of East Africa while that of the Thomson's gazelle does not. Grant's gazelle requires about 33.3% more water per kg body mass than the Thomson's gazelle in a simulated desert environment (12 hr day^{-1} at 22 ºC alternating with 12 hr day^{-1} at 40 ºC). This paper tries to resolve this apparent paradox by investigating the response of the 2 gazelles to short, but very intense, heat loads. Most of the water loss in a simulated desert is through evaporation and helps keep the animal cool. Intense solar radiation occurs together with high air temperatures in the arid regions of Africa. During a short period at mid-day, Grant's gazelle might frequently encounter a more severe heat load than the air temperature of 40 ºC provided in the simulated desert. At high ambient air temperatures both gazelles dissipate heat primarily by panting. When dehydrated neither gazelle began to pant until air temperatures exceeded 40 ºC and steady state rectal temperature was higher than air temperature. This effect was greater in the desert-dwelling Grant's gazelle than in the Thomson's gazelle. For example, when air temperature was 45 ºC body temperature of the Grant's gazelle was as high as 46.5 ºC while that of the Thomson's gazelle did not exceed 42.3 ºC. The higher body temperature and lower evaporation of the Grant's gazelle at air temperatures exceeding 40 ºC help to resolve the apparent paradox between water requirements and habitat of the gazelles.

Taylor, C. R. and C. P. Lyman. 1967. A comparative study of the environmental physiology of an East African antelope, the eland and the Hereford steer. Physiological Zoology 40:280-295.

The water requirements and physiological adaptations to arid environments were studied in the eland (*Taurotragus oryx*) and Hereford steer were studied under laboratory conditions. Water intake, turnover, evaporative water loss, oxygen consumption, respiratory water loss, and minimum water requirements were determined at 22 and 40 ºC. Overall average water loss did not differ between eland and Hereford steer, however the routes of water loss did differ between species. Hereford steer had higher fecal water loss than the eland. Variations in body temperature were much higher in the eland than in the Hereford steer. The eland also had a narrower thermoneutral zone than the Hereford steer.

Taylor, C. R. and C. P. Lyman. 1972. Heat storage in running antelopes: independence of brain and body temperatures. American Journal of Physiology 222:114-117.

This study tried to determine how much of this heat was stored and to find out if antelopes possess unusual physiological mechanisms for coping with high body temperatures when antelope run at high speeds. Large increases in rectal temperature of Thomson's gazelles (*Gazella thomsonii*, wt 15 kg) were measured during running: +3.9 ºC after 5 min at 40 km hr^{-1}; +4.6 ºC after 11 min at 25 km hr^{-1}; and +4.3 ºC after 20 min at 15 km hr^{-1}. Heat storage accounted for 80 - 98% of the calculated heat production during running. Brain temperature rose more slowly than rectal or carotid artery temperature. After a 5 min run at 40 km hr^{-1}, the brain was 2.7 ºC cooler than blood in the carotid artery. Blood supplying the brain appears to be cooled via a countercurrent heat exchange with cool blood draining the nasal mucosa (in the carotid rete). Elands (*Taurotragus oryx*, mass 200 kg) sweated profusely and their rectal temperature equilibrated after a few minutes of running at a slightly higher level: +0.8 ºC at 25 km hr^{-1}; 0.8 ºC at 20 km hr^{-1}; +0.7 ºC at 15 km hr^{-1}; and +0.5 ºC at 10 km hr^{-1}.

Taylor, C. R., C. Spinage, and C. P. Lyman. 1969a. Water relations of the waterbuck, an East African antelope. American Journal of Physiology 217: 630-634.

The water relations of the waterbuck (*Kobus defassa*) was studied in a climate controlled laboratory setting. We found that in a moderate environment (22 ºC) the waterbuck required 25% more water than a domestic Hereford steer. At 40 ºC the waterbuck lost water equal to about 12% of its body mass in 12 hr. This degree of dehydration could not be tolerated for prolonged periods at 40 ºC. When water intake was restricted, fecal water loss was reduced, but urine volume and evaporation were unchanged. Oxygen consumption was not altered by dehydration and this helps explain the relatively unchanged water loss with the restricted water intake. The unusually high water requirement of the waterbuck is in accord with its restricted habitat near water.

Taylor, C. R., D. Robertshaw, and R. Holmann. 1969b. Thermal panting: a comparison of wildebeest and Zebu cattle. American Journal of Physiology 217:907-910.

Thermal panting of wildebeest (*Connochaetes taurinus*) and Zebu cattle was studied under laboratory conditions. At 50 ºC both wildebeest and zebu cattle maintained their rectal temperatures about 10 ºC below ambient temperature. At higher air temperatures, preventing cutaneous evaporation had no observable effect on the wildebeest's ability to regulate its temperature whereas it seriously impaired the zebu's ability. The wildebeest developed respiratory alkalosis only at air temperatures of about 50 ºC whereas in the zebu, with cutaneous evaporation blocked, this happened at about 43 ºC. To avoid alkalosis the wildebeest could increase its effective dead space as it pants. Morphological studies indicate that the wildebeest have a larger anatomical dead space, larger nasal passages, and larger openings into the paranasal sinuses than cattle. Ventilation of the paranasal sinuses may contribute to increased dead space as the wildebeest pants.

Taylor, C. R. and G. M. O. Maloiy. 1967. The effects of dehydration and heat stress on intake and digestion of food in some east African bovids. International Congress of Game Biologists 8:324 (Abstract).

The effect of an intermittent heat load (a daily cycle of 12 hours at 22 ºC and 12 hours at 40 ºC) and a 15% level of dehydration, with ad without the heat load, on food intake and digestibility of a poor quality hay was investigated in the Grant's gazelle (*Gazella granti*), and oryx (*Oryx beisa*); the arid domestic Turkana goats, fat-tailed sheep, and zebu cattle, and the non-arid Thomson's gazelle (*G. tompsonii*), and wildebeest (*Connocaetes taurinus*). An intermittent heat load with water available ad libitum depressed the food intake of zebu cattle and Turkana goats more than 40%. It had no significant effect on intake of any of the other species. Dehydration at 22 ºC caused a depression in food intake of all the species investigated. Dehydration together with heat load caused no further reduction in food intake of the arid Grant's gazelle and oryx, or in goats but did cause a further reduction in the other species. The digestibility of food by the Thomson's gazelle is found to be much higher than that of any other species.

Taylor, C. R., R. Dmi'el, A. Shkolnik, D. Baharav, and A. Borut. Heat balance of running gazelles: strategies for conserving water in the desert. American Journal of Physiology 226:439-442.

The effect of exercise on water balance of mountain gazelle (*Gazella gazella*) was determined in the laboratory. Heat lost through evaporation, Nonevaporative means, and the amount stored as animals rested at various air temperatures and ran at various speeds was determined. The same proportion of the heat production was lost by evaporation at 3 km hr^{-1} as at rest, whereas 30 – 40% more of the heat produced while running at 6 – 9.5 km hr^{-1} was lost by evaporation. At speeds exceeding 15 km hr^{-1}, most of the heat produced was stored. However, when the recovery period after a sprint was included (while body temperature returned to normal levels), the same proportion of the heat production was lost by evaporation as at rest. Since gazelles normally either move slowly as they graze or sprint to avoid predators, it seems reasonable to conclude that exercise would not have a major effect on their water balance.

Thorton, R. F. and H. G. Yates. 1968. Some effects of water restriction on apparent digestibility and water excretion in cattle. Australian Journal of Agricultural Research 19:665-672.

An experiment is described in which digestibility and water excretion was investigated in cattle using metabolism crates during periods of unrestricted feed and water, of water restriction, and of feed restriction. During water restriction, increased dry matter and acid detergent fiber digestibilities could not be wholly accounted for by decreased intake of dry matter. Reduced fecal water output was more important than changes in urine output in conserving water. It is suggested that the hindgut has a regulatory role in the observed responses to water restriction.

Thorton, R. F. and H. G. Yates. 1969. Some effects of water restriction on nitrogen metabolism of cattle. Australian Journal of Agricultural Research 20:185-189.

The effect of water restriction on the metabolism of nitrogen was studied in cattle using metabolism crates. Water restriction was found to decrease nitrogen retention in cattle when compared with periods of similar digestible energy intake but unrestricted water intake. The decreased nitrogen retention was associated with increases in fecal nitrogen output and urinary excretion. The rise in urinary urea nitrogen excretion appeared to be mediated through increased plasma urea nitrogen concentration.

Till, A. and A. Downes. 1962. The measurement of total body water in sheep. Australian Journal of Agricultural Research 13:335-342.

The measurement of total body water in sheep was studied. After intravenous injections of titrated water were given to sheep, about 5 hr was required for the dose to equilibrate with the total body water. A standard procedure for estimating the total body water of sheep was adopted, in which blood samples were taken 6 and 7 hr after an intravenous injection of titrated water. The specific activity of the water from the 2 samples was measured and the mean value used for the calculation of total body water. As a result of a study of the errors in this method, it was concluded that the value obtained for the total body water in about 2% of the body mass higher than the true value, and on measuring the rate of fall in specific activity of the total body water. This specific activity fell exponentially with time, with turnover half-times ranging from 3.5 to 16.3 days for sheep housed indoors.

Tomkiewicz, S. M. 1979. Heterothermy and water turnover in feral burros (*Equus asinus*) of the desert southwest. Masters thesis, Arizona State University, Tempe, Arizona, USA.

Body temperature and subcutaneous temperature of 5 free-ranging and 15 captive burros were monitored by temperature sensitive implants. Body temperature and subcutaneous temperature were related to environmental parameters and activity. Titrated water turnover rates were monitored on 2 free-ranging and 12 captive burros. Relationships between season, age, and body weight were examined. Burros exhibited a pronounced heterothermy (35.0 – 41.6 ºC). Mean body temperature was lower in free-ranging burros than in captive burros. In both free-ranging and captive burros, body temperature was dependent on time of day and air temperature. Males maintained consistently lower body temperature (mean 36.5 ºC) than females (mean 38.2 ºC) in summer. During summer, burros remained quiescent throughout most of the day and were active nocturnally. Males engaged in more strenuous activities during periods of maximum summer heat load than did females. Fighting or copulation resulted in a rapid increase in body temperature of males (0.1 ºC min^{-1}). During winter, activities were not restricted during the daytime and burros were observed at greater distances from permanent water. A sexual difference in body temperature did not exist in winter. Water turnover rates were higher in summer than winter. Absolute water loss increased with age and weight during summer and winter. Weight specific water loss increased with age and weight in summer; however, in winter, weight specific water loss was lower in colts than in adults. An ecophysiological model was developed to explain the breeding biology of feral burros in the desert southwest.

Turner, J. C. 1973. Water, energy, and electrolyte balance in the desert bighorn sheep, *Ovis canadensis*, Ph. D. Thesis, University of California, Riverside, California, USA. 132 p.

Bighorn sheep were studied in the Santa Rosa Mountains, California. Animals were captured and maintained in an enclosure; water and energy requirements, seasonal changes in body fluid distribution, and effects of water deprivation on food consumption, body temperature, excretion, and distribution of body fluids were determined. Captive animals had daily water requirements equivalent to 3 - 4% of their body mass during the summer. During winter and spring daily water requirements were 1 - 2% of body weight. Seasonal investigations of water balance were determined by dividing investigations into 3 periods, 5 days of ad libitum water, 5 days of water deprivation, and 5 days of ad libitum water. Total body water, extracellular fluid, plasma, blood, and rumen volume were measured. Measurement of water turnover, weight change and body temperature were also made. Rumen normally contained 20% of body water. After 2 days of deprivation, rumen fluid volume decreased by 56% and after 5 days decreased by 80% and supplied 50% of the total water lost by bighorn sheep during dehydration. Bighorns were capable of surviving water loss equivalent to 20% of body mass after 5 days of water deprivation during summer. Almost 90% of water loss was extracellular fluid; plasma volume was decreased by 48% and interstitial volume by 20%. Normal interstitial and plasma fluid volumes increased during the summer and fall periods. Total body water did not increase, but fluid shifts from the intracellular fluid space accounted for the increase in extracellular fluid. Fecal water content was reduced to 4.1 g water kg^{-1} body mass day^{-1} after 5 days of water deprivation. Urinary water loss was reduced to 1.5 g water kg^{-1} body mass day^{-1} at a concentration of 3.9 osm. Under normal conditions of water availability, Na was excreted in urine at levels below 30 meq L^{-1}, K at 300 meq L^{-1}. After water restriction, Na levels in urine increased to 170 meq L^{-1} and K to almost 1,000 meq L^{-1}.

Turner, J. C. 1979. Osmotic fragility of desert bighorn sheep red blood cells. Comparative Biochemistry and Physiology 64A:167-175.

Desert bighorn sheep (*Ovis canadensis cremnobates*) exposed to 5 days dehydration lost 17 – 22% of their body mass, which they were capable of replacing within 1 hr after water was made available. Dehydrated bighorn tolerated a 48% loss of their initial plasma volume. After less than 4 hr postrehydration, more than 50% of the lost plasma volume was replaced. The absorption of water from the postrehydration rumen occurred at moderate rate (1 – 2 L hr^{-1}) with 13% of the initial postrehydration fluid volume absorbed during the first hr of rehydration. Within 9 hr postrehydration, less than 50% of the imbibed rumen volume remained. The osmotic fragility of the bighorns red blood cells improved with increased dehydration. Control values for 50% lysis in hyposmotic saline decreased from 77 mM NaCl to 68 mM NaCl after 5 days dehydration. Plasma concentration increased from 304 mOsm L^{-1} to 345 mOsm L^{-1} after dehydration and became regulated to control levels 4 hr postrehydration. Red blood cells osmotic concentrations remained constant at an average of 252 mOsm L^{-1} during dehydration, rising to 279 mOsm L^{-1} 1 hr postrehydration and achieved control levels 5 hr post rehydration.

Turner, J. C. 1984. Seasonal variation of red blood cell survival in desert bighorn sheep (*Ovis canadensis cremnobates*). Canadian Journal of Zoology 62:1227-1231.

The life span of red blood cells (RBCs) in captive and free-ranging desert bighorn sheep (*Ovis canadensis cremnobates*) was measured with [^{32}P]diisopropylfluorophosphate. The mean winter RBC life-span (156.6 days) was not significantly affected by season for captive animals maintained on a high nutritional plane and water, ad libitum. Free-ranging bighorn demonstrated a significant difference between mean winter (155.9 days) and summer (209.9 days) RBC survival. Dehydration of captive bighorn significantly increased RBC survival, closely approximating that found in summer free-ranging animals. Desert bighorn RBCs exhibited a seasonal facultative response to the availability of water. Red blood cell life-span was significantly increased from 153.5 to 197.7 days in animals experiencing extreme dehydration. The large spleen, relative to body mass, may accommodate extensive fluctuations in total RBC volume measured during dehydration and rehydration, preventing premature RBC degradation and an increased water requirement.

Updike, D. 1977. Growth, energetics, and water balance of California mule deer fawns. M.S. thesis, California State University, Fresno, California, USA. 44p.

Growth, energetics, and water balance were assessed in California mule deer (*Odocoileus hemionus californicus*) fawns. Titrated water was used to determine water turnover rate. Mule deer fawns lost an average of 624 ml day^{-1} compared to a predicted value of 1,350 ml day^{-1} based on allometric calculations. The water turnover rate of California mule deer fawns was not significantly different than predicted based on its body mass, however it was at the lower end of the 95% confidence interval for mammals with similar body mass.

Valtonen, M. H. 1980. Effects of dietary nitrogen and sodium chloride content on water intake and urine excretion in reindeer. Pages 274-277 *in* Reimers, E., E. Garre, and Skjenneberg, editors, Proceedings of the Second International Reindeer/caribou Symposium, Roros, Norway.

The influence of nitrogen and NaCl load on water intake and urinary excretion was studied in reindeer (*Rangifer tarandus*) housed in temperature controlled stalls and fed low and high protein diets with and without a daily supplement of 10 g of salt. The effects of lichen diet were also studied. Increasing the dietary nitrogen resulted in a highly significant increase in water consumption, urine flow, and osmolality. However, even on high protein diet the urine osmolality was only 650 ± 97 mOsm kg^{-1} water (mean ± SD). The effect of supplementary salt on water intake was slight. Salt increased the urine osmolality on low protein diet, but on high protein diet it raised urine flow. Excretion rates of nitrogen, sodium, and potassium reflected the differences in dietary intake. On lichen diet with moisture content of 67% the reindeer did not drink any water. The urine osmolality was below that of plasma, but urea excretion remained the same low level as it did on the low protein diet. The surplus water is well excreted by reindeer kidney, but increased intake of dietary protein presupposes liberal water supply.

Wesley, D. E. 1971. Energy and water flux in pronghorn. Ph.D. dissertation, Colorado State University, Fort Collins, Colorado, USA. 93p.

Energy and water flux were studied in pronghorn (*Antilocapra americana*) using titrated water methods. Four trials conducted at 21 ºC with 4 female pronghorn aged 1 – 12 mo. showed that average body water decreased from 71.5 to 61.3% during this period. Water intake, flux, and turnover were higher for 1-month-old pronghorn than adult animals. Two-month-old pronghorn exposed to 32 ºC significantly increased water intake, flux and turnover compared to exposure at 21 ºC. Energy metabolism trials conducted at 21 ºC with animals of 4 ages from 2-month to 18 months indicated that 2-month-old animals showed higher energy intake, apparent digestible energy, and metabolizable energy (N corrected), energy retention, total heat production, and fasting metabolic rates than animals older than 7.5 months of age.

