

# Mechanisms of Thermoregulation and Water Balance in Desert Ungulates

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## Abstract

*Desert ungulates must contend with high solar radiation, high ambient temperatures, a lack of water and cover, unpredictable food resources, and the challenges these factors present for thermoregulation and water balance. To deal with the conflicting challenges of maintaining body temperature within acceptable limits and minimizing water loss, desert ungulates use a variety of physiological, morphological, and behavioral mechanisms. The mechanisms involved in thermoregulation and water balance have been studied in many domestic and wild African and Middle Eastern ungulates; studies involving ungulates inhabiting North American deserts are limited in comparison. Our objectives were to review available scientific literature on thermoregulation, water balance, and the effects of dehydration in desert ungulates. We discuss the physiological, morphological, and behavioral mechanisms used by ungulates to maintain temperature and water balance in arid environments, and the implications for research and management of desert ungulates in western North America. (WILDLIFE SOCIETY BULLETIN 34(3):570–581; 2006)*

## Key words

*adaptations, Africa, arid environments, dehydration, deserts, ecophysiology, Middle East, North America, physiology, ruminants, water restriction.*

Ungulates have broad ecologic distribution and inhabit every major terrestrial biome. Because of this distribution, ungulates exhibit a range of physiological patterns for temperature and water regulation (Yousef 1976). Desert ungulates must contend with high solar radiation, high ambient temperatures, a lack of water and cover, unpredictable food resources, and the challenges these factors present for thermoregulation and water balance (Feldhamer et al. 1999). The factors that influence the heat load imposed on an animal by the environment include direct and reflected solar radiation, thermal radiation, air temperature, wind speed, and vapor pressure deficit; the environmental heat load plus the metabolic heat produced by the animal compose the overall heat load (Porter and Gates 1969). When body temperatures are higher than ambient temperatures, animals lose heat to the environment passively by radiation, convection, and conduction (Mitchell 1977). If the temperature gradient between the animal and the environment becomes too small or when ambient temperature exceeds body temperature, evaporative cooling must be used to maintain body temperature within acceptable limits (Taylor 1977). Desert ungulates use a variety of physiological, morphological, and behavioral mechanisms to deal with the conflicting challenges of maintaining body temperature within acceptable limits and minimizing water loss.

Desert ungulate physiological responses to dehydration have been studied in many domestic and wild African and Middle Eastern species. Studies on thermoregulation and water balance of North American ungulates have been largely limited to animals from more temperate regions or focused on thermoregulation

during winter (Wesley et al. 1970, Chappell and Hudson 1978, Parker and Robbins 1984, Renecker and Hudson 1986). Few studies have been conducted in the arid areas of North America (Turner 1973, 1979, 1984, Sargeant et al. 1994). Therefore, comparatively little is known about thermoregulation and water balance of ungulates inhabiting North American deserts relative to African and Middle Eastern species.

Because the climate of many areas of the Middle East, Africa, and southwestern North America is similar, ungulates inhabiting these areas face similar environmental conditions and thermoregulatory challenges. Mean maximum daily air temperatures during summer were 43.5, 38.0, 32.5, 40.8, and 41.6°C in Saudi Arabia, Israel, South Africa, southwestern Arizona, USA, and southeastern California, USA, respectively (Silanikove and Tadmor 1989, Owen-Smith 1998, Ostrowski et al. 2003, Western Regional Climate Data Center 2005). Annual precipitation is low and was 73.5, 168, and 99 mm in Saudi Arabia, southwestern Arizona, USA and southeastern California, USA respectively; relative humidity during summer is commonly <45% (Silanikove and Tadmor 1989, Ostrowski et al. 2003, Western Regional Climate Data Center 2005).

Our objectives were to review available scientific literature on thermoregulation, water balance, and the effects of dehydration in desert ungulates. We discuss the physiological, morphological, and behavioral mechanisms used by ungulates to maintain temperature and water balance in arid environments, and the implications for research and management of desert ungulates in western North America.