Wesley, D. E., K. L. Knox, and J. G. Nagy. 1970. Energy flux and water kinetics in young pronghorn antelope. Journal of Wildlife Management 34:908-912.

Energy flow trials with 4 pronghorn (*Antilocapra americana*) ranging from 108 to 182 days of age, produced results similar to those described for other ruminants with the possible exceptions of total heat production and fasting metabolic rate. The comparatively high heat production may be related to the higher metabolism of younger animals. Fasting metabolic rates were above the interspecies mean of 70 kcal $kg^{0.75}$ day^{-1}; similar results have occurred with other wild ruminants. Pronghorn, under the conditions tested, had a slightly higher content of body water than reported for other ruminants. This is feasible since pronghorn probably have a lower fat content than do most domestic or laboratory animals. Water flux in antelope is similar to that in domestic sheep and mule deer (*Odocoileus hemionus*). Noticeable differences existed between water kinetics of male and female pronghorn.

Whisler, S. L. S. and S. L. Lindstedt. 1983. Physiological responses to water deprivation in pronghorn antelope. Journal of the Colorado-Wyoming Academy of Sciences 15:58 (Abstract).

Pronghorn (*Antilocapra americana*) are found in arid and semi-arid precipitation zones in the western United States. As droughts are common in these regions, we hypothesized that pronghorn possess physiological water conserving mechanisms. We measured water loss parameters in pronghorn given ad libitum water intake and dehydrated pronghorn maintained at 15% weight loss. During dehydration, with evaporative water losses declining markedly, exhaled air temperature was lowered that alone would result in a 30% respiratory water savings. Basal respiratory rate decreased and panting during rumination ceased. During dehydration, food intake fell dramatically, lowering urine output. Urine urea nitrogen levels elevated slightly although total urine osmolality was constant (2,000 mOsm kg^{-1}) regardless of hydration state. Also unchanged were plasma osmolality and hematocrit values. Fecal water loss fell to 10% of control values due to a smaller quantity of drier food. When faced with water shortage pronghorn lower their metabolic rate, thus reducing food intake, urine and fecal production, and oxygen consumption. This leads to reductions in urine, fecal, and evaporative water losses. Reductions in exhaled air temperature and fecal moisture also contribute to the drastic reduction in water turnover in dehydrated antelope. These physiological adaptations make pronghorn well suited to their dry environment.

Williams, C. K. and B. Green. 1982. Ingestion rates and aspects of water, sodium, and energy metabolism in caged swamp buffalo, (*Bubalus bubalis*) from isotope dilution and material balances. Australian Journal of Zoology 30:779-790.

In February 1976, 5 swamp buffalo (*Bubalus bubalis*, 1 intact males and 4 steers) were placed into separate metabolism cages and fed Lucerne chaff, Lucerne pellets and water. Swamp buffalo were injected with ^{22}Na in sodium chloride solution and titrated water to estimate food intake rate using turnover rates of ^{22}Na and ^{3}H. Exchanges in dry matter, sodium, water and energy were then measured. Tritium equilibrated in 6 hr and ^{22}Na in 12 hr. The daily rate of water turnover was 34.7 ± 2.3 l, approximately 3 times that expected based on body size, reflecting an adaptation to tropical swamp habitat. Swamp buffalo had a high rate of inhibition, 30.8 ± 2.2 l day^{-1}. Daily rates of water loss were partitioned as: fecal, 9.99 ± 0.76 l, urinary, 10.4 ± 0.76 l, pulmocutaneous, 14.3 ± 1.4 l. Swamp buffalo are not likely to be able to satisfy their daily water requirements from food alone during the dry season in Australia. Daily sodium turnover rate was 6.3 ± 0.4 mmol kg^{-1} W^{-1}. Sodium levels in were low (8.3 ± 0.9 mmol kg^{-1}). Apparent digestible energy (DE) intake per day for maintenance was 651 ± 41 kJ kg^{-1} W^{-1}. Daily rates of evaporative heat loss were high, 481 ± 33 kJ kg^{-1} $W^{-0.75}$, exceeding the non-evaporative component of DE, 321 ± 35 kJ kg^{-1} $W^{-0.75}$, evaporative processes may have contributed to the high maintenance DE.

Williamson, D. T. and E. Delima. 1991. Water intake of Arabian gazelles. Journal of Arid Environments 21: 371-378.

The free water intake of 2 gazelle species, *Gazella gazella* and *G. subgutturosa*, was measured for a year, during which period shade temperatures ranged from a minimum of 1 ºC to a maximum of 49 ºC. There was significant individual variation in water intake in both species. The relationship between temperature and mean water intake was non-linear and temperature explained 90 - 98% of the variance in mean daily water intake. No evidence was found for Arabian gazelles having uniquely low water requirements and it was therefore inferred that their adaptation to aridity includes additional physiological and or behavioral mechanisms. The two species met their water requirement in different ways, but both responded to increased temperatures not only by drinking more but also by changing their diet to select for food with high moisture content.

Wilson, A. D. 1970. Water economy and food intake of sheep when watered intermittently. Australian Journal of Agricultural Research 21:273-281.

The water economy and food intake of medium-wool Merino, fine-wool Merino, and Border Leicester wethers were compared when water was made available only every 3 or 4 days. The comparisons were made on penned sheep with 2 diets at both low (max. 12 ºC) and high (max 36 ºC) temperatures. The Border Leicester used more water than the two groups of Merinos (20 – 40%), but they also ate more food per unit of body mass (15 – 18%). In proportion to food intake, the Border Leicesters and medium-wool Merinos drank 6 – 20% more water than fine-wool Merinos. It was concluded that although economy of water use may assist survival when water is unavailable, it appeared to be inversely related to food intake and therefore of limited value in selecting sheep for arid climates. The Border Leicesters lost more water in their feces than the Merinos, but similar amounts of water as urine. The volume of urine appeared to be related to the amounts of potassium and sodium excreted, since on the second to fourth day without water the concentration of potassium + sodium was maintained at 600 – 800 meq L^{-1} while the nitrogen concentration varied from 0.9 to 2.4 g 100 ml^{-1}. Nitrogen and potassium excretion in urine remained relatively constant, but sodium excretion varied from around 20meq day^{-1} on the first 1 – 2 days without water to 100 – 120 meq day^{-1} on the final 1 – 2 days.

Wilson, A. D. 1974. Water consumption and water turnover of sheep grazing semi-arid pasture communities in New South Wales. Australian Journal of Agricultural Research 25:339-347.

The water consumption and water turnover of Merino sheep grazing on 3 natural pastures of southwestern New South Wales, Australia were recorded throughout 1 year, and supplementary data on the water consumption of sheep on some pastures were collected for a further 2 - 4 years. On *Danthonia caespitosa* grassland, water was consumed for up to 7 months each year over the summer months. Maximum intakes were 3.0 - 3.5 L/sheep/day, but this was reduced for 1-2 weeks after rain of less than 25 mm and for longer periods after heavier falls. The provision of shade reduced water turnover by a maximum of 0.3 - 0.5 L day^{-1} on some occasions only, which indicates that shade, is of little importance to woolled sheep. On the saltbush (*Atriplex vesicaria*) and belah-rosewood (*Casuarina cristata – Heterodendrum oleifolium*) communities, water intakes were up to 6-7 L day^{-1} in summer. In the particularly dry summer of 1972 - 72, water intakes of the sheep on saltbush rose to 12 L day^{-1} for several months. The higher water intakes of these sheep were attributed mainly to the high mineral content of the *Atriplex* and *Bassia* spp. eaten by them, although the sheep on *Danthonia*, those on the bush communities consumed significant amounts of water throughout the winter in years of low rainfall.

Wilson, R. T. 1989. Ecophysiology of the Camelidae and desert ruminants. Springer-Verlag, Berlin, Germany.

This book provides a review of the climate, types, and locations of deserts of the world. Physiological mechanisms of camels, sheep, goats, oryx (*Oryx beisa*), eland (*Taurotragus oryx*), springbok (*Antidorcas marsupialis*), dorcas gazelle (*Gazella dorcas*), Grant’s gazelle (*G. granti*), Thomson’s gazelle (*G. thomsonii*), and Dik-dik (*Rhynchotragus kirki*) for thermoregulation, water balance, kidney function, and nutrition are reviewed.

Wright, D. E. 1982. Applications of labeled water in animals nutrition and physiology. I. Measurement of individual intakes of grazing animals. Pages 69-76 *in* Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

Methods for measuring individual animal intakes of food or liquid labeled with tritium or deuterium are reviewed. The errors associated with these techniques have been measured and the methods for estimating individual food, water, or milk intakes are discussed.

Wright, D. E. 1982 Applications of labeled water in animal nutrition and physiology. II. Measurement of milk intake. Pages 77-88 *in* Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

The application and validity of isotopic water to measure the milk intake of suckling lambs and calves are discussed. A method using 2 isotopes of iodine is described. Partitioning the intake of water in the offspring into that from milk and that from other sources, using double-labeled technique (tritium or deuterium) is also presented.

Wright, D. E. 1982. Use of labeled water in studies on the nutrition and physiology of grazing ruminants in New Zealand. Pages 91-102 *in* Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

Application of isotopic water in animal production studies of grazing ruminants in New Zealand is described. These include the seasonal and nutritional effects on water metabolism of dairy cattle and meat breeds of sheep, milk intakes of calves and lambs, and individual intakes of dietary supplements to control diseases.

Woodall, P. F. and J. D. Skinner. 1993. Dimensions of the intestine, diet, and fecal water loss in some African antelope. Journal of Zoology 229:457-471.

Measurements of the intestine of 16 species of antelope were allometrically analyzed. Moisture content of the digesta showed greatest interspecific variation in the spiral and distal colon. Small intestine length showed positive allometry, its circumference showed negative allometry, resulting in a surface area, which was isometric or related to metabolic rate. Dimensions of the villi were non-allometric. Grazers had lower surface areas of the small intestine than intermediates/concentrate selectors owing to smaller circumferences. In the large intestine, the dimensions of the distal colon showed the greatest interspecific variation. Lengths of the large intestine showed positive allometry except for the caecum, which was isometric. Circumferences and areas of the large intestine were isometric or related to metabolic rate. Species producing dry dung had larger lengths and areas of the large intestine but smaller circumferences of the proximal and spiral colon and showed greater drying of digesta per unit area than those producing wetter dung. Grazers had smaller lengths, circumferences, and areas of the large intestine than intermediates/concentrate selectors.

Woodall, P. F., V. J. Wilson, and P. M. Johnson. 1999. Size and moisture content of fecal pellets of small African antelope and Australian macropods. African Journal of Ecology 37:471-474.

The authors compare the fecal moisture content of eight species of small African antelope and 12 species of Australian macropod representing species with habitats that range from arid to mesic. Antelope had fecal moisture contents between 50 – 58% and macropods had fecal moisture contents between 61 – 80%. All antelope species had similar fecal moisture contents, whereas macropod species from arid environments had lower fecal moisture contents than those from more mesic environments.

Yagil, R. 1985. The desert camel: comparative physiological adaptation. Karger, New York, New York, USA.

The overall physiology of the camel is described. Thermoregulation and metabolism, urea metabolism, respiration and acid base balance, cardiovascular system and plasma, endocrine system, lactation, and reproduction are reviewed.

Yagil, R. and G. M. Berlyne. 1976. Sodium and potassium metabolism in the dehydrated and rehydrated Bedouin camel. Journal of Applied Physiology 41:457-461.

The effects of 10 days dehydration and rapid rehydration on the sodium and potassium metabolism in the one-humped camel were examined. The research was carried out during 2 periods in the summer, a cool and hot period. In the hot period the effects of dehydration were found to be more severe. The potassium metabolism was more affected than that of the sodium. The concentrations of potassium in the urine declined while those of sodium increased. There were also marked changes in the filtered loads, excreted loads, and reabsorption of the two cations. Following rehydration significant changes in the cation metabolism were recorded within 15 - 45 min. It is suggested that antidiuretic hormone and not aldosterone caused the changes in the two-cation metabolism.

Yagil, R. and G. M. Berlyne. 1977. Glucose loading and dehydration in the camel. Journal of Applied Physiology 42:690-693.

Five female Bedouin camels were subjected to large infusions of glucose, both when water was readily available and following 10 days of water deprivation. When camels were hydrated the extra glucose was readily given off in the urine with only a slight increase in blood levels. Following dehydration, the blood glucose levels increased greatly while the urinary excretion was limited. Dehydration led to decreased blood insulin levels, while glucose infusion led to increased levels. The data showed that the acclimatization of the camel to dehydration is not only a question of long-term adaptation to desert conditions but that even following acute nonphysiological stress, i.e., glucosuria, excess loss of body water was prevented.

Yagil, R. and G. M. Berlyne. 1977. Renal handling of creatine in various stages of hydration in the camel. Comparative Biochemistry and Physiology 56A:15-18.

The renal creatine handling of camels was examined when the animals were hydrated, dehydrated, and rehydrated. A rise in the creatine and inulin clearance ratios was found following dehydration and a decrease following rehydration. When exposed to heat and also when dehydrated, the camels had gross changes in renal creatine handling with a tendency to tubular secretion. It is concluded that endogenous creatine determinations are no measure of glomerular filtration rate in the camel.

Yagil, R. and G. M. Berlyne. 1978. Glomerular filtration rate and urine concentration in the dromedary camel in dehydration. Renal Physiology 1:104-112.

The glomerular filtration rate, effective renal plasma flow, urine osmolality, urine flow rate, urea extraction, osmolar clearance, and free water reabsorption were measured in 5 female camels in control conditions and also after 10 days dehydration in both early and mid-summer. There was a loss of 23% in mean body mass and a fall of 75% in glomerular filtration rate in severe dehydration, with a parallel reduction in the effective renal plasma flow and in urine flow rate. Urine osmolality reached a maximum of 1,466 mOsm kg^{-1} in severe dehydration of mid-summer, the highest individual osmolality being 2,372 mOsm kg^{-1}. Osmolar clearance, free water absorption, and urinary urea excretion were lower in dehydration. Urea/inulin clearance ratio was significantly lower in dehydration. Sodium excretion did not change in dehydration. Fractional reabsorption of urea was higher in dehydration, reaching a maximum value of 74% of the filtered load. The fall in urinary urea concentration was one of the factors contributing to the poor concentrating ability of the severely dehydrated camel kidney, probably caused by the fall in glomerular filtration rate and increase in tubular reabsorption of urea, rather than by protein deprivation.

Yagil, R., H. Amir, Y. Abu-Rabiya, and Z. Etzion. 1986. Dilution of milk: a physiological adaptation of mammals to water stress? Journal of Arid Environments 11:243-247.

A study was carried out on the effect of dehydration on the milk water content of humans and cows. Milk from Bedouin women was examined in winter and in summer, when urine analysis confirmed that the mothers were lacking drinking water. The milk content of cows not getting enough to drink because of a mechanical fault in the watering system, was compared with cows getting water ad libitum. There was a dilution of the milk, in both partially dehydrated Bedouin women and the partially dehydrated cows. It is surmised that dilution of milk, when drinking water is scarce is a physiological phenomenon for the survival of the young in arid areas. It is postulated that there is an endocrine regulation system for the dilution of milk; the hormones governing milk secretion – prolactin – oxytocin – act like the hormones responsible for water homeostasis (ADH and aldosterone). Water is therefore withdrawn from the intestine and kidneys and secreted into the milk.

Yagil, R., U. A. Sod-Moriah, and N. Meyerstein. 1974. Dehydration and camel blood I: red blood cell survival in the one-humped camel, *Camelus dromedarius*. American Journal of Physiology 226:298.300.

Half-life and survival time of camel red blood cells were determined by labeling with ^{51}Cr. The determinations were made on 3 separate occasions, the first in summer, and then in wither with water ad libitum followed by a summer of chronic dehydration. The shortest red blood cell survival time was recorded in winter, and the longest survival and half-life times were recorded under chronic dehydration n the summer. Normal summer determinations with water ad libitum were similar to those found in other ruminants. The lengthening of the red blood cell life span during dehydration may contribute to the ability of the camel to preserve water.

Yagil, R., U. A. Sod-Moriah, and N. Meyerstein. 1974. Dehydration and camel blood II: shape, size, and concentration of red blood cells. American Journal of Physiology 226:301-304.

This experiment examined the changes that occur in the red blood cells during hydration, dehydration, and intervals after rehydration. With dehydration the cell size diminishes but the shape does not change. These changes were confirmed in hypertonic saline solutions. Only in 20% saline solution was beveling of the membrane observed. After repaid rehydration the cells increased in size, as was found in hypotonic saline solutions. Hemolysis was observed in 0.2% saline. The hematocrit, number of cells, and hemoglobin content also changed during the various states of hydration. It is concluded that the red blood cell plays an important role in the ability of the camel to survive extreme environmental conditions.

Yagil, R., U. A. Sod-Moriah, and N. Meyerstein. 1974. Dehydration and camel blood III: osmotic fragility, specific gravity, and osmolality. American Journal of Physiology 226:305-308.

Camel blood was examined to determine whether dehydration and rapid rehydration affect the osmotic fragility of the red blood cells. The critical hemolytic volume, specific gravity, and osmolality were also determined. It was found that the red blood cells of the dehydrated camel are more resistant to hypotonic saline solutions than those of a hydrated camel. The fragility changes together with the state of hydration. Changes are also found in critical hemolytic volume, density, and osmolality. It is concluded that despite changes in the red blood cell, it remains functional in extreme environmental conditions. This fact contributes to the camel's ability to withstand prolonged dehydration and rapid rehydration.

Yagil, R. and Z. Etzion. 1979. The role of antidiuretic hormone and aldosterone in the dehydrated and rehydrated camel. Comparative Biochemistry and Physiology 63A:275-278.

The role of antidiuretic hormone and aldosterone in the dehydrated and rehydrated camel was studied in 6 female camels maintained outdoors in pens. Aldosterone secretion was higher in normally watered camels in summer than in winter. Aldosterone and antidiuretic hormone secretion increased following dehydration. It is suggested that the antidiuretic hormone besides its water reabsorptive functions in the kidney, initiates aldosterone secretion. The aldosterone then works primarily on the colon causing absorption of salt and water. When camels were rehydrated the aldosterone and antidiuretic hormone secretion diminished, but to prevent hemodilution great amounts of aldosterone were secreted 24 hr following drinking.

Yagil, R. and Z. Etzion. 1980a. Effect of drought condition on the quality of camel milk. Journal of Dairy Research 47:159-166.

Ten-day periods of water restriction flowed by 2 hr ad libitum water caused changes in camel milk. The changes were different from those reported in other mammals. At the end of each dehydration period there were increased water percentages in the milk when compared with milk in hydrated camels. The content of fat, lactose, and protein declined. Concentrations of Na, K, phosphate, and chloride in milk increased while Ca and Mg concentration declined. The urea concentration of the milk was unchanged. The young suckling calves showed no signs of stress during the dehydration periods. It was concluded that the milk of dehydrated camels is an excellent human food in arid areas, as the water and salt content are high while the nutritive value remains good.

Yagil, R. and Z. Etzion. 1980b. Milk yield of camels (*Camelus dromedarius*) in drought areas. Comparative Biochemistry and Physiology 67A:207-209.

The milk yield was determined in camels in the heat of summer when drinking water was restricted to once per week for 2 hr. The amount of milk was determined by dilution of tritium in the calves. A steady amount of 6 L day^{-1} camel^{-1} was produced. The calves had no other source of water except their mother's milk. It is concluded that the capability of the camel to produce milk of good composition and quantity for human consumption when water is severely restricted is of extreme importance.

Yagil, R., Z. Etzion, and G. M. Berlyne. 1975. Acid-base parameters in the dehydrated camel. Tijdschrift voor Diergeneeskunde 100:1105-1108.

The effect of prolonged (10 days) dehydration on acid-base parameters of camel was examined. The pH and PCO_2 levels rose significantly in the course of dehydration. This state was comparable with compensated non-respiratory alkalosis found in other animals. The plasma sodium, and magnesium levels rose significantly also. The plasma oxygen and calcium levels declined significantly. There was no significant change in potassium and phosphate levels. It is concluded that the changes found in acid-base status following dehydration are further evidence of water preservation mechanisms in the dehydrated camel.

Yagil, R., Z. Etzion, and J. Ganani. 1978. Camel thyroid metabolism: effect of season and dehydration. Journal of Applied Physiology 45:540-544.

The thyroid function of normally hydrated and dehydrated camels was examined in winter, spring, and summer. The thyroid was stimulated in summer when water was available, but inhibited flowing dehydration. It is concluded that the decline in thyroid function, as gauged by hormone secretion during dehydration in the summer, aids in preservation of body water by decreasing pulmonary water loss and dropping basic metabolism.

Yesberg, N. E., M. Henderson, and O. E. Budtz-Olsen. 1973. Hydration and vasopressin effects on glomerular filtration rate in sheep. Australian Journal of Experimental Biology and Medical Science 51:191-197.

Hydration of sheep has been shown to result in a diuresis, which is accompanied by a significant increase in glomerular filtration rate. Antidiuretic hormone has also been shown to cause an increase in glomerular filtration rate, observable only in those sheep where the initial glomerular filtration rate has not been raised by prior hydration. It is suggested that antidiuretic hormone has a two-fold effect on water excretion; an increase in water loss through its glomerular filtration rate-augmenting effect and a decrease in water loss through its ability to increase tubular water reabsorption. The diuretic effect of antidiuretic hormone frequently observed in non-hydrated sheep, where glomerular filtration rate initially is low and tubular water reabsorption high, is probably due to a relatively large change in the former and a minor change in the latter of these two effects.

Yousef, M. K., D. B. Dill, and M. G. Mayes. 1970. Shifts in body fluids during dehydration in the burro, *Equus asinus*. Journal of Applied Physiology 29:345-349.

The mechanisms underlying the dehydration tolerance in the burro were studied. A study was conducted using 2 burros to partition body fluid compartments before and after dehydration. Dehydration for 48 hr including a 10-h walk reduced body mass about 18%. Intracellular fluid volume decreased from 77.9 to 82.9 L, extracellular fluid volume, from 53.2 to 45.8 L, and plasma volume, only from 9.0 to 8.4 L. The ability of the burro to conserve blood volume and presumably to maintain circulatory adequacy gives a likely explanation of its well being even after 20% dehydration. The difference in water loss between 2 nonexercising burros is found to be behavioral and partly related to the time spent in the sun. Rehydration was rapid and overhydration did not occur. Water content of dehydrated burros was similar to that of desert antelopes but greater than values reported on the camel.

Zervanos, S. M. 2002. Renal structural adaptations among three species of peccary. Southwestern Naturalist 47:527-531.

Several morphological characteristics of the kidney were studied to determine the degree of interspecific and intraspecific adaptation that might occur within 3 species of peccary from arid, semi-arid, and moist habitats. Paired kidney samples were collected from collared (Tayassu tajacu), Chacoan (Catagonus wagneri), and white-lipped (T. pecari) peccaries from habitats varying in water availability. Two indexes for renal concentrating ability, the relative medullary thickness and relative medullary area, exhibited higher values for animals from arid and semi-arid habitats than for those from moist habitats. Relative kidney mass also was higher for collared peccaries from dry environments. It was concluded that renal structures are flexible in response to environment variation, and the differences observed were related to the adaptability of renal concentrating structures.

Zervanos, S. M. and G. I. Day. 1977. Water and energy requirements of captive and free-living collared peccaries. Journal of Wildlife Management 41:527-532.

In 1974 – 1976, water and energy requirements of captive collared peccaries (*Dicotyles tajacu*) at the Phoenix Zoo, Phoenix, Arizona and free-living wild peccaries at the Three-bar Wildlife Area, Gila County, Arizona were studied. Titrated water was used to determine water turnover in both captive and free-living collared peccaries. Hydrated captive peccaries turned over 1.58 L of water day^{-1}, whereas turnover rates for the dehydrated captive group were only 0.55 L day^{-1}. Free-living peccaries under field conditions lost 1.35 L water day^{-1} in summer and 1.17 L day^{-1} in winter. A seasonal determination of field energy requirements was made using the water loss value for free-living peccaries. To meet daily field energy requirements in summer a peccary ate 1.54 kg (wet mass) of cactus, while in winter a peccary are 1.47 kg. The energy assimilated from this amount of cactus was determined to be 825.7 kcal day^{-1} and 897.5 kcal day^{-1}, respectively.

Zervanos, S. M. and J. A. Kauffman. 1981. Water and salt balance of free-ranging ponies on Assateague Island. Proceedings of the Pakistan Academy of Sciences 55:35-36.

Field collections and observations were conducted to evaluate some of the physiological and ecological parameters affecting salt and water balance of free-ranging feral ponies inhabiting Assateague Island National Seashore, Maryland in June 1978 to July 1980. A total of 592 hours of direct field observation and sample collection was accumulated. The ponies' major avenue of water gain was in preformed water contained in the grasses consumed. This amounted to 65.5 ml kg^{-1} day^{-1}. The major avenue of water loss was evaporative with an estimated loss of 69.0 ml kg^{-1} day^{-1}. Total water balance amounted to 110.8 ml kg^{-1} day^{-1}. It was calculated that the ponies consumed 288.8 mg kg^{-1} body mass of sodium and 282.2 mg kg^{-1} Cl day^{-1} by grazing on marsh cord grass. The major avenue of loss of these ions was through urine production. Urine concentrations averaged 204.8 neq L^{-1} for sodium and 248.6 neq L^{-1} for Cl. Comparing these values with other equids indicates that the ponies have not acquired any special adaptation to conserve water, even with their high salt diets.

Zervanos, S. M. and S. Naveh. 1988. Renal structural flexibility in response to environmental water stress in feral hogs. Journal of Experimental Zoology 247:285-288.

Several morphological characteristics of the kidney were studied at the Pennsylvania State University Swine Research Laboratory at University Park, Pennsylvania, to determine the degree of acclimatization that may occur in 3 groups of feral hogs live-captured in different environments. Two groups of hogs were living in the wild, while another was raised in captivity for 3 generations and was directly descended from 1 of the wild-living groups. The 2 groups of wild hogs were living under 2 different types of water stress conditions. One group experienced periodic drought, and the other ate a high salt diet. The captive hogs were given food and water ad libitum. The captive-raised hogs had significantly lower relative medullary thickness (RMT) and relative medullary area (RMA) values (RMT of 2.35; RMA of 0.35) than either group of hogs living in the wild (RMT of 2.70 and 2.69; RMA of 0.41 and 0.44). Because the feral hogs living in the wild were exposed to a higher degree of water stress than the captive-raised hogs, it was concluded that the differences in observed kidney structure were due to acclimatization.

Marsupial Mammals

Barboza, P. S. 1993. Effects of restricted water intake on digestion, urea recycling and renal function in wombats (Marsupialia: vombatidae) from contrasting habitats. Australian Journal of Zoology 41:527-536.

The effects of restricted water intake on digestion, urea recycling and renal function in wombats (Marsupialia: Vombatidae) from contrasting habitats. Responses to limited water availability were studied in two species of wombats from mesic (*Vombatus ursinus*) or xeric (*Lasiorhinus latifrons*) habitats. Four *Vombatus* and three *Lasiorhinus* were fed a low-quality straw-based diet containing 0.6% nitrogen and 68% neutral detergent fiber (dry-matter basis). Restriction to 50% of ad libitum intakes of drinking water reduced dry-matter intakes by 30% but did not alter digestibilities of fiber or nitrogen. Nitrogen balances were negative and similar between species and water intakes. Urea pool size (^{14}C-urea) increased during water restriction but urea-entry rates and the proportion of urea recycled to the gut were similar between water intakes (78-89%). Titrated water was given to wombats in single intramuscular or intraperitoneal doses. Times to equilibrium of tritium in urinary water were large and variable (45 ± 36 hr). Urinary tritium concentrations often declined erratically after equilibrium, and were 14 ± 14% lower than the tritium concentration in the blood. The irregular kinetics for titrated water suggest that the water-dilution method requires validation for the wombats. Urinary and fecal water losses were reduced by 60% during water restriction. Water was mainly lost in the feces, which were drier in *Lasiorhinus* (41% dry matter) than in *Vombatus* (31%). As blood hematocrit and plasma osmolality were similar between water intakes, extracellular spaces were apparently maintained during water restriction. Glomerular filtration rates (creatinine clearance) were low (12 ml min^{-1}) and similar between water intakes. Therefore, more concentrated urine was produced by tubular reabsorption in water-restricted wombats. *Lasiorhinus* had greater urinary osmolalities and urine: plasma rations of creatinine, which reflected a greater urine-concentrating ability than *Vombatus*. Apparent water intakes and the ability to reduce urinary and fecal water losses in the wombats are similar to those of kangaroos. The contrasting abilities of *Vombatus* and *Lasiorhinus* to minimize both these water losses are directly related to their separate distributions.

Blaney, C. E., T. J. Dawson, H. C. K. McCarron, R. Buffenstein, and A. K. Krockenberger. 2000. Water metabolism and renal function and structure in eastern grey kangaroos (*Macropus giganteus*): responses to water deprivation. Australian Journal of Zoology 48:335-345.

The effect of water deprivation on water metabolism and renal function in eastern grey kangaroos (*Macropus giganteus*) were studied using titrated water and compared to those of the red kangaroo (*M. rufus*) which inhabits more arid habitats than the eastern grey kangaroo. Free-ranging animals were captured so that blood could be drawn and titrated water injected then released. Indices of relative medullary thickness and medullary to cortical ratio, derived from kidney morphology are indicators of renal concentrating ability. In *M. giganteus* both of these values were lower than in *M. rufus*; 5.24 ± 0.15 (mean ± SE) for M. giganteus and 6.00 ± 0.10 for *M. rufus.* Maximal measured urine concentrations were 2,444 ± 59 (*M. giganteus*) and 3,135 ± 165 mOsm kg^{-1} (*M. rufus*), with individual concentrations being 2,752 and 4,054 mOsm kg^{-1}. Kidney function in hydrated and dehydrated *M. giganteus* was assessed via glomerular filtration rates, urine flow rate, and concentration index. As measured by these parameters, *M. giganteus* had renal water-conserving capacities similar to or superior to, those of many comparable-sized arid-zone-inhabiting placental mammals, but below those of *M. rufus*. Water metabolism, as measured by water turnover, showed a similar pattern.

Bradshaw, S. D., K. D. Morris, and F. J Bradshaw. 2001. Water and electrolyte homeostasis and kidney function of desert-dwelling marsupial wallabies in Western Australia. Journal of Comparative Physiology 171B: 23-32.

Prolonged drought, necessitating conservation of water, is one of the major environmental challenges faced by many Australian marsupials. Radioactive isotopes of water and sodium were used to assess the ability of 2 species of marsupial wallabies to maintain water and electrolyte balance during periods of extreme water deprivation in the arid Pilbara region of Western Australia in 1987 and 1988. The spectacled hare-wallaby, (*Lagorchestes conspicillatus*) has the lowest mass-specific rate of water turnover at 27.5 ml $kg^{-0.82}$ day^{-1} yet reported for any mammal and was 2 to 3 orders of magnitude lower than that of the Rothschild's rock-wallaby, (*Petrogale rothsdchild*). Studies of renal function show that the hare-wallaby conserves water by producing highly concentrated urine under the influence of lysine vasopressin (LVP), the anti-diuretic hormone in macropodid marsupials. In contrast, rock-wallabies show unusual renal responses to water deprivation, with no change in LVP levels and a limited response to water deprivation involving a reduction in renal plasma flow and glomerular filtration rate, with no significant change in tubular function. Both species are able to maintain water and electrolyte homeostasis during periods of drought, highlighting the efficacy of their differing adaptive solutions to the problem of water scarcity, although the hare-wallaby is superior to the rock-wallaby in this respect. Rock wallabies appear to rely primarily on behavioral rather than physiological responses for their survival in the Pilbara and appear to be more vulnerable to extinction in the event of significant habitat modification. The secure nature of their rock habitat, however, means that they have suffered less than hare-wallabies in the recent past.

Buffenstein, R., H. C. K. McCarron, and T. J. Dawson. 2001. Erythrocyte osmotic fragility of red (*Macropus rufus*) and grey (*Macropus fuliginosus* and *Macropus giganteus*) kangaroos and free-ranging sheep of the arid regions of Australia. Journal of Comparative Physiology 171B:41-47.

The mean corpuscular fragility (MCF) of erythrocytes may reflect phylogenetic characteristics as well as an animal's ability to respond to the osmotic challenges associated with cyclic dehydration and rehydration. This type of ecophysiological stress is commonly encountered by animals living in arid regions and low MCF may contribute to their ability to survive and thrive in these xeric habitats. The eastern grey kangaroo has only in recent times extended its range into the arid zone, and is considered a more mesic inhabitant than the red kangaroo. We therefore compared the ability of eastern grey kangaroos and red kangaroos to handle prolonged periods of water restriction, as well as the MCF of the erythrocytes of free-ranging red, eastern grey and western grey kangaroos found at the Fowlers

Gap field station, New South Wales, Australia. In addition, the MCF of free ranging sheep inhabiting the same pastures were used as an experimental control; they are phylogenetically unrelated yet are subject to the same acclimatization stresses. While red kangaroos exhibited greater tolerance of dehydration compared to eastern grey kangaroos, the MCF of all 3 kangaroos species was similar and more resilient to osmotic stresses (MCF, 130 mOsm kg^{-1}) than erythrocytes of sheep (MCF, 220 mOsm kg^{-1}). The MCF did not change with water restriction, however, the erythrocytes of long-term captive populations fed a comparatively better quality diet were more resistant to osmotic shock than the free-ranging animals. Phylogenetic commonality rather than ecophysiological responses to life in the arid zone appeared to influence MCF. The MCF values of sheep corresponded to that of other ovines; similarly the MCF of kangaroos concurred regardless of their preferred habitats, ecological history and differential success in the arid zone.

Dawson, T. J., M. J. S. Denny, E. M. Russell, and B. Ellis. 1975. Water usage and diet preferences of free-ranging kangaroos, sheep, and feral goats in the Australian arid zone during summer. Journal of Zoology 177:1-23.

In much of the arid rangelands of Australia the common large mammalian herbivores are the native marsupials, the red kangaroo (*Megaleia fufa*) and the Euro (*Macropus robustus*), and the introduced eutherian species, the domestic sheep and the feral goat. In the north west of New South Wales a study was carried out to examine the patterns of water usage during summer of these species when they were free ranging in the same area. Drinking frequencies, water turnovers, electrolyte concentrations and diet preferences were determined and information on movements and dispersal from watering points. The marsupials had a much lower water usage than either of the eutherians. The titrated water turnover of the goats was three times and that of the sheep four times the value obtained for kangaroos. While much of the difference between the marsupials and eutherians appeared to be due to fundamental physiological differences the high water usage of sheep was in part related to the high intake of halophytic plants in their diets. The water turnovers of the red kangaroos and Euros were not found to be different. Drinking studies and urine osmolalities suggested, however, that the open plains-dwelling red kangaroos had a higher water requirement than the hill inhabiting Euro. The principle components of the diets of the red kangaroo were grasses; of the Euro, grasses and shrubs; of goats, trees and shrubs; of sheep halophytic shrubs.