## Physiological Mechanisms

### **Water Economy and Responses to Dehydration**

**Water loss and total body water.**—There are 4 primary routes of water loss in mammals: cutaneous and pulmonary evaporation,

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feces, and urine. Lactation is an additional route of water loss for females. 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 of water loss (McNab 2002). For example, camels (*Camelus dromedarius*) and Bedouin goats (*Capra hircus*) can survive water losses amounting to 30–40% of body mass, whereas in other species (e.g., waterbuck [*Kobus ellipsiprymnus*]) a 15% loss can result in mortality (Taylor et al. 1969, Louw 1984).

Total body water of mammals often is viewed as being composed of separate compartments: the intracellular fluid within cells and the extracellular fluid consisting of rumen fluid, blood plasma fluid, and interstitial fluids; however, 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). Ungulates such as camels and 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 sufficient to prevent circulatory failure during dehydration (Yousef et al. 1970, Choshniak and Shkolnik 1977, Choshniak et al. 1984).

**Water turnover rates.**—Water turnover rates vary among species and are lower in wild ungulates 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, Degen 1977, Nagy and Peterson 1988). In normally hydrated ungulates, water turnover rate increases with increasing temperature and is lower in winter than in summer (e.g., mule deer [*Odocoileus hemionus*], 1,750–8,050 mL/d], pronghorn [*Antilocapra americana*], 1,940–2,420 mL/d], desert bighorn sheep [*Ovis canadensis*], 4,850–7,010 mL/d]; Longhurst et al. 1970, Wesley et al. 1970, Nagy and Peterson 1988). When ungulates are dehydrated, water turnover rates decrease regardless of ambient temperature (Maloiy 1973b). In addition, water turnover rates have been found to differ between captive and free-living animals of the same species (Nagy and Peterson 1988, Parker et al. 1993).

Reproductive status also can affect water turnover rates. Water turnover rates are 40–50% higher in pregnant and lactating animals than in nonlactating animals (Macfarlane and Howard 1972, Maloiy et al. 1979, Hassan et al. 1988). Water deprivation during lactation can result in decreased milk production (Maltz and Shkolnik 1980, Wilson 1989, Hossaini-Hilali et al. 1994). Dehydration during lactation also can result in a reduction in the concentration of fat and nonfat solids and an increase in water content of milk. This is viewed as an adaptation to ensure that nursing young receive adequate water during times of limited water availability (Mittal 1980, Yagil and Etzion 1980, Yagil et al. 1986). A similar mechanism may be used in North American species; however, no studies have been published on the effect of dehydration on milk production in wild ungulates of North America.

**Water loss in feces and urine.**—Reduction in water content of feces, urine volume, 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 [*Antidorcas marsupialis*], gemsbok [*Oryx gazella*]) to 70–80% in species adapted to more mesic areas (e.g., cattle [*Bos taurus*], waterbuck; Maloiy et al. 1979, Louw and Seely 1982, Woodall et al. 1999). Water is reabsorbed in the colon; 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 [*Taurotragus oryx*], impala [*Aepyceros melampus*]; Woodall and Skinner 1993). Reductions in fecal moisture content of 17–50% have been found in some species (e.g., dorcas gazelle [*Gazella dorcas*], eland, cattle, camel, impala, desert bighorn sheep) when dehydrated (Ghobrial and Cloudsley-Thompson 1966, Maloiy and Hopcraft 1971, Turner 1973).

Arid-adapted ungulates typically have reduced urine output and greater urine concentration than do temperate species (Louw and Seely 1982). 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 more concentrated urine, and arid-adapted mammals have longer loops of Henlé than do other species (Schmidt-Nielsen and O'Dell 1961, Louw and Seely 1982, McNab 2002). 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. Therefore, relative medullary thickness often is used as an index of kidney concentrating ability and is correlated with the environment and diet of the animal (McNab 2002, Zervanos 2002). For example, the relative medullary thickness of the kidney in desert bighorn sheep is nearly twice that of domestic sheep and urine concentrations of 3.9 osmole 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, Ali et al. 1982, Mohamed et al. 1988). 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). Reductions in urine volume ranging from 0–76% and increases in urine osmolality ranging from 3–239% have been documented in comparisons of normally hydrated and dehydrated ungulates (e.g., camel, dorcas gazelle, hartebeest [*Alcelaphus buselaphus*], impala, and desert-adapted goats and sheep (Maloiy and Hopcraft 1971, Ali et al. 1982, Etzion and Yagil 1986, Mohamed et al. 1988).