Denny, M. J. S. and T. J. Dawson. 1972. Water metabolism of kangaroos. Australian Mammalogy 1:66-67 (Abstract).

Studies on the total body water and water turnover in several species of macropodid are described using a method incorporating a radioactive hydrogen isotope to label the water molecule. The methods are described including the estimation of the equilibrium time for large kangaroos. Results of yard studies on 5 species of macropodid show that water turnover during winter is less than that found in eutherians and that the total body water values are generally higher. A description of a technique used to study water metabolism of kangaroos in the field is given.

Denny, M. J. S. and T. J. Dawson. 1973. A field technique for studying water metabolism of large marsupials. Journal of Wildlife Management 37:574-578.

A study was undertaken on the euro (*Macropus robustus*), a large arid zone kangaroo to develop techniques for the investigation of the water metabolism of large free-living mammals. A two-sample method using titrated water is described. This method requires the capture of an experimental animal at least twice over a period of 2 weeks, but gives reliable values for total body water content and water turnover rates.

Denny M. J. S. and T. J. Dawson. 1975. Effects of dehydration on body-water distribution in desert kangaroos. American Journal of Physiology 229:251-254.

Thermoregulatory studies have been carried out on 2 species of desert kangaroos, the red kangaroo, (*Megaleia rufa*), and the euro or hill kangaroo, (*Macropus robustus*). These animals, like other marsupials, differ markedly from eutherian mammals in several aspects of temperature regulation. The basis of these differences is the lower metabolic rate of marsupials, the level of metabolism in marsupials being 30 – 35% below that of eutherians of similar size. At low air temperatures the kangaroos compensated for their low level of metabolism by having a high total body (core to fur tip) insulation. As expected from the environment in which they live both the red kangaroo and the euro have good thermoregulatory abilities at high ambient temperatures. The low level of metabolism may be advantageous under these conditions because less metabolic heat has to be dissipated by the evaporation of water. Panting appears to be a major avenue of evaporative heat loss in both species. However, preliminary studies suggest that sweating also may be important in the red kangaroo. A difference in the modes of evaporative heat loss would be consistent with the microhabitat selection of the two kangaroos. On hot summer days the red kangaroo is found residing in the sparse shade of small desert trees. The euros, however, are found around rocky outcrops in caves and under rock ledges. The greater reliance of the euro on respiratory water loss can be appreciated since in small caves air movement is low and humidity may be high.

Freudenberger, D. O. and I. D. Hume. 1993. Effects of water restriction on digestive function in two macropodid marsupials from divergent habitats and the feral goat. Journal of Comparative Physiology 163B:247-257.

The effects of water restriction on digestive function in the euro (*Macropus robustus erubescens*) found in the arid zone of inland Australia, the eastern wallaroo (*M.r. robustus*) from more mesic regions of the eastern Australia, and the feral goat found throughout the range of *M. robustus*, were compared to examine some physiological adaptations required by herbivores for the exploitation of arid environments. Eight animals of each species were held in individual metabolism cages in temperature-moderated rooms and given a chopped hay diet ad libitum. Half the animals were restricted to 40 ml water $kg^{-0.80}$ day^{-1}. This was 40%, 32%, and 57% of voluntary drinking water intake in the euro, wallaroo and goat, respectively. All species responded to water restriction by reducing fecal, urinary and evaporative water losses in association with reductions in feed intake. All animals increased urine osmolality and electrolyte concentrations but not to maximal levels, while packed-cell volume and plasma osmolality and electrolyte concentrations were unaffected by water restriction. The euro displayed a suite of characteristics that separated it from the wallaroo in terms of physiological adaptation, including lower voluntary water intake, an increase in fiber digestibility and maintenance of nitrogen balance during water restriction, and lower fecal water efflux associated with a consistently lower fecal water content (54% versus 59% water in the wallaroo during water restriction, $P < 0.05$). The euro's colon was 37% longer ($P < 0.01$) than that of the wallaroo. The goat had the lowest fecal water efflux ($P < 0.05$) and the longest colon ($P < 0.001$). Water restriction did not affect water content in digesta, nor short-chain fatty acid concentrations or production rates in vitro. Total body water, as a proportion of body mass, was depressed ($P< 0.05$) in the macropodids, but not in the goat. The reduction in dietary nitrogen intake, which accompanied water restriction, was partially compensated by an increase in urea degradation in the gut from 68% to 76% of urea synthesis water-restricted macropodids. These responses to water restriction are discusses in relation to those reported in other macropodid and ruminant species.

Hume, I. D. 1982. Water metabolism in Australian marsupials. Pages 195-206 *in* Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

Several studies are discussed in which titrated water has been used to investigate water metabolism in Australian marsupials, particularly arid-zone species. Equilibration of injected titrated water in large kangaroos was slower than in smaller marsupials and similar to that in ruminants and camels, presumably because of the high gut water space of all large forestomach fermenters. Loss of titrated water in urine, and insensible water during equilibration was also similar to that in ruminants. Total body water was similar whether estimated by equilibration or extrapolation. Total body water of small marsupial species (16 g to 6.5 kg body mass) was usually in the range found for small eutherian mammals (56 to 68% of body mass). However, in the larger kangaroos total body water ranged from 73 to 78% of body mass, possibly due to the low body fat content and the high ratio of gut contents to total body mass of kangaroos. In general, the water turnover rate of marsupials is about 30% below that of eutherians; this has been related to their lower metabolic rate. Nevertheless, significant differences in water turnover have been found between some species. It has been suggested that there may be a correlation between water turnover rates measured under ad libitum water availability and the aridity of the animal's habitat. However, this is not always so; differences in behavior and in the water content of the natural diet explain why some marsupials with high ad libitum water turnovers can survive in desert environments. The physiological state of the animals (e.g., lactation) has also been shown to affect water turnover, both in the laboratory and in the field.

Kennedy, P. M. and G. E. Heinsohn. 1974. Water metabolism of two marsupials--the brush-tailed possum, *Trichosurus vulpecula* and the rock-wallaby, *Petrogale inornata* in the wild. Comparative Biochemistry and Physiology 47A:829-834.

Water metabolism of the brush-tailed possum (*Trichosurus vulpecula*) and the rock-wallaby (*Petrogale inornata*) in the free-living, wild animals captured from 1970 – 1972 in the Hervey Range, Australia was studied using titrated water. The water turnovers of wild brush-tailed possums and plain rock-wallabies living in the same environment were determined at intervals throughout 2 years. The water turnover of non-lactating animals of both species did not vary significantly with season and averaged 89.3 ml kg^{-1} day^{-1} for the possums and 80.7 ml kg^{-1} day^{-1} for the rock-wallabies. Lactating females had an increased water turnover and higher titrated water space than non-lactating animals. The daily water turnover of rock-wallabies in cages was 112 ml kg^{-1} in the presence of drinking water, and 80.8 ml kg^{-1} without drinking water.

McCarron, H. C. K., R. Buffenstein, F. D. Fanning, T. J. Dawson. 2001. Free-ranging heart rate, body temperature and energy metabolism in eastern grey kangaroos (*Macropus giganteus*) and red kangaroos (*Macropus rufus*) in the arid regions of south east Australia. Journal of Comparative Physiology 171B: 401-411.

Eastern grey kangaroos (*Macropus giganteus*) are generally regarded as mesic inhabitants. Even though access to drinking water in permanent stock watering troughs is commonly available, these animals are still found in only low densities in arid pastoral areas. We hypothesized that the differential success of red (*Macropus rufus*) and grey kangaroos in the arid zone may be due to higher energy requirements of *M. giganteus* with a concomitant need for increased food rather than limitations imposed by inadequate water access. We test this by indirectly measuring energy expenditure through the monitoring of heart rate by radiotelemetry in semi-free ranging eastern grey and red kangaroos at the University of New South Wales arid zone research station at Fowlers Gap, New South Wales, Australia. Radiotelemetry measurements of heart rate were calibrated against oxygen consumption of animals maintained in an 8-ha enclosure in the arid zone of southeast Australia. Heart rate provided a reliable estimate of oxygen consumption. This well-correlated relationship was curvilinear and was established for each individual. Behavioral observations revealed that both kangaroo species spent most of the day in low energy demanding activities. *M. rufus* were most active at night while *M. giganteus* were more active in the early mornings and late afternoons. Like other marsupials, both species had low field metabolic rates (FMRs). However, *M. giganteus* in keeping with their mesic history had higher FMRs than the more arid-adapted *M. rufus*, particularly during water restriction. Body temperature telemeters revealed a further species difference in that under hot conditions when water is freely available, *M. rufus* exhibits a higher and more labile daytime body temperature than *M. giganteus*. During the hottest part of the day *M. giganteus* maintain body temperature, relying upon increased evaporative cooling mechanisms, such as licking. Indeed, only when access to drinking water was restricted was thermolability evident in *M. giganteus*. Differences in behavior and concomitant energy expenditure may thus contribute substantially to the divergent distribution and abundance of the 2 kangaroo species.

Nagy, K. A., C. Meienberger, S. D. Bradshaw, and R. D. Wooller. 1995. Field metabolic rate of a small marsupial mammal, the honey possum (*Tarsipes rostratus*). Journal of Mammalogy 76:862-866.

Doubly-labeled-water measurements of field metabolic rates and water influx rates in free-ranging honey possums (mean mass = 9.9 g) during late winter of 1986 in Western Australia indicated that these nectarivores had lower daily energy expenditures than did insectivorous, dasyurid marsupials of similar body mass. Honey possums are capable of using torpor, and some individuals apparently did so during this study. Honey possums have an unusually high basal metabolic rate, and their field metabolic rate is ca. 2.7 times the basal rate, which is much lower than the 4.6 - 4.9 times the basal rate in small insectivorous marsupials. Nevertheless, the daily cost of living we measured for honey possums is 75% greater than for eutherian mammals of similar body mass. Small marsupials in general have much higher energy and food requirements in the field than do small eutherian mammals.

Nagy, K. A. and G. C. Suckling. 1985. Field energetics and water balance of sugar gliders, *Petaurus breviceps* (Marsupialia: Petauridae). Australian Journal of Zoology 33:683-691.

Field energetics and water balance of sugar gliders (*Petaurus breviceps*) were studied near South Gippsland, Australia. Doubly labeled water measurements in free-ranging sugar gliders (121 g) indicated that field metabolic rates (FMRs) averaged 62.5 L CO_2 kg^{-1} day^{-1}, which is equivalent to 169 kJ $animal^{-1}$ day^{-1} (3.8 times basal metabolic rate). The females, most of which had small pouch young, weighed significantly less than males (112 v. 135 g), but mass specific FMRs did not differ significantly between sexes. Rates of water influx (mass-specific) also did not differ between sexes, and averaged 208 ml/kg/day. The diet consisted of about two-thirds acacia gum, one-third mixed arthropods, and traces of bark (on a dry mass basis). Percentage apparent assimilation of dietary substances was 88% for dry matter, 89% for energy, 86% for nitrogen and 61% for water. Gliders consumed 11.2 g dry matter of food per animal each day. The diet contained 44% water (fresh mass basis), and provided about half of the water gliders obtained. The other half presumably was ingested as rainwater. In comparison with the ecologically similar Leadbeater's possums (129 g), sugar gliders had much lower metabolic rates while active outside their nests (17.4 v. 31.4 kJ hr^{-1} for possums), primarily because possums spent energy for activity 2.5 times faster than did sugar gliders. This suggests that gliding affords sugar gliders a considerable energetic saving, but portion of time abroad spent foraging and resting, and distribution, abundance and predictability of food resources may also account for this difference.

Nagy, K. A., R. S. Seymour, A. K. Lee, and R. Braithwaite. 1978. Energy and water budgets in free-living (*Antechinus stuartii*) (Marsupialia: Dasyuridae). Journal of Mammalogy 59:60-68.

Rates of water flux and CO_2 production were measured in the Brown Antechinus (*Antechinus stuartii*) in the field in 1974 - 1975 near Healsuilie, Australia, using doubly labeled water. Itemized dry matter, energy, and water budgets were determined for captive animals, and were used to estimate feeding rate and energy and water fluxes in free-living animals. In winter, steady state, field *A. stuartii* ingested 807 kcal kg^{-1} day^{-1} and metabolized 670 kcal kg^{-1} day^{-1}. They consumed about 60% of their body mass in arthropods each day. There were no significant differences between metabolic rates of nonbreeding adult (July) males and females and breeding (August) females; satisfactory data for breeding males were not obtained. Energy expenditures of *A. stuartii* were similar to those of several free-living, small eutherians, after accounting for differences in ambient temperature and body size. However, this comparison is complicated by the use of burrows and occurrence of torpor in some of these mammals. The energetic impact of *A. stuartii* in temperate evergreen forest lies between 60 and 370 kcal kg^{-1} day^{-1}. These rates are similar to those obtained for small eutherian insectivores in other communities. Water fluxes did not differ between males and females in the field, but mean flux rate in steady-state, adult *A. stuartii* in August (734 ml kg^{-1} day^{-1}) was higher than in July (539 ml kg^{-1} day^{-1}), apparently because they ingested rain water that fell abundantly in August. Laboratory results indicate that field animals obtain much more water than they need to maintain water balance.

Nagy, K. A., S. D. Bradshaw, and B. T. Clay. 1991. Field metabolic rate, water flux, and food requirements of short-nosed bandicoots, *Isoodon obesulus* (Marsupialia: Peramelidae). Australian Journal of Zoology 39:299-305.

Field metabolic rates (FMRs) and water influx rates of free-living short-nosed bandicoots (*Isoodon obesulus*) were measured via the doubly labeled water technique on the Harry Waring Marsupial Reserve, Australia, from 14 - 20 April 1980. Bandicoots ranging in body mass from 775 to 1,825 g (mean = 1,230 g) had FMRs averaging 0.908 ml CO_2 g^{-1} hr^{-1}, or 644 kJ day. This is about 2.7 times predicted basal metabolic rate. Water influx rates during the summer measurement period were comparatively low, averaging 88.8 ml kg^{-1} day^{-1}, or 103 ml day^{-1} for a 1,230 g animal. Feeding rate (dry matter intake) was estimated to be 45 g day^{-1}, assuming that the food was half invertebrates and half plant tissues (dry matter intake). Preformed and metabolically produced water from the food can completely account for total water intake, indicating that bandicoots did not drink the rainwater or pond water that was available. The study population (estimated density = 0.63 bandicoots/ha) consumed food at a rate of about 62 g fresh matter ha^{-1} day^{-1} (equivalent to 27 g dry matter or 605 kJ ha^{-1} day^{-1}), which is similar to the food requirements of populations of small eutherian and marsupial insectivores in other habitats.

Small Eutherian Mammals

Alkon, P. U., A. A. Degen, A. Cohen, and H. Pollak. 1986. Seasonal energy requirements and water intakes of Indian crested porcupine (*Hystrix indica*) in captivity. Journal of Mammalogy 67:333-342.

Four adult male Indian Crested Porcupines (*Hystrix indica*), held in covered outdoor enclosures in the Negev Desert, Israel during the summer 1981 and winter 1982, were offered ad libitum water and a dry rodent ration (16.5% protein; 9% fiber; 19.2 kJ g^{-1} dry matter) at four nutritional planes (100%, 80%, 60%, and 49% of ad libitum intake) during consecutive 10-day feeding trials in summer (July - August) and winter (January - February). Water intakes were significantly higher in summer (137 ± 60 ml kg^{-1} day^{-1}; mean ± SD) than winter (53 ± 7 ml kg^{-1} day^{-1}). There were no seasonal differences in ad libitum food intake, in dry matter digestibility (annual mean = 76.5%), or in gross energy digestibility (80.9%). Moreover, maintenance energy requirements (estimated from body mass changes) were similar in both seasons, and averaged 220 kJ kg^{-1} day^{-1}. These results, supported by limited data from free-ranging *H. indica*, indicate that *Hystrix* porcupines are capable of substantial formation and mobilization of fat reserves. This is a useful adaptation in seasonally fluctuating arid environments. Large inverse changes in the proportional composition of body water and body solids are likely such that body mass is an inadequate index to body condition.

Arad, Z. and C. Korine. 1993. Effect of water restriction on energy and water balance and osmoregulation of the fruit bat (*Rousettus aegyptiacus*). Journal of Comparative Physiology 163B:401-405.

The energy, water balance, and osmoregulation of the fruit bat (*Rousettus aegyptiacus*) were studied during normal hydration and during water restriction (oven-dried apple diet) in the laboratory at the Israel Institute of Technology, Haifa, Israel. The water input and output were balanced during both normal hydration and water restriction. The kidney of the fruit bat is well adapted to handle the water load from its fruit diet by excreting large volumes (14% of the body mass per day) of dilute urine (113 ± 25 mOsm kg^{-1} water) as well as reducing urine volume (-95%) and increasing urine concentration (555 ± 280 mOsm kg^{-1} water) during water restriction. The hemocrit, plasma hemoglobin, and total protein concentrations did not increase during water restriction and heat exposure, suggesting the conservation of plasma volume. Gross energy intake was not affected by water restriction. However, digested energy intake and digestibility were significantly reduced. The effective regulation of energy and water budgets during water restriction suggests that the fruit bat can cope with seasonal climatic changes and with variable fruit supply during various seasons.

Baverstock, P. R. and C. H. S. Watts. 1975. Water balance of small lactating rodents--I. ad libitum water intakes and effects of water restriction on growth of young. Comparative Biochemistry and Physiology 50A:819-825.

Ad libitum water consumption of lactating and non-lactating females of the xeric-adapted rodents (*Notomys alexis, N. cervinus, N. mitchellii, Pseudomys australis,* and *Mus musculus*) was studied in the laboratory. The increase in ad libitum water consumption during lactation was surprisingly small, particularly at small litter sizes. The effects of restricting the water intake of the lactating female on growth of the young were studied in *N. alexis* and *M. musculus*. In both species, lactation was sustained during water restriction but at reduced levels. The young were able to survive the reduced milk intake, but grew at a depressed rate.

Baverstock, P. R., L. Spencer, and C. Pollard. 1976. Water balance of small lactating rodents--II. Concentration and composition of milk of females on ad libitum and restricted water intakes. Comparative Biochemistry and Physiology 53A:47-52.

The concentration and composition of the milk of lactating rodents (*Notomys alexis, N. mitchellii, N. cervinus, Pseudomys australis*, and *Mus musculus*) on ad libitum and restricted water intakes was determined. Australian desert mice and laboratory house mice produced milk at concentrations above the average eutherian level. The major solid constituent of milk in all species was fat. During lactation, percent fat increased, but sugar and protein did not change. Water restriction tends to increase solid concentration in *N. cervinus, P. australis*, and *M. musculus*, with the increase being entirely due to fat. Milk concentration does not appear to be important in the water-balance of lactation of Australian desert rodents.

Bell, G. P., G. A. Bartholomew, and K. A. Nagy. 1986. The roles of energetics, water economy, foraging behavior, and geothermal refugia in the distribution of the bat, *Macrotus californicus*. Journal of Comparative Physiology 156B:441-450.

Energy metabolism, thermoregulation, and water flux of (*Macrotus californicus*) the most northerly representative of the Phyllostomidae, were studied in 1983 - 1984 in the laboratory at the University of California, Los Angeles, using standard methods, and energy metabolism and water fluxes were studied in the field using the doubly labeled water method together with a time budget. Daily energy expenditures of free-living bats averaged 22.8 kJ during the winter study period. Approximately 60% of this was allocated to resting metabolism costs while in the primary roosts (22hr day^{-1}). *Macrotus californicus* is unable to use torpor. The thermoneutral zone (TNZ) in this species is narrow (33 to 40 ºC) and metabolic rate increased rapidly as ambient temperature decreased below the TNZ. Basal metabolic rate was 1.25 ml O_2 g^{-1} hr^{-1}, or 24 J g^{-1} hr^{-1}. Total thermal conductance below the TNZ was 1.8 mW g^{-1} ºC, similar to values measured for other bats. Evaporative water loss showed a hyperbolic increase with increasing ambient temperature, and was approximately 1% of total body mass hr^{-1} in the TNZ. The success of these bats as year round residents in the deserts in the southwestern United States is probably not due to special physiological adaptations, but to roosting and foraging behavior. They use geothermally-heated winter roost sites (stable year-round temperatures of approximately 29 ºC), which minimize energy expenditures, and they have an energetically frugal pattern of foraging that relies on visual prey location. These seem to be the two major factors that have allowed *M. californicus* to invade the temperate zone.

Bintz, G. L. and W. W. Macken. 1980. The effect of water availability on tissue catabolism during starvation in Richardson's ground squirrels. Comparative Biochemistry and Physiology 65A:181-186.

Richardson's ground squirrels were starved for 6 days with no water or with limited water to compare the effect of these stresses on nitrogen catabolism and excretion. Starved ground squirrels fed 5.0 g of celery daily for five days catabolized 16% of the carcass mass, whereas starved ground squirrels with no water catabolized 25% of the carcass mass and excreted 57% more nitrogen in the urine. The availability of water had a protein sparing effect during starvation, despite the fact that animals of both groups derived more than four-fifths of their energy requirements from adipose tissue. Ground squirrels did not appear to retain large amounts of catabolized nitrogen during starvation to reduce urinary water loss.

Buffenstein, R. 1985. The effect of a high fiber diet on energy and water balance in two Namib Desert rodents. Journal of Comparative Physiology 155B:211-218.

The effect of dietary fiber content on food consumption, digestive ability, and water balance was studied in the rock rat (*Aethomys namaquensis*) and pygmy gerbil (*Gerbillurus paeba*) in the Namibian Desert. In addition changes in these factors were monitored when water was withheld. Daily energy expenditure (DEE) for *A. namaquensis* remained fairly constant and similar to that predicted by mass despite changes in food and water regimes. The DEE of *G. paeba* was more variable. On a millet (low-fiber) diet with ad libitum water DEE was 35% higher than the expected value. This increased still further within the first week of water deprivation before dropping back to pre-water deprivational levels once mass had stabilized. On the high fiber diet, the DEE of *G. paeba* was similar to that predicted by mass when water was freely available. This was reduced by half when the animals were water stressed, suggesting that *G. paeba* might employ torpor under these circumstances. Water balance was assessed by measuring water intake and loss. Fecal water content when maintained on a millet diet was similar in both species, irrespective of whether water was freely available or withheld. However, urine concentrations and estimated evaporative water losses were higher in *G. paeba*. Observed differences in water loss are largely a function of variables related to weight specific metabolic rate. Differential water losses were offset by differences in metabolic water production, enabling both species to attain a positive water balance and survive indefinitely on a millet diet. When provided with a more fibrous diet, low assimilation efficiency and the resulting increase in fecal production, coupled with increased fecal water content, increased fecal water loss to such an extent that it precluded the maintenance of a positive water balance in either species. Despite increased urine concentration and a decline in evaporative water loss, both species rapidly succumbed to chronic water deprivation.

Chevalier, C. D. 1989. Field energetics and water balance of desert-dwelling ringtail cats, *Bassariscus astutus* (Carnivora: procyonidae). American Zoologist 29:8A.

Field metabolic rates (FMR), water flux rates (WFR), and total body water (TBW) were estimated using doubly labeled water (tritium and oxygen-18) for non-reproductive, adult ringtail cats during late summer in the Sonoran Desert, central Arizona. Male and female ringtail cats differed in mass (males 838.1g, SE = 11.919; females, 656.3 g, SE = 22.844; *P* = 0.02) and in TBW:Mb ratio (males 0.697, SE = 0.025; females 0.781 g, SE 0= 0.006, *P* = 0.02; combined: .739 g, SE = 0.020). No other differences between sexes were detectable, and no character scaled with mass. The data for sexes were combined for further analyses. Field metabolic rates averaged 19.49 (SE = 1.278) L CO_2 day^{-1} (approximately 472 kJ day^{-1}). This value approximated 81% of predicted FMR for desert eutherians, and 2.69 times minimum resting metabolism. Ringtail cats experienced no significant mass change and water intake, which was only slightly greater than water loss was 141% of predicted field WFR for desert eutherians and 153% of predicted standard WFR for arid-dwelling mammals.

Culebras, J. M., G. F. Fitzpatrick, M. F. Brennan, C. M. Boyden, and F. D. Moore. 1977. Total body water and the exchangeable hydrogen II. A review of comparative data from animals based on isotope dilution and desiccation, with a report of new data from the rat. American Journal of Physiology 232:R60-65.

Total body water determined by tritium space could be factitiously elevated by exchangeable H^+ contained within water-soluble chemical configurations. Should this nonaqueous exchangeable H^+ total body water measurement by titrated water dilution would display a systematic upward and nonrandom error. Total body water was measured by titrated water dilution and subsequently by total body desiccation in 21 rats (*Rattus norvegicus*). Total body water was 71.4 ± 2.4% by titrated water dilution and 70.2 ± 1.5% by body desiccation. Analysis of variance of total body water vs. body weight showed a highly significant correlation both with desiccation and dilution. Covariance analysis of both methods showed no difference in slope. There was a difference in variance and means. Tritium space is 1.2% of body mass larger than total body water measured by desiccation. Total body water measured by titrated water dilution is accurate to within < 2% error.

Deavers, D. R. and J. W. Hudson. 1979. Water metabolism and estimated field water budgets in two rodents (*Clethrionomys gapperi* and *Peromyscus leucopus*) and an insectivore (*Blarina brevicauda*) inhabiting the same mesic environment. Physiological Zoology 52:37-152.

Water metabolism and field water budgets were estimated in 2 rodents (*Clethrionomys gapperi* and *Peromyscus leucopus*) and an insectivore (*Blarina brevicauda*) captured in Tompkins County, New York. At an ambient temperature of 20 ºC shrews and voles lose water at about twice the rate predicted from body mass, while the white-footed mouse loses about one-third more water per day than predicted. Cold exposure (5 ºC) caused significant increases in water loss in the three species, and this increase was due to increased fecal and urinary losses while evaporative loss was not significantly changed; during cold exposure *P. leucopus* lost much less water than shrews and voles. When drinking water was reduced to the minimum requirements at both 5 ºC and 20 ºC, the three species showed marked reductions in urinary, fecal, and evaporative losses. Minimum water requirements of *P. leucopus* were much lower than those of shrews or voles. On minimum water regimes urine concentration was significantly higher in *P. leucopus* (2,953 mOsm L^{-1}) than in shrews (1,802 mOsm L^{-1}) or voles (1,758 mOsm L^{-1}), and ability to concentrate urine in these three as well as numerous other mammals correlated well with relative medullary thickness of the kidneys. Water budgets for the three species were calculated based on energy requirements; the protein, salt and water intake resulting from feeding and obligatory water loss. These calculations revealed: (1) shrews and voles, despite their high water requirements, are in effect forced to consume large quantities of low-caloric and high water-content food with consequent intake of large quantities of preformed water and probably remain in water balance throughout the year; (2) *P. leucopus* may need to supplement their diet with small amounts of drinking water in the winter, but their summer diet probably supplies sufficient water.

Degen A A. 1997. Ecophysiology of Small Desert Mammals. Springer-Verlag, Berlin, Germany, 296p.

This book reviews the ecophysiology of small desert mammals including issues related to body size and allometry, heat transfer and body temperature, behavioral adaptations, water requirements and water balance, energy requirements and energy flux, and reproduction

Degen, A. A. and M. Kam. 1992. Water intake in two coexisting desert rodents, *Acomys cahirinus* and *Gerbillus dasyurus*. Journal of Mammalogy 73:201-206.

The common spiny mouse (*Acomys cahirinus*) and Wagner's gerbil (*Gerbillus dasyurus*), are omnivorous Old World rodents that coexist in rocky habitats in the deserts of Israel. They differ in their diets in that *A. cahirinus* consumes proportionately more snails and animal matter than *G. dasyurus* and *G. dasyurus* consumes proportionately more seeds than *A. cahirinus*. Rodents were offered seeds and either water ad libitum, ca. 50% of ad libitum. Total water intake, or denied water. Both species were able to maintain steady state body mass on both ad libitum and 50% ad libitum water. Furthermore, both species lost body mass when denied water. However, the daily rate of loss of body mass of *G. dasyurus* was slower than that of *A. cahirinus* both in absolute (0.72 and 1.72 g) and in relative (10.9 and 21.9% body mass $g^{-0.54}$) terms. Dry matter digestibility and metabolizable energy from seeds were similar between species on the ad libitum and 50% ad libitum water treatments and both species combined averaged 90.9% of dry matter and 88.8% of gross energy, respectively. These values were similar to those found for granivorous rodents in general.

Downs, C. T. and M. R. Perrin. 1990. The effect of diet on water and energy turnover rates of four *Gerbillurus* species in captivity. Journal of Zoology 222:215-233.

The effects of diets differing in energy and water content on the energy turnover rates and water flux of four *Gerbillurus* species live-trapped during 1986 and 1987in South West Africa/Namibia and the Cape Province, South Africa were examined in the laboratory. *Gerbillurus tytonis*, a dune species, had higher than predicted daily energy expenditure (DEE) and high water turnover rates (WTR) for a small desert mammal. The large *G. setzeri*, which occurs on gravel plains, has slightly lower than predicted DEE and WTR than the other gerbil species studied. The *Gerbillurus* species examined have DEE and WTR that are affected by the protein content and potential water yield of food eaten. The importance of diet selection for water and energy budgets are discussed as adaptive strategies employed for survival and reproduction within the southern African arid zone.

Duxbury, K. J. and M. R. Perrin. 1992. Thermal biology and water turnover rate in the Cape gerbil, *Tatera afra* (Gerbillidae). Journal of Thermal Biology 17:199-208.

Oxygen consumption (V_{O2}), thermal conductance (C_d and C_{min}), body temperature (T_b) and evaporative water loss (EWL) of the Cape gerbil (*Tatera afra*) were measured in the laboratory at in the laboratory at the University of Natal, South Africa, at ambient temperatures (T_a) between 5 and 35° C. *T. afra* is not well adapted to high T_a. Above 30° C, hyperthermia occurs, despite elevated C_d, C_{min} and EWL. Peripheral vasodilation, salivation and urination are short-term responses that contribute to delaying the onset of hyperthermia. The water turnover rate (WTR) is higher (48%) in the field than in the laboratory owing to activity associated with foraging behavior, predator avoidance and socialization. The relatively mild and mesic environment permits a higher WTR than in arid zone gerbils. Basal metabolic rate (BMR) is higher (49%) than the average value for other cricetid rodents. It is hypothesized that this is associated with herbivory and a relatively low T_a.

Farrell, B. C. and D. P. Christian. 1987. Energy and water requirements of lactation in the North American porcupine, *Erethizon dorsatum*. Comparative Biochemistry and Physiology 88A:695-700.

Energy and water requirements of lactation in the North American porcupine (*Erethizon dorsatum*) were studied at the University of Minnesota, Duluth. Energy and water requirements of lactating porcupines were compared with results of previous studies on energetics of reproduction in small-bodied rodents. Mass-specific food and water intake of control and lactating porcupines was examined throughout the 68 - 78 days of lactation. Water intake of lactating females was 16% higher than that of non-lactating animals. Digestive efficiency of porcupines fed commercial rabbit chow was 54 - 60%; there was no significant difference in efficiency between lactating and non-lactating animals. Total mean energetic intake throughout lactation was only 17% greater than that of non-lactating animals. Reproductive rate and costs of lactation in porcupines are considerably less than in other rodents and other comparably sized mammals, but the amount of energy allocated to each offspring is quite high. The reproductive pattern of porcupines is associated with low juvenile mortality and long adult lifespan (both of which reflect the porcupine's protective morphology), and may be related to the quality of winter diets.

Gettinger, R. D. 1984. Energy and water metabolism of free-ranging pocket gophers, *Thomomys bottae*. Ecology 65:740-751.

Seasonal influences on the patterns of energy and water metabolism by free-ranging pocket gophers, (*Thomomys bottae*), were investigated using $^3H_2$ ^{18}O procedures. Metabolic rates of adult, nonreproductive gophers did not differ significantly in summer, winter, or spring (CO_2, 2.34 ml g^{-1} hr^{-1}; 1416 kJ kg^{-1} day^{-1}). Efficiency of energy assimilation (54%) by gophers consuming natural diets in the laboratory did not differ between summer and winter, even though composition of the diet changes seasonally. Calculated feeding rates (dry food, 119 g kg^{-1} day^{-1}), also did not differ with season. Harvesting rates were more than two times feeding rates. Construction of energy budgets revealed that if annual vegetation is abundant, precluding the necessity for gophers to burrow extensively for food, energy is not limited in any season. Gophers remained in water balance (influx = efflux) in all seasons. However, influx was significantly greater during spring (518 ml kg^{-1} day^{-1}) than during summer or winter (256 ml kg^{-1} day^{-1}). In free-ranging gophers, water influx was three to six times the minimum water flux of gophers than were maintained on water-restricted diets in the laboratory. In spite of their existence in arid macroenvironments, gophers appear to be "water-dependent." Diet selection and occupation of humid burrow systems appear to be prerequisites for existence in such habitats.

Grenot, C. J. 1989. Ecophysiological characteristics of small mammals in arid zones (North America, Australia, Namibia, Sahara). Mammalia 53:478. (Abstract).

A variety of physiological and behavioral solutions are employed by small mammals to challenge the desert environment. A comparative study of the ecophysiological responses to water stress was carried out with species from different arid regions. Various rodents conserve water and energy effectively, obtain adequate water, and energy throughout the year without drinking, by varying their diet appropriately among seed, vegetation and arthropods. Despite their taxonomic differences, ecophysical similarities can occur in various small mammals form different intercontinental arid regions. A rich diversity of desert adaptations remains to be found. It seems that each species copes differently in response to the highly variable and unpredictable climatic conditions. The plasticity of mammal physiology and behavior has been underestimated and future studies have to be pursued for each species, with the same methodology and careful control.

Hayes, J. P., C. A. Bible, and J. D. Boone. 1998. Repeatability of mammalian physiology: evaporative water loss and oxygen consumption of *Dipodomys merriami*. Journal of Mammalogy 79:475-485.