The excretion of water and electrolytes by the kidney is under hormonal control, primarily vasopressin (antidiuretic hormone [ADH]) and aldosterone. Water reabsorption is controlled by ADH in a negative feedback loop. As animals become dehydrated, plasma concentration increases, stimulating the release of ADH from the pituitary gland. Antidiuretic hormone causes an increase of permeability of the renal tubules and collecting ducts, and water then leaves the renal tubules by osmosis. In addition, ADH also increases the transport of sodium and urea by the renal tubules

into the medulla, helping to maintain the osmotic gradient that allows for the formation of hyperosmotic urine (Willatts 1987, Bentley 2002)

Aldosterone is secreted by the adrenal glands and regulates the transfer of sodium from the nephron to the blood. When sodium levels in the blood fall, aldosterone is released, causing the distal renal tubules to increase reabsorption of sodium and the secretion of potassium, causing water to flow into the blood by osmosis (Willatts 1987, Bentley 2002).

**Diet and water balance.**—Dependence on free water sources and rates of forage consumption 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 free water (Maloiy 1973a, Kay 1997). The amount of preformed water contained in the food has been associated with free water requirements of some ungulate species (e.g., oryx [*Oryx beisa*], Grant's gazelle [*Gazella grantii*], springbok). Preformed water provides a significant portion of the total water intake and is related to the ability of some species to survive long periods without free water (Taylor 1968, 1969a, Schmidt-Nielsen 1979, Jhala et al. 1992). Some populations of desert ungulates in North America are believed to obtain sufficient moisture from forage (Mendoza 1976, Alderman et al. 1989, Krausman et al. 1989, Warrick and Krausman 1989).

Dehydration causes an increase in saliva osmolality and a reduction in saliva flow, eventually resulting in a decrease in the rate of forage intake (dry matter intake) in some species (e.g., white-tailed deer [*Odocoileus virginianus*], zebu cattle [*Bos taurus*], domestic sheep, desert bighorn sheep), whereas others (e.g., dorcas gazelle, Bedouin goat, camel) maintain forage intake even when dehydrated (Turner 1973, Brosh et al. 1986, Lautier et al. 1988). Increases in apparent dry matter digestibility have been documented in dehydrated ungulates, including Bedouin goat, cattle, Thomson's gazelle, (*Gazella thomsonii*), Grant's gazelle, and desert bighorn sheep (Thornton and Yates 1969, Maloiy 1973b, Turner 1973, Silanikove 1985). 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 and nutrient absorption (Brosh et al. 1983, 1986, Choshniak et al. 1988).

**Metabolic rate.**—Reduction in standard metabolic rate (i.e., metabolic rate of resting animal with body temperature in thermoneutral zone) can minimize metabolic heat gain and reduce water loss in ungulates; when examined under similar environmental conditions, desert-adapted ungulates of similar body size typically have lower metabolic rates than do other ungulates (Macfarlane et al. 1971, Shkolnik et al. 1972, Haim and Skinner 1991). 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 ungulates (e.g., camel, eland, oryx, zebu cattle) have lower metabolic rates than when normally hydrated (Schmidt-Nielsen et al. 1967, Taylor 1969a, Finch and King 1982). This mechanism also may be important for North American species; we did not find any published studies

confirming changes in metabolic rates in North American ungulates in response to dehydration.

**Role of the rumen in water balance.**—The rumen helps maintain water balance in 2 ways. First, the rumen of hydrated ungulates and the foregut of camels contain a large volume of water, approximately equal to 20% of body weight, and may buffer ungulates against short-term water deprivation (Hoppe et al. 1975, Silanikove 1994). During the first few days of dehydration, fluid contained in the rumen is used to maintain water balance of blood and body tissues and represents a large portion (50–70%) of the water lost during dehydration (Maloiy et al. 1979, Louw and Seely 1982, Silanikove 1994). Second, after dehydration in some species, the rumen plays a role in the prevention of hemolysis and osmotic tissue shock during rapid rehydration. Desert-adapted species (e.g., Somali donkey [*Equus asinus*], camel, Bedouin goat) are able to drink water equivalent to 20–40% of their body mass in one visit to a water source, which is initially retained in the rumen (Maloiy 1970, Choshniak and Shkolnik 1977, Turner 1979, Silanikove 1994). The rumen is then involved in 2 conflicting necessities: the need to retain all water imbibed until all tissues are fully rehydrated and osmotic homeostasis restored and the prevention of hemolysis and osmotic shock to tissues due to the creation of a large osmotic gradient between the rumen fluid and the blood due to the consumption of the large volume of water (Choshniak and Shkolnik 1977, Etzion et al. 1984, Silanikove 1994). Increases in the secretion of hypotonic saliva following drinking recycles water back to the alimentary tract, allowing retention of water, and transfers large amounts of sodium from the blood, helping to reduce plasma osmolality to normal levels (Silanikove 1994).

The function of the rumen (or foregut) 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, 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 and allows for rapid rehydration while minimizing hemolysis (Yagil et al. 1974, Turner 1979).

**Blood plasma volume.**—Reductions in plasma fluid volume from dehydration can affect blood constituents. The reduction in plasma volume results in an overall increase in plasma osmolality due to increases in plasma proteins, Na<sup>+</sup>, Cl<sup>-</sup>, K<sup>+</sup>, and urea (Laden et al. 1987, 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). Species able to withstand severe dehydration maintain plasma volume and prevent circulatory failure by losing relatively less water from blood plasma fluid than from other compartments (e.g., rumen, body tissues) or are able to move fluid from other compartments to maintain plasma volume

(Yousef et al. 1970, Choshniak and Shkolnik 1977, Choshniak et al. 1984).

### **Thermoregulation**

**Nonevaporative heat loss.**—In environments with moderate temperatures (i.e., within the animal's thermoneutral zone), thermoregulation is achieved largely through behavioral modification and nonevaporative heat loss. An animal gains heat from the environment through convection, radiation, and conduction, at rates proportional to both the temperature gradient between the animal and the environment and the surface area of the animal (Mitchell 1977, Taylor 1977, Sokolov 1982). Animals continue to lose heat to the environment as long as the gradient between ambient temperature and body temperature is sufficient; however, once the total heat load exceeds that which can be dissipated by nonevaporative means, evaporative cooling must be used for the dissipation of excess heat. There are 2 types of evaporative water loss from animals: insensible water loss is water that passively diffuses through the skin and respiratory tract and is lost by evaporation, and active evaporative water loss is water loss from sweating or panting for thermoregulation. In addition to the physiological mechanisms discussed here, animals also influence the magnitude of the temperature gradient using behavioral and morphological adaptations.

**Regional blood flow.**—The circulation of blood transfers metabolic heat produced in deep body tissues to the skin where it is lost to the environment by convection, radiation, and conduction (Hales 1974, Mitchell 1977). Changes in circulation aid in maintaining thermal homeostasis; dilation and constriction of blood vessels regulate the transfer of heat to the skin (Hales 1973, 1974). During heat stress, heart rate and cardiac output increase, vasodilation decreases peripheral resistance, maintaining relatively constant blood pressure, and blood flow to the skin increases (Whittow 1976). Cardiac output can increase 1–2%, blood flow to the skin can increase 2-fold, and there is an overall redistribution of blood flow from nonrespiratory deep body tissues (e.g., gut, nonrespiratory skeletal muscle) to tissues important in heat exchange (e.g., skin, nasal region; Hales 1973, 1976, Whittow 1976). In addition to nonevaporative heat loss, changes in regional blood flow also are important in effective evaporative heat loss; the increase in blood flow and heat transfer from deep body tissues to the skin and respiratory tissues of sweating or panting animals can have a significant influence on the effectiveness of evaporative cooling.