Phenotypic measurements (e.g., body mass, metabolic rate) made at 1 point in time are often assumed to represent measurements made at other times. However, if traits are not repeatable over time, inferences about ecological, environmental, or other correlates of the trait could be misleading. We found that evaporative water loss, oxygen consumption, resting metabolic rate, and their residuals from body mass were significantly repeatable (intraclass correlations generally > 0.6) in Merriam's kangaroo rats (*Dipodomys merriami*). Nevertheless, our data, plus a review of the scant data on repeatability of mammalian physiological traits, show that repeatability typically is less than perfect (i.e., <1). Consequently, investigators studying physiological performance of mammals should not assume that the traits they study are good indicators of performance at other points in time.

Hewitt, S., J. F. Wheldrake, and R. V. Baudinette. 1981. Water balance and renal function in the Australian desert rodent N*otomys alexis*: the effect of diet on water turnover rate, glomerular filtration rate, renal plasma flow and renal blood flow. Comparative Biochemistry and Physiology 68A:405-410.

Water balance and renal function were studied in the Australian desert rodent (*Notomys alexis*) at Flinders University, Australia. Water turnover rate, glomerular filtration rate and renal plasma and blood flow rates have been measured in individuals of the Australian desert rodent under conditions of acute and chronic water deprivation and high nitrogen diet. When these parameters are compared with values predicted allometrically the extreme ability of the species to conserve water is apparent only in those groups subjected to water stress. While a reversible reduction in renal function is evident upon water deprivation, the major function in water conservation under these conditions is the renal reabsorption of water at a post-filtration stage.

Holleman, D. F. and R. A. Dieterich. 1973. Body water content and turnover in several species of rodents as evaluated by the titrated water method. Journal of Mammalogy 54:456-465.

Body water content and turnover were determined for deer mouse (*Peromyscus maniculatus*), meadow vole (*Microtus pennsylvanicus*), tundra vole (*M. oeconomus*), insular vole (*M. abbreviatus*), vesper mouse (*Calomys ducilla*), collared lemming (*Dicrostonyx groenlandicus*), Egyptian spiny mouse (*Acomys cahirinus*), gerbil (*Meriones unguiculatus*), Norway rat (*Rattus norvegicus*), chinchilla (*Chinchilla laniger*), Guinea pig (*Cavia porcellus*), and muskrat (*Odonata zibithicus*) using the titrated water method. All experimental rodents were maintained under similar laboratory conditions. Measurements of body water content indicated wide variability in the degree of body fatness. Mean values of body fat as a percentage of body mass ranged from 3.0 to 38.8% for the 12 species. The equation, WTR = n $(LBM)^b$, was used to relate water transfer rate (WTR) to lean body mass (LBM). The overall exponent (b) for the 12 species of rodents equaled 0.78 ± 0.044 (SD) and represents the interspecies estimate. The exponent computed for three species of the genus *Microtus* equaled 0.69 ± 0.093. Specific water transfer rates ranged from 0.34 to 1.76 ml $g^{-0.69}$ day^{-1}. In general, water transfer rates ere correlated with water availability in the natural habitat of each species. Species inhabiting moist areas had higher specific water transfer rates while species inhabiting arid regions had lower specific water transfer rates.

Horowitz, M. and J. H. Adler. 1983. Plasma volume regulation during heat stress: albumin synthesis vs. capillary permeability. A comparison between desert and non-desert species. Comparative Biochemistry and Physiology 75A:105-110.

Plasma albumin synthesis was measured in rats (*Rattus norvegicus*) and sand rats (*Psammomys obesus*) during heat acclimation (34 ºC) and following thermal dehydration (37 ºC) in a laboratory using ^{3}H l-leucine as a tracer. In rats, heat acclimation resulted in 48% reduction in albumin synthesis. In sand rats, synthesis increased by 160%. Both species achieved a new stabilization of the synthetic system on the fifth day of acclimation. Following thermal dehydration albumin synthesis increased in rats and decreased in sand rats. Acclimation did not alter this response. In our dehydrating system plasma volume was maintained via maintenance of adequate albumin mass. In rats, albumin synthesis apparently contributes to this process. In sand rats, vascular permeability rather than albumin synthesis plays this role.

Kam, M. and A. A. Degen 1992. Effect of air temperature on energy and water balance of *Psammomys obesus*. Journal of Mammalogy 73:207-214.

Fat sand rats (*Psammomys obesus*) are diurnal, desert-dwelling gerbillid rodents that can survive while consuming solely the saltbush (*Atriplex halimus*), a chenopod high in electrolytes. To reduce electrolyte intake, fat sand rats scrape off the outer layers of leaves with their teeth before consuming them. We measured energy and water balances of fat sand rats offered *A. halimus* and maintained at 15, 21, and 34 ºC. They maintained body mass at 21 ºC, gained body mass at 34 ºC, but lost body mass at 15 ºC. The dry matter intake was not significantly different among treatments, but dry matter digestibility and metabolizable energy of *A. halimus* was higher for fat sand rats at 34 ºC than at 15 and 21 ºC. Fat sand rats at 34 ºC produced the most concentrated urine and scraped off the most leaf material. As a result these fat sand rats secreted the lowest volume of urine, thus providing them with water required for evaporative cooling.

Kitahara, E. 1993. Relationships between habitat and renal function in water conservation in the Anderson's red-backed vole, *Eothenomys andersoni* on the Kii Peninsula, Japan. Japan. Forestry and Forest Products Research Institute Bulletin No 364:115-124.

The present study on the distribution and renal structure of *E. andersoni* on the Kii Peninsula revealed the following: 1) the distribution of *E. andersoni* was vertically broad and horizontally limited to a certain range in a part of Nara, Mie and Wakayama Prefectures; 2) the distribution was strongly influenced by the amount of annual rainfall in the areas of Kii Peninsula, Japan, from 1985 - 1990. *E. andersoni* alone occurred in areas whose annual rainfall exceeded 3,000 mm and coexisted with *E. smithii* in areas of about of about 2,500 to 3,000 mm, while only *E. smithii* was caught in areas with a rainfall of less than 2,000mm; and 3) there were significant differences (P<0.05) in the thickness (PMT) and area of the renal medulla measured at the midsagittal section between E. *andersoni* (PMT 73.1 ± 2.3, PMA 41.3 ± 3.6, n = 6) and *E. smithii* (PMT 77.7 ± 4.6, PMA 48.4 ± 4.9, n = 9); consequently *E. andersoni* had the weaker kidney against water shortage stress in comparison with *E. smithii*.

Korine, C. and Z. Arad. 1993. Effect of water restriction on temperature regulation of the fruit-bat *Rousettus aegyptiacus*. Journal of Thermal Biology 18:61-69.

The thermoregulatory responses of the fruit-bat (*Rousettus aegyptiacus*) were studied over a wide range of ambient temperature during normal hydration and during water restriction in Hiafa, Israel. The thermoneutral zone of the normally hydrated fruit-bat ranged between 31 - 36 ºC. Oxygen consumption in this range averaged 0.95 ± 0.15 ml g^{-1} hr^{-1}. Evaporative water loss and respiration frequency during normal hydration increased as power functions of ambient temperature and were significantly correlated ($P <$ 0.02). The normally-hydrated, heat exposed fruit-bat effectively regulated its body temperature and dissipated the total metabolic heat production by evaporative cooling. In bats fed on oven-dried apples (water restriction), body mass decreased by 20.72 ± 2.78%. Oxygen consumption between 32 - 36 ºC increased significantly and body temperature was relatively high. Evaporative water loss decreased significantly, except at 36 ºC where evaporative water loss was not significantly different from that during normal hydration, suggesting the preference for body temperature regulation at the cost of increased water loss. At this ambient temperature, dry thermal conductance increased significantly compared to normal hydration, facilitating non-evaporative heat loss. We conclude that the Israeli population of *Rousettus aegyptiacus* is adapted to the relatively warm climate and can cope with decreased water content in its exclusive fruit diet and effectively regulate its body temperature and metabolic rate.

Lindstedt, S. L. 1980. Energetics and water economy of the smallest desert mammal. Physiological Zoology 53:82-97.

The physiological and ecological coupling of the desert shrew (*Notiosorex crawford*) to its environment has been examined in wild captured shrews from Cochise and Pima counties, Arizona. Mean standard metabolism between 32 and 36 ºC equaled 17.12 W/kg. Below 32 ºC metabolic rate increased linearly to a high of 79 W/kg at 10 C. The heat transfer coefficient was 3.05 W kg^{-1} $ºC^{-1}$ below 32 ºC. At 37 ºC air temperature, heat lost by the evaporation of water equaled one-half of the total metabolic heat production. The kidney medullary thickness of the desert shrew is high, suggesting a considerable urine concentrating ability and only scant urinary water losses. By thus minimizing urinary and respiratory water losses, the desert shrew can maintain water balance without drinking even when some water is required for thermoregulation. The climate space of the desert shrew was determined and found to differ from that of the masked shrew. The desert shrew can tolerate higher temperatures than can the masked shrew in full sunlight (23 vs. 6 ºC) in its nest (38 vs. 24 ºC) and under the night sky (42 vs. 35 ºC). Energy metabolism, water loss, and daytime activity are all lower in the desert shrew than in other shrew species.

MacMillen, R. E. 1983. Water regulation in *Peromyscus.* Journal of Mammalogy 64:38-47.

New-World mice of the genus *Peromyscus* are nearly ubiquitous, and their omnivorous diets are accompanied by intermediate efficiency in water regulation when compared to dry-food or moist-food specialists among rodents. In virtually all aspects of water economy thus far studied (mass and urinary responses to water deprivation and saline drinking solutions, rates of evaporative water loss), the performances of *Peromyscus* are modest, with the single exception of *P. crinitus*; this is a small desert rodent species that is nearly independent of dietary preformed water. Among *Peromyscus* there is considerable interspecific variability in efficiency of water regulation, and nearly as great intraspecific variability within west coast races of *P. maniculatus*. This variability appears to be related to food habits and/or habitat climate, but the specific roles of these factors have yet to be elucidated. The most striking adaptation to drought among *Peromyscus* is the use of torpor and summer dormancy by *P. eremicus*, enabling prolonged escape from demanding surface conditions of water stress. These thermoregulatory adjustments may be common among arid-inhabiting *Peromyscus* and contribute substantially to their powers of water regulation.

Mangione, A. M., D. Dearing, and W. Karasov. 1998. A plant secondary metabolite increases minimum water requirements of desert woodrats. American Zoologist 38:114A. Final Program and Abstracts of the Annual Meeting of the Society for Integrative and Comparative Biology, Denver, Colorado, January 6-10, 1999 (Abstract)

The effects of plant secondary metabolites on water balance has received little attention. Desert woodrats (*Neotoma lepida*) fed a diet with phenolic resin extracted from creosote bush (*Larrea tridentata*) increased their ad libitum water intake (3 – 12 ml day^{-1}) depending on diet resin concentration. This increase, if obligatory, would reflect at least a doubling of the minimum preformed water requirement of desert woodrats. The hypothesis that creosote bush phenolic resin would increase the minimum water requirements of woodrats was tested. In two experiments the minimum water requirement of woodrats fed dry diet (alfalfa pellets) with and without resin added was examined. Drinking water was offered in decreasing amounts until woodrats could just maintain constant body mass. In both experiments the minimum drinking water of woodrats fed resin was significantly higher than controls by about 15% (ca. 1 ml day^{-1}). Several potential causes of increased water loss associated with the increase in preformed water requirements were tested. Fecal water loss rate was significantly higher in woodrats eating resin. Neither water content of the urine, urine water loss rate, nor evaporative water loss rate was significantly affected by resin.

McManus, J. J. 1974. Bioenergetics and water requirements of the redback vole, *Clethrionomys gapperi*. Journal of Mammalogy 55:30-44.

The effects of temperature on food consumption, assimilation efficiency, oxygen uptake, and water requirements of the redback vole (*Clethrionomys gapperi*) were studied in a laboratory at Cornell University, Ithaca, New York. Gross and net caloric intakes varied inversely with temperature and the relationships were geometric rather than linear. Assimilation efficiency was maximal at 25 ºC (78.9%) and lowest at 10 ºC (72.2%). Manometric measurements of oxygen consumption indicated a resting metabolic rate of 31.4 ml O_2 g^{-1} hr^{-1}, a thermoneutral zone from 25 to 28 ºC, and a thermal conductance of 0.255 ml O_2 g^{-1} hr^{-1} ºC^{-1}. Water consumption increased with temperatures above and below 15 ºC. Minimum water requirements, including free water, food moisture, and metabolic water, were 0.64 g water g^{-1} day^{-1} at 15 ºC. These date are compared to those of other small mammals.

Muller, E. F. 1979. Energy metabolism, thermoregulation and water budget in the slow loris (*Nycticebus coucang*, Boddaert 1785). Comparative Biochemistry and Physiology 64A:109-119.

Energy metabolism, thermoregulation and water budget was studied in captive slow loris (*Nycticebus coucang*) in a laboratory setting. At ambient temperatures from 5 - 37 ºC the mean rectal temperature varied from 32.2 - 38.5 ºC. The thermoneutral zone extended from 25 - 33 ºC, the basal metabolic rate (0.229 - 0.244 ml O_2 g^{-1} hr^{-1}) being only 40% of the mammalian standard. An excellent thermal insulation provided by the thick fur and a counter current heat-exchange in the limbs could be demonstrated. Thermoregulatory responses at ambient temperatures above 35 ºC were insufficient, mainly due to restricted capacities for evaporative cooling. The daily fresh water consumption was very low (9 ml water day^{-1}). The slow loris kidney is able to produce a rather highly concentrated urine (3,000 mOsm kg^{-1} water). The results were used to establish a daily energy budget under thermoneutral conditions.

Mutze, G. J., B. Green and K. Newgrain. 1991. Water flux and energy use in wild house mice (*Mus domesticus*) and the impact of seasonal aridity on breeding and population levels. Oecologia 88:529-538.

Water turnover rate (WTR), urine concentration and field metabolic rate (FMR) were examined in house mice, *Mus domesticus*, permanently inhabiting roadside verge areas and seasonally invading crops in semi-arid wheatlands in South Australia. FMR was approximately proportional to body mass $^{0.5}$ and mean values varied from 4.8 ml CO_2 g^{-1} hr^{-1} (2.9 kJ g^{-1} day^{-1}) in autumn and winter, to 7.0 ml CO_2 g^{-1} hr^{-1} (4.2 kJ g^{-1} day^{-1}) in maturing crops during spring. WTR was independent of body mass, indicating that larger mice were selecting a diet containing moister foods. WTR was low in summer and high in winter, and in mice from crops varied from 165 ml L^{-1} body water day^{-1} (122 ml kg^{-1} day^{-1}) to 1,000 ml L^{-1} day^{-1} (725 ml kg^{-1} day^{-1}). Seasonal changes in WTR were less extreme on the roadside, where a greater diversity of food was available. In the crops, breeding occurred throughout the summer during two of three years, but the population increased only in the one summer when mice had marginally higher WTR. On the roadside, breeding and population growth were continuous during summer, except in a drought year. Average urine concentration was inversely related to WTR, and varied form 2.0 to 4.8 osm L^{-1}. The data indicate that the water conserving abilities of mice equal those of many desert rodents. The water conserving abilities of mice living in crops during summer were fully extended, and in some year aridity limited breeding success and population levels. The degree of moisture stress to which mice are exposed during summer appears to depend not only on rainfall but also on other factors such as availability of food and shelter, and the level of weed infestation in crops.

Nagy, K. A. 1994. Seasonal water, energy and food use by free-living, arid-habitat mammals. Australian Journal of Zoology 42: 55-63.

In arid ecosystems, the dry season is probably an especially challenging time for animals to find adequate food and water resources. Both stressful and benevolent times of the year can be identified by measuring rates of water and energy use (with doubly labeled water), diet and behavior throughout a year in free-ranging animals. Seasonal water, energy and food use were studied in free-living jackrabbits (*Lepus californicus*), Merriam's kangaroo rats (*Dipodomys merriami*), and antelope ground squirrels (*Ammospermophilus leucurus*) in the Mojave Desert, California, and springbok, antelope (*Antidorcas marsupialis*) in the Kalahari Gemsbok National Park in Southern Africa. Jackrabbits are strict herbivores, and most Mojave Desert individuals have no access to drinking water, and depend on their food for their water. When vegetation dries up during the summer drought, most jackrabbits apparently die of dehydration and malnutrition, but populations are replenished by bountiful reproduction after winter rains. However, springbok antelope, also strict herbivores, can maintain water and energy balance throughout the year in the Kalahari in southern Africa by drinking water is available, but, if not, they obtain enough water from dietary plants, probably by feeding before dawn, when food items have taken up water from the humid air. Antelope ground squirrels are omnivorous in the Mojave Desert, and are active diurnally. They have lower water and energy requirements than non-desert mammals of the same body mass, like many desert mammals, but their ability to find succulent plant or animal foods in all seasons appears to be their primary survival tool. On the other hand, Merriam's kangaroo rats are essentially nocturnal, and were thought to be strict granivores that never drank. A recent study, done throughout a year in the Mojave Desert, confirms their lack of drinking, but revelas that they eat much green vegetation in late winter and spring, probably in connection with reproduction. They obtain additional water throughout the year by caching dry seeds in humid burrows, where seeds take up water hydroscopically before being eaten. Although springbok, antelope ground squirrels and Merriam's kangaroo rats were in negative energy and water balance at times during the year, only jackrabbits were severely stressed by the dry season. Each species has a unique suite of desert survival mechanisms. Future research should include carnivores as well as arid-habitat marsupials.

Nagy, K. A. and M. J. Gruchacz. 1994. Seasonal water and energy metabolism of the desert-dwelling kangaroo rat (*Dipodomys merriami*). Physiological Zoology 67:1461-1478.

Free-living Merriam’s kangaroo rats (*Dipodomys merriami*) were studied in the Mojave Desert, California in 1988 – 1989; kangaroo rats did not drink, even when abundant rainwater was available for short periods in winter and summer, but they still obtained much more water than expected from a diet of dry seeds alone. Year-round measurements of water influx rates and field metabolic rates (via doubly labeled water), diet composition (stomach content analysis), and body mass changes were used to evaluate water and energy balance during each month of the year. From late spring (May) through midwinter (December), kangaroo rats ate primarily the seeds of creosote bush (*Larrea tridentata*) and were able to maintain water and energy balance on this diet even during summer drought. Dry seeds collected at the surface apparently were cached in burrows where hydroscopic uptake of water from humid air increased the succulence of seeds before ingestion. In late winter and early spring, kangaroo rats obtained abundant water and energy from their diet of green vegetation (90% dry mass) and arthropods (10%). Only in late April and early May did these animals lose body mass, but that was primarily due to reproductive effort (lactation) by females. Thus, at no time of year were kangaroo rats distressed by their comparatively dry, hot, and barren desert habitat. Field metabolic rates were highest in winter, which suggests that these animals did not use torpor or hibernation. On an annual basis, an individual free-living kangaroo rat (mean body mass 33.9 g) consumed nearly 1 kg (dry matter) of food, and population (density, 17.5 animals ha^{-1}) consumed over 17 kg ha^{-1}. This is a small fraction of net primary productivity but can be a large proportion of seed production.

Nagy, K. A., V. H. Shoemaker, and W. R. Costa. 1976. Water, electrolyte, and nitrogen budgets of jackrabbits (*Lepus californicus*) in the Mojave Desert. Physiological Zoology 49:351-363.

Seasonal changes in water flux rates and diet (stomach content analysis) were determined in jackrabbits (*Lepus californicus*) kept in 0.4 ha field enclosures that contained natural Mojave Desert vegetation in San Bernardino County, California. The water, electrolyte, and nitrogen contents of food plants were measured at different seasons. Itemized water, electrolyte, and nitrogen budgets in jackrabbits were obtained by measuring food utilization in caged animals fed natural diets. Field jackrabbits maintained body mass and obtained excess water while eating succulent annual plants in spring, but in summer and winter animals could not maintain mass or water balance while eating the drier vegetation present during those seasons. Diet utilization studies indicated that (1) jackrabbits could not maintain nitrogen balance on the winter diet, (2) ion regulation was no problem in spring or summer, and (3) jackrabbits can produce fairly concentrated urine (2.5 - 3.6 osm), very dry feces (38% water), and can reduce evaporative water loss about 70% when water is restricted. Despite these mechanisms for conserving water, jackrabbits in the field have relatively high water requirements. We estimate that in summer a jackrabbit would require about 120 ml water kg^{-1} day^{-1} to maintain water balance, and that its diet must contain no less than 68% water in order to meet this requirement. As long as food plants contain sufficient water, their digestibility, nitrogen, and electrolyte content will probably also be suitable.

Reese, J. B. and H. Hines. 1978. Effects of dehydration on metabolic rate and fluid distribution in the jackrabbit, (*Lepus californicus*). Physiological Zoology 51:155-165.

Jackrabbits (*Lepus californicus*) captured in Oklahoma and New Mexico were used to study the effects of dehydration on metabolic rate and fluid distribution in a laboratory setting at the University of Oklahoma. Chronic water restriction resulted in a 30% decrease in metabolic rate and an over 50% decrease in evaporative loss in jackrabbits with no change in body temperature. Thus, evaporative cooling as a means of maintaining body temperature was minimized. Accommodation to measuring technique may account for part of the decrease in O_2 consumption. Fractional water content increased, and solids decreased associated with a 10.6% weight loss due to a chronic restriction, whereas plasma and extracellular volume decreased in proportion to weight loss. The biological half-life of water was increased from 5.8 to 11.6 days while water exchange decreased from 13.0% to 5.9% of the body water per day. In acutely dehydrated jackrabbits (3 - 5 days without water at 25 ºC), all body fluid compartments lost equal proportions (10.7%) with no change in metabolic rate. Similarly, oxygen consumption was unaffected, and plasma volume decreased in proportion to weight loss (5.5%) in jackrabbits acutely dehydrated in hyperthermic conditions (12 - 14 hr at 35 - 40 ºC). The jackrabbit is similar to several other desert species in that it minimizes the loss of plasma volume when exposed to several other desert species in that it minimizes the loss of plasma volume when exposed to dehydration. Evan's Blue space of 8.6% of body mass was shown to be a 36% overestimation of plasma volume as measured with iodinated (^{125}I) albumin (6.3% of body mass).

Reid, E. D. and R. J. Brooks. 1994. Effect of water on retention time and food consumption in deer mice. Canadian Journal of Zoology 72:1711-1714.

Experiments were conducted to assess the effect of water on food consumption and retention time in deer mice (*Peromyscus maniculatus*). We tested whether increased intake of water, preformed in food or free drinking water, affects mean retention time and consumption of food. Mean retention times for diets of sunflower seeds (*Helianthus annuus*), commercial rat chow, and insect-seed mixtures were estimated by using 2-mm red thread markers. For all diets, mean retention times decreased more rapidly with increased water content for sunflower seeds than for rat chow, suggesting that food type also may be important. Granivorous rodents may consume wet food items during periods of low water availability to increase energy intake rather than to satisfy water requirements.

Rhodes, D. H. and M. Richmond. 1987. Water metabolism in free-ranging pine voles (*Microtus pinetorum*). Comparative Biochemistry and Physiology 86A:213-215.

Water metabolism in free-ranging pine voles (*Microtus pinetorum*) was studied in 1981-1982 in New Paltz, New York. Rates of body water turnover in free-ranging pine voles exceeded those reported for a large number of similarly sized mammals. Concentration of urine obtained from free-ranging pine voles were significantly lower than values published for other free-ranging mammals and also for laboratory-maintained members of this species. Rates of body water turnover in this species were not correlated with seasonal changes in soil temperatures.

Richards, G. C. 1979. Variation in water turnover by wild rabbits, *Oryctolagus cuniculus*, in an arid environment, due to season, age group and reproductive condition. Australian Wildlife Research 6:289-296.

Rates of water turnover were measured in free-living rabbits (*Oryctolagus cuniculus*) during a period of wide variation of climate and water availability in New South Wales, Australia. Mean rate of water turnover was positively correlated with the hydration of the pasture ($r = 0.987$). Mean turnover rates per day ranged from 214.3 ml kg^{-1} in cool, wet conditions to 55.4 ml kg^{-1} in a moderate summer drought. The lowest individual rate was 46.1 ml kg^{-1} day^{-1}. The rate of water turnover in young rabbits (1-2 months old) was significantly higher than that of adults measured at the same time; this may contribute to the low survival of young rabbits in dry seasons. A comparison of the rates of water turnover from lactating rabbits in wet and dry season shows that the estimated milk production under dry pasture conditions is below that required to maintain a litter of young.

Sasidharan, T. O., S. P. Goyal, P. Chand, and P. K. Ghosh. 1990. The effects of water deprivation and salt load on water conservation efficiency in two Indian desert gerbils. Journal of Comparative Physiology 160B:413-422.

The effects of water deprivation and intraperitoneal salt loading on urine volume and on various urinary constituents have been examined in 2 gerbil species of the Rajasthan Desert, the Indian desert gerbil (*Meriones hurrianae*) and the Indian gerbil (*Tatera indica indica* Hardwicke). During summer, hydrated *T. indica* excreted 0.782 ml urine $100g^{-1}$ day^{-1}, which was about 60.5% higher than the volume of urine excreted by hydrated *M. hurrianae* (0.487 ml $100g^{-1}$ day^{-1}). During winter, both species excreted around 1.5 ml urine $100g^{-1}$ day^{-1}. The experimental treatments caused reductions in urine volume in *M. hurrianae* from 40 to 76% during summer and from 35 to 71% in winter. Similar treatments in *T. indica* caused reductions in urine volume of 50 - 82% in summer and 5-60% in winter. The mean increase in urine osmolarity following various salt loading treatments in *T. indica* ranged form 3,800 to 5,761 mOsm and from 4,034 to 6,255 mOsm during summer and winter, respectively. The mean values of urine osmolarity for hydrated *T. indica* were 2,831 and 3,189 mOsm during summer and winter, respectively. In *M. hurrianae* salt loading treatments caused increases of urine osmolarity between 3,381 and 5,646 mOsm and between 4,032 and 5,434 mOsm during summer and winter, respectively, over the values recorded for hydrated animals (summer = 3,292; winter = 3,294 mOsm). A maximum urine osmolarity of around 7,000 mOsm was found in both species when subjected to 2% salt loading treatment. The treatments used in this study increased urinary urea level in both *T. indica* (3,039 – 4,056 mM) and in *M. hurrianae* (1,900 - 2,180 mM) compared to the level in their respective hydrated controls (*T. indica* = 1,628 mM; *M. hurrianae* = 1,372 mM). The results indicate that *T. indica* may be better adapted to produce more concentrated urine than *M. hurrianae*.

Seymour, R. S., P. C. Withers, and W. W. Weathers. 1998. Energetics of burrowing, running, and free-living in the Namib Desert golden mole (*Eremitalpa namibensis*). Journal of Zoology, 244:107-117.

The Namib Desert garden mole (*Eremitalpa granti namibensis*) is a small (ca. 20g), blind, sand-swimming, chrysochlorid insectivore that inhabits the sand dunes of one of the driest and least productive areas of the world. Its food, largely termites, is sparse and occurs in widely distributed patches, and free water is unavailable. The moles forage by running on the surface and burrowing below the sand. Moles were live-captured at the Kuiseb River, Namibia in 1996. We estimated their daily energy expenditure in the field to be 11.8 kJ day^{-1} by constructing a "distance-energy budget" based on measurements of tracks in the sand and the energy cost of running (4.2 kJ day^{-1}), burrowing (3.2 kJ day^{-1}), and resting (4.4 kJ day^{-1}). We also measured field metabolic rate (12.5 kJ day^{-1}) and water turnover (2.3 ml day^{-1}) independently with doubly-labeled water. The resting metabolic rate (0.5 ml O_2 g hr^{-1} at 35 ºC) is about a fifth of that predicted for a normal insectivorous mammal, and the daily field energy expenditure and water turnover are about a half. The low daily energy expenditure stems mainly from the low resting metabolic rate, which is associated with low body temperatures and metabolic depression. Moles save more energy during foraging by running on the surface of the sand, rather than burrowing under it. The gross energy cost of sand-swimming (80 J m^{-1}) is 26 times more expensive than running on the surface

(3.0 J m^{-1}), but is less than a tenth of the energy required by mammals that tunnel through compact soil. Nevertheless, it would be energetically impossible for the moles to obtain enough food by foraging only underground at our study site. The mean track length was 1.4 km, but only 16 m of it was below the surface. There is evidence that the track length and fraction underground depend on food abundance, which is influenced by rainfall.

Schmidt-Nielsen, B. and K. Schmidt-Nielsen. 1950. Pulmonary water loss in desert rodents. American Journal of Physiology 162:31-36.

Water evaporation was measured in Merriam kangaroo rat (*Dipodomys merriami*), banner-tailed kangaroo rat (*D. spectabilis*), pocket mouse (*Perognathus* sp.), Norway rat (*Rattus norvegicus*), Syrian golden hamster (*Cricetus aureus*), canyon mouse (*Peromyscuc crinitus*), and house mouse (*Mus musculus*). Evaporation from the lungs was 0.54, 0.57, 0.50, 0.94, 0.85, 0.59, and 0.54 mg water ml^{-1} O_2 in Merriam kangaroo rat, Banner-tailed kangaroo rat, pocket mouse, Norway rat, house mouse, Syrian golden hamster, and canyon mouse, respectively. In desert rodents, hamsters, and wild mice pulmonary evaporation was considerable less than in Norway rats and house mice and is likely an adaptation to maintaining water balance.

Schmidt-Nielsen, B. and K. Schmidt-Nielsen. 1957. A complete account of the water metabolism in kangaroo rates and experimental verification. Journal of Cellular and Comparative Physiology 38:165-181.

A complete account of the water intake and water output of Merriam’s kangaroo rats (*Dipodoyms merriami*) maintained on a dry grain diet is presented. Calculations are based on data of evaporative water loss and urine concentration presented in previous publications and on additional data on water loss through and moisture determinations in pearled barley fed to the animals. Kangaroo rats are in positive water balance when fed a diet of dry pearled barley without drinking water at all atmospheric humidities above 2.2 mg water L^{-1} air (10% relative humidity at 25 ºC). Kangaroo rats could not maintain body mass below atmospheric humidities of 2.5 mg water L^{-1} air. White rats (*Rattus norvegicus*) fed the same diet were in negative water balance and were unable to maintain body mass at all atmospheric humidities below 21 mg water L^{-1} air.

Stalling, D. T. and H. Haines. 1982. Effect of dehydration on water-turnover rates and hematocrits in the rice rat, *Oryzomys palustris*. Comparative Biochemistry and Physiology 72A:301-306.

Effect of dehydration on water-turnover rates and hematocrits was studied in the rice rat (*Oryzomys palustris*). Water turnover rate (WTR) was determined in rice rats, using titrated water, under conditions of ad libitum water (hydrated), water restriction (dehydrated), and restoration of ad libitum water (rehydrated). Hydrated WTR's were similar to other mesic rodents, but water restriction revealed this species inability to conserve water. WTR's of hydrated, dehydrated, and rehydrated animals in ml $kg^{-0.82}$ day^{-1} was 140.3, 94.9 and 158.1 respectively. Hematocrit decreased during dehydration, possibly due to red cell loss. Hematocrit in rice rats was high as compared to cricetid rodents (50 vs. 44% in similarly sized cricetids) and this was evaluated as an adaptive feature.

Stallone, J. N. 1979. Seasonal changes in the water metabolism of woodrats. Oecologia 38:203-216.

Seasonal changes in the water metabolism of dusky-footed (*Neotoma fuscipes*) and desert woodrats (*N. lepida*) was studied in San Diego County, California in 1972 - 1973. The effects of seasonal aridity upon the water conserving abilities of these species were assessed through measurements of water conserving abilities and kidney structure of animals captured in summer and winter, and through measurements of animals' abilities to acclimate to differing water availabilities in the laboratory. Urine concentrating ability was the water conserving mechanism most responsive to changes in the availability of water. Summer and summer-acclimated *N. fuscipes* (431.7 and 459.4 meq Cl L^{-1}) demonstrated urine Cl concentrating abilities substantially greater than those of winter and winter-acclimated *N. fuscipes* (245.7 and 337.4 meq Cl L^{-1}). Summer, winter-acclimated, and winter *N. lepida* exhibited urine Cl concentrations equivalent to those of winter *N. fuscipes*; summer-acclimated *N. lepida* exhibited markedly greater values (466.7 meq Cl L^{-1}) equivalent to those of summer and summer-acclimated *N. fuscipes*. Measurement of relative thickness of renal cortex and medulla yielded no significant differences among the experimental groups of *N. fuscipes* and *N. lepida*, thus suggesting that both species possess equal abilities to concentrate urine. These data are confirmed by urine concentrations of summer-acclimated animals of both species. Water conserving abilities of both species correlate well with climatic and dietary plant water content data. Thus, during the dry, warm summer months (when plant moisture is reduced) *N. fuscipes* conserves water mainly through increased urine concentration. The laboratory acclimation data and differences between summer and winter animals strongly suggest that *N. fuscipes* undergoes an acclimatization to the seasonal aridity which increases gradually during summer and peaks in late summer, thus enabling this water-dependent species to exist on reduced water requirements. The uniformly low water conserving abilities of winter-acclimated, winter, and summer *N. lepida* physiologically verify the previous reports that this species satisfies its water requirements through utilization of succulent cactus, thereby avoiding the stress of summer aridity in its habitat. The fact that both species exhibit equal capacities to conserve water indicates that the much greater geographic distribution of *N. lepida* is not the result of differences in physiological water conserving abilities, but instead may be the result of specific physiological adaptation by *N. lepida* to utilization of cactus and other plants containing noxious or toxic compounds.

Tracy, R. L. and G. E. Walsberg. 2000. Unappreciated tolerance to high ambient temperatures in a widely distributed desert rodent, *Dipodomys merriami*. Physiological and Biochemical Zoology 73:809-818.

A long-held assertion has been that nocturnality is an escape mechanism for many nocturnal desert rodents because of limited tolerances to heat. To test this claim, we used a treadmill to examine the tolerances to high ambient temperatures (T_as) of 1 subspecies of desert rodent, Merriam's kangaroo rat, (*Dipodomys merriami merriami*) from contrasting environments in Yuma and Gila counties, Arizona, and in the laboratory at Arizona State University, Tempe, Arizona. We simultaneously measured body temperature (T_b), evaporative water loss, and metabolic rates at an ecologically relevant speed (0.6 km hr^{-1}) at different ambient temperatures (T_a = 25 - 42.5 ºC). We hypothesized that kangaroo rats from a more xeric site would have greater abilities to remain active and maintain stable T_b than those from a more mesic site, but mesic and xeric-site animals had comparable tolerances and were active until T_b = 42 ºC. At T_a = 42.5 ºC, however, T_b of mesic-site animals increased more quickly than in xeric-site animals. Although most animals could not run more than 18 min at T_a = 42.5 ºC, most could run at T_a = 40 ºC for at least 30 min. Benefits of nocturnality for this species may reside more in purposes of water conservation and avoidance of predation and less on the direct regulation of T_b as T_b is more labile than commonly thought.

Turlejska, E. and J. Lyszczarz. 1986. Dehydration does not influence the summer versus winter thermal adaptation changes in rabbits (*Oryctolagus cuniculus*) living in natural photoperiod. Journal of Thermal Biology 11:41-45.

Resting metabolic rate of laboratory rabbits kept indoors is susceptible to seasonal fluctuations and is higher than in summer. Thermoneutral zone of rabbits under these conditions may shift downwards in winter and upwards in summer. Both of these adjustments in thermoregulation seem to be related to the seasonally changing photoperiod. Dehydration did not influence these thermoregulatory adaptive changes.

Vorhies, C. T. 1945. Water requirements of desert animals in the southwest. Technical Bulletin 107. University of Arizona, Agricultural Experiment Station, Tucson, Arizona, USA.

Abiotic characteristics (e.g. temperature, relative humidity) of microclimates used by and food habits of banner-tailed kangaroo rat (*Dipodomys spectabilis*), wood rat (*Neotoma albigula*), round-tailed ground squirrel (*Citellus tereticaudus*), and jackrabbits (*Lepus* spp.) were studied on the Santa Rita Experimental Range, Arizona in relation to water conservation and heat balance. Comparisons are also made between the microclimate conditions of mesquite (P*rosopis velutina*) and the surrounding desert.

Willems, N. J. and K. B. Armitage. 1975. Thermoregulation and water requirements of semiarid and montane populations of the least chipmunk, (*Eutamias minimus*)--ii. Water balance. Comparative biochemistry and physiology 52A:109-120.

Acclimation of semiarid and montane populations of the least chipmunk (*Eutamias minimus*) at a high ambient temperature was studied. Acclimatization at 34 ºC results in a reduction of metabolism, body temperature (T_b), and evaporative heat loss (EHL) and an increase in dry heat conductance as compared to values reported for chipmunks acclimatized at 22 ºC. At high ambient temperatures, the semiarid population, as compared to the montane population, maintains a lower T_b under all conditions examined. The lower T_b occurs because of a higher EHL when water is available and because of reduced metabolism when dehydrated. Adaptation of *E. minimus* to the semiarid habitat has involved changes in response to acute and chronic heat and water stress, which increase the time the chipmunks, can survive exposures to high ambient temperature, regardless of water availability.

Withers, P. C. 1963. Effect of diet and assimilation efficiency on water balance for two desert rodents. Journal of Arid Environments 5:375-384.

Differences in preformed water content and digestive assimilation efficiency of three diets, millet seed, soy bean and bran had profound effects on energy balance and water balance in two species of North American desert rodents, *Peromyscus maniculatus* and *Perognathus parvus* captured in central and eastern Oregon in 1980. Digestive assimilation efficiency was over 90% for millet, 85% for soybean and 65% for bran. The assimilation efficiency was correlated with the fiber content of the diet. The daily energy assimilated by animals with ad libitum water was similar for the three diets. Both species survived chronic water deprivation when consuming seed, but not when consuming soybean or bran. Tolerance to water deprivation was inversely related to assimilation efficiency. This is attributed to the high fecal water loss of mice consuming soybean or bran, since fecal water loss is inversely proportional to assimilation efficiency. A low digestive assimilation efficiency automatically precludes the concomitant maintenance of positive water and energy balance for animals without available drinking water.

Yahav, S., S. Simson, and E. Nevo. 1989. Total body water and adaptive water turnover rate in four chromosomal species of subterranean mole rats of the *Spalax ehrenbergi* superspecies in Israel. Journal of Zoology 218:461-469.

Total body water (TBW) and water turnover rate (WTR) were measured in 24 subterranean mole rats comprising 4 populations, each belonging to a different chromosomal species of the (*Spalax ehrenbergi*) superspecies in Israel. The 4 species range in different climates: humid-cool percentage of body mass, measured by titrated water (HTO), was 72.4% ± 4.7, significantly ($P < 0.05$) higher than the similar estimates of 61.7% ± 7.2, and 59.4% ± 5.3, respectively. A comparison of HTO space, as a percentage of TBW, closely approximated TBW, ranging from 97% to 108%. WTR was high, 218.1 and 230.9 ml $kg^{-0.75}$ day^{-1} in the mesic populations of. By contrast, WTR estimates were significantly lower, ($P < 0.001$), 150.2 and 148.9 ml $kg^{-0.75}$ day^{-1} in the xeric populations, respectively. The biological half-life time was similar and faster, 32.7 and 27.9 hours in the mesic populations, as compared with slower, 47.9 and 40.8 hours in the xeric populations. Urine osmolality (737 ± 45 mmol kg^{-1}) in the most xeric northern Negev steppe populations was significantly ($P < 0.001$) higher than in the other species. We conclude that adaptive radiation in the *Spalax ehrenbergi* superspecies involves speciation in semiarid and arid climates by the physiological adaptations of kidney water conservation, along with multiple morphological, physiological and behavioral syndromes of climatic adaptations to increasing aridity.

Yousef, M. K., H. D. Johnson, W. G. Bradley, and S. M. Seif. 1974. Titrated water-turnover rate in rodents: desert and mountain. Physiological Zoology 47:153-162.

Water-turnover rate in were studied in rodents desert and mountain environments suing titrated water. Eight species of rodents were studied; species arranged in increasing order of daily water turnover rates are: *Dipodomys deserti, D. merriami, D. microps, Spermophilus tereticaudus, Ammospermophilus leucurus, Neotoma lepida, Spermophilus lateralis, and Eutamius palmeri*, were studied. Influences of phylogeny, ecologic distribution, diet, behavior, and metabolic rate on water turnover rates are discussed.

Zhi-long, L., L. Zhong-min, and S. Ru-yong. 1992. Seasonal water turnover rates of free-living Brandt's voles *Microtus brandti.* Physiological Zoology 65:215-225.

Seasonal changes in water turnover rates were determined in free-living Brandt's voles (*Microtus brandti*) of arid steppes of inner Mongolia using isotopically labeled water method. The water flux of laboratory-maintained Brandt's voles was also measured. Voles remained in water balance in all seasons. Water influx of free-living voles was lowest in April (180 ml kg^{-1} day^{-1}) and highest during June and August (270 ml kg^{-1} day^{-1} and 280 ml kg^{-1} day^{-1}, respectively). The pattern of seasonal changes of water turnover rates of free-living Brandt's voles was similar to that of other herbivores. Water influx during October (217 ml kg^{-1} day^{-1}) was higher than that during April. Foraging and burrow digging activity are suggested as reasons for this increase. Also, the months of March and April may be the water-stressed period.

Techniques and Methodology

Holleman, D. F., R. G. White, and J. R. Luick. 1982. Application of the isotopic water method for measuring total body water, body composition, and body water turnover. Pages 9-32 *in* Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

The theory and application of the isotopic water method in body water and body composition studies are discussed, including the underlying assumptions and the effects of inaccuracies and the problems of recycling. The application of the method for estimating intake of water and water additives is outlined.

Knox, K. L., A. Chappell, J. A. Gibbs, D. N. Hyder, and R. E. Bement. 1970. Sampling methods for water kinetics. Journal of Dairy Science 53:1279-1282.

In a Holstein steer, jugular blood, saliva, 24-hour urine collection, urine by palpation, and respired-water were compared to determine their reliability and convenience for tritium assay in water kinetic studies. No significant differences in rate of tritium dilution occurred among the various procedures. However, the collection and assay of respired-water was the most convenient method. Further comparison of jugular blood and respired-water collected from 12 lambs revealed no significant difference in tritium dilution.

Lifson, N. and R. McClintock. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. Journal of Theoretical Biology 12:46-74.

The theory is developed for the use of the isotopically determined turnover rates of the hydrogen and oxygen of body water for measurement of total energy and material balance of an animal. After a consideration of several simplifying assumptions, a summary is given of tests of the extent to which theoretical expectations are realized. The results of these appear to be in general accord with theoretical expectations.

Nagy, K. A. 1975. Water and energy budgets of free-living animals: Measurement using isotopically labeled water. Pages 227-245 *in* N. F. Hadley, editor, Environmental physiology of desert organisms. Dowden, Hutchinson, and Ross, Inc. Stroudsburg, Pennsylvania, USA.

This book chapter reviews techniques used to measure water, energy, and material fluxes in free-living animals using isotopically labeled water. It briefly covers methodologies, water and energy budgets, water flux calculations, metabolic rate calculations, isotope assays, and potential sources of error. It also contains a discussion of results of labeled water studies with reference to a study conducted on chuckwalla (*Sauromalus obesus*).

Nagy, K. A. 1980. CO_2 production in animals: analysis of potential errors in the doubly labeled water method. American Journal of Physiology 238:R466-473.

Laboratory validation studies indicate that doubly labeled water measurements of CO_2 production are accurate to within ± 8% in 9 species of mammals and reptiles, a bird, and an insect. However, in field studies, errors can be much larger under certain circumstances. Isotopic fraction of labeled water can cause large errors in animals whose evaporative water loss comprises a major proportion of total water efflux. Input of CO_2 across lungs and skin caused errors exceeding +80% in kangaroo rats exposed to air containing 3.4% unlabeled CO_2. Analytical errors of ±1% in isotope concentration can cause calculated rates of CO_2 production to contain errors exceeding ± 70% in some circumstances. These are 1) when little decline in isotope concentrations has occurred during the measurement period, 2) when final isotope concentrations closely approach background levels, and 3) when the rate of water flux in an animal is high relative to its rate of CO_2 production. The following sources of error are probably negligible in most situations: 1) use of an equation that does not correspond to the patterns of change in total body water, 2) variations in rates of water or CO_2 flux through time, 3) use of $^2H_2\,^{18}O$ dilution space as a measure of body water volume, 4) exchange of ^{18}O between water and organic compounds in animals (including excrement), 5) incomplete mixing of isotopes in the animal, and 6) input of unlabeled water via lungs and skin. Errors in field measurements of CO_2 production can be related to acceptable levels (<10%) by appropriate selection of study subjects and recapture intervals.

Nagy, K. A. and C. C. Peterson. 1988. Scaling of water flux rates in animals. University of California Press, Berkeley, California, USA. 172p.

Studies of water flux rates measured using titrated or deuterated water in eutherian and marsupial mammals, birds, reptiles, fishes, arthropods, and mollusks were summarized and analyzed allometrically. Water flux is strongly correlated with body mass within taxa and scales differently in captive vs. free-living animal, among animals in different taxa, and among animals having different habitats and diets. This indicates that ecological conclusions based on laboratory studies of captive animals are suspect. Water fluxes are highest in water-breathing animals, intermediate in air-breathing endotherms, and lowest in air-breathing ectotherms. Analyses of the water economy index (amount of water used per unit energy metabolized, as determined using doubly labeled water in free-living animals) indicate that the low water fluxes of air-breathing ectotherms (compared to endotherms) are primarily due to their low metabolic rates, rather than to supposedly more effective water economies. Desert ectotherms and endotherms have lower water fluxes and water economy index values than their nondesert relatives, reflecting the importance of physiological, behavioral, and morphological adaptations for achieving water balance in desert animals living under natural conditions.

Nagy, K. A. and D. P. Costa. 1980. Water flux in animals: analysis of potential errors in the titrated water method. American Journal of Physiology 238:R454-465.

Laboratory studies indicate that titrated water measurements of water flux are accurate to within -7 to + 4% in mammals, but errors are larger in some reptiles. However, under conditions that can occur in field studies, errors may be much greater. Influx of environmental water vapor via lungs and skin can cause errors exceeding ± 50% in some circumstances. If water flux rates in an animal vary through time, errors approach 15% in extreme situations, but are near ± 3% in more typical circumstances. Errors due to fractional evaporation of titrated water may approach ±9%. This error probably varies between species. Use of an inappropriate equation for calculating water flux from isotope data can cause errors exceeding ±100%. The following sources of error are either negligible or avoidable: use of isotope dilution space as a measure of body water volume, loss of nonaqueous tritium bound to excreta, binding of tritium with nonaqueous substances in the body, radiation toxicity effects, and small analytical errors in isotope measurements. Water flux rates measured with titrated water may be expected to be within ±10% of actual flux rates in most situations.

Robertshaw, D. 1982. Potential errors in the technique for estimating total body water and water turnover using titrated water. Pages 33-42 *in* Use of titrated water in studies of production and adaptations in ruminants. International Atomic Energy Agency, Vienna, Austria.

If the assumption is made that the body is unable to differentiate between water and titrated water, the dilution of administered titrated water should give a measure of the total body water and its subsequent rate of dilution will measure total water intake, or output if the water pool size remains constant. In general, estimates of body water content from the dilution of titrated water overestimates body water measured directly by desiccation. Likewise, water turnover measured from the rate of dilution will be overestimated. The reasons for this error are not known but several factors may contribute. Loss of titrated water during equilibration will result in either an overestimate or underestimate of body water when water losses during equilibration are, respectively, greater or less than the specific activity of the final equilibration value. Incorporation of the isotope into non-aqueous compounds is thought to account for part of the error. Fractionation of titrated water in the water of evaporative water loss also induces an error and is due, in part, to the ability of the skin to selectively retain titrated water and, in part, to the lower vapor pressure of titrated water when compared to water. Fractionation of the isotope will lead to an underestimate of body water and water turnover rate. Evidence exists that there is an exchange of water from the air with that of the body at the skin and respiratory mucosal surfaces, and that the magnitude of the error is directly proportional to the ambient humidity. This is probably the major source of error.

Speakman, J. R. 1997. Doubly labeled water: theory and practice. Chapman and Hall, London, United Kingdom. 399 p.

This book reviews the energetics, theory, biochemical basis, isotope turnover in the body, assumptions for use, practice, methodology, and considerations, and analysis of the use of doubly labeled water in physiological research both in the laboratory and in field situations.

General Desert Ecophysiology

Adolph, E. F. 1947. Water metabolism. Annual Review of Physiology 9:381-408.

The review summarizes published information on water metabolism from 1945 to 1946. Topics reviewed include water turnover, water excesses, dehydrations, water uptake, nonexcretory water loss, excretion of water, neurohypophyisis and water diuresis, and water content and redistributions.

Chew, R. 1961. The water metabolism of desert-inhabiting vertebrates. Biological Review 36:1-31.

This review summarizes the water metabolism of desert-inhabiting vertebrates, including amphibians, reptiles, birds, and mammals. Behavioral adaptations, resistance to water loss and water uptake through the skin, kidney and bladder function, tolerance to dehydration and total physiological response of amphibians. Cutaneous and urine water loss and uricotelism and ureotelism are reviewed for reptiles.

Evaporative water loss, water balance, thermoregulation, drinking, kidney and cloaca function, and behavioral mechanisms of birds are also reviewed. For desert dwelling mammals, water intake, water loss, and kidney function are reviewed.

McArthur, A. J. and J. A. Clark. 1988. Body temperature of homeotherms and the conservation of energy and water. Journal of Thermal Biology 13:9-13.

This paper considers the reasons for the narrow range of body temperatures of homeotherms. Analysis of heat and water balance suggests that the observed range is consistent with the conservation of energy in the cold and water in heat. Poorly insulated "homeotherms" can economize on both water and energy needs if they accept a thermolabile body temperature.

Schmidt-Nielsen, K. and B. Schmidt-Nielsen. 1952. Water metabolism of mammals. Physiological Review 32:135-166.

The physiological problems associated with obtaining enough water for normal functioning of the body and heat regulation are reviewed in desert mammals with emphasis on the kangaroo rats (*Dipodomys* spp.). Water balance, intake, and output in kangaroo rats are discussed including mechanisms associated with kidneys, and evaporation. The review also discusses mammals that do not use water for regulation of heat as well as those that regularly use water in heat regulation. The review of mammals that use water in heat regulation includes: man, dog, cattle, sheep, donkey, and the camel.

Schmidt-Nielsen, B. and K. Schmidt-Nielsen. 1961. Structure and concentrating mechanism in the mammalian kidney. American Journal of Physiology 200:1119-1124.

In a number of mammalian kidneys a close correlation was found between renal medullary thickness and ability to concentrate electrolytes in the urine, indicating that both outer and inner zone of the medulla act as a countercurrent multiplier system. Further evidence for this assumption was furnished through studies of the distribution of urea and electrolytes in different kidney types during antidiuresis. The beaver with 100% short-looped nephrons, the rabbit with 44% long-looped nephrons, and the desert rodent *Psammomys* with 100% long-looped nephrons were studied. In all 3 kidney types sodium and urea concentrations increased to approximately the same level in the outer zone of the medulla. In the rabbit and *Psammomys* kidneys a considerable increase in sodium concentration was found through the inner zone of the medulla. This can best be explained if we assume that the sodium pump, which has been demonstrated in the thick ascending limb of the loop of Henlé, functions in a similar manner in the thin limb.

Yousef, M. K. 1971. Titrated water turnover rate in desert mammals. Pages 333-341 *in* A. A. Moghissi and M. W Carter, editors, Tritium. Messenger Graphics, Phoenix, Arizona, USA.

Water turnover rates of large and small desert adapted mammals are compared using titrated water. Small mammals have faster water turnover rates in proportion to body mass. Relative proportions of body water content and body solids content are compared among large mammals. It is concluded that water turnover rates exhibit interspecific differences on the basis of water use for thermoregulation, reabsorption, and water loss through urine and feces.