**Evaporative cooling.**—Animals use evaporative cooling (i.e., sweating and panting) when their total heat load exceeds levels that can be dissipated by nonevaporative means. Whether animals rely primarily on cutaneous or respiratory evaporation for thermoregulation is related to body size. Small animals ( $\leq 40$  kg) tend to rely more on respiratory than cutaneous evaporation, and large animals ( $> 40$  kg) tend to rely more on cutaneous evaporation (Robertshaw and Taylor 1969, Maloiy et al. 1979). Large animals must rely more on cutaneous evaporation because their low surface-area-to-volume ratios result in low rates of nonevaporative heat loss, and respiratory evaporation alone is not sufficient to dissipate heat generated during exercise (Robertshaw and Taylor 1969, Robertshaw 1976, Taylor 1977, Maloiy et al.

1979). Maximal rates of evaporative heat loss are higher for cutaneous evaporation than respiratory evaporation (Taylor 1977).

Evaporation of water through the skin occurs by passive diffusion and sweating, and removes approximately 580 cal heat/g water evaporated (Taylor 1977). Most artiodactyls and perissodactyls have sweat glands; however, the number of glands and rate of sweating varies among species (Robertshaw and Taylor 1969, Sokolov 1982). In addition, the combination of the large number of arteriovenous anastomoses in the skin, increased blood flow to the skin, and sweating function to maximize heat loss in certain regions of the body (Robertshaw and Taylor 1969, Hales 1974). Within a given species, rates of cutaneous water loss are affected by season, animal age, nutritional status, state of hydration, and site of measurement (Parker and Robbins 1984, 1985, Taylor 1970a, Maloiy and Hopcraft 1971). The stimuli that influence the regulation of sweating include core body temperature, skin temperature, and solar radiation (Robertshaw and Taylor 1969, Finch 1972a, Parker and Robbins 1984). The fact that exposure to solar radiation is important in the stimulation of sweating in ungulates has significant implications for physiological research; cutaneous water loss often is higher in animals outdoors than in indoor metabolic chambers (Maloiy and Hopcraft 1971, Finch 1972b, Borut et al. 1979, Dmi'el and Robertshaw 1983). The magnitude of heat loss by cutaneous evaporation is related to sweating rate, wind speed, and vapor pressure gradient.

Some desert-adapted ungulates employ facultative use of cutaneous evaporation, depending on the extent of their hydration or dehydration. When hydrated, sweating and cutaneous evaporation rate generally increases with body temperature. However, when dehydrated, some species (e.g., Grant's gazelle, Thomson's gazelle, oryx, eland, wildebeest [*Connochaetes taurinus*], impala, camel) reduce sweating and the rate of cutaneous evaporation by 12–89% (Schmidt-Nielsen et al. 1957, Schoen 1968, Maloiy 1970, Taylor 1970b). Also, the body temperature at which dehydrated animals begin sweating often is higher than that of normally hydrated animals (Schmidt-Nielsen et al. 1957, Taylor 1969a, 1970a,b).

In addition to gas exchange, the respiratory tract also performs a thermoregulatory function. When ambient temperatures are below body temperature, a portion of the heat lost via the upper respiratory tract is due to the difference in temperature between inspired and expired air and is independent of the evaporation of water (Parker and Robbins 1985). When ambient temperatures increase, evaporation of water is required to lose heat from the upper respiratory tract. As body temperature increases, ungulates increase evaporative heat loss by increasing both respiratory frequency and volume to maximize the movement of air across the evaporative surfaces of the upper respiratory tract (Finch 1972a, Hales 1976, Robertshaw 1976). Scrotal temperature also has been shown to influence the initiation and respiratory frequency during panting in domestic sheep (Waites 1962, Hales and Hutchinson 1971). However, increasing respiratory rate without also adjusting rates of oxygen consumption can lead to respiratory alkalosis (Hales 1974, Robertshaw 1976, Taylor 1977). Increasing the ventilation of the lungs without increasing the rate of oxygen consumption causes CO<sub>2</sub> concentration in the lungs to decline, which results in an increase in blood pH (Hales 1974, 1976,

Robertshaw 1976, Taylor 1977). Animals can avoid respiratory alkalosis by increasing dead space ventilation relative to that of alveolar space, thereby increasing total ventilation across the evaporative surfaces in the upper respiratory tract without increasing alveolar ventilation (Hales 1974, 1976, Robertshaw 1976).

Respiratory rates in normally-hydrated animals increase with increasing ambient temperature, resulting in increased respiratory evaporation (Taylor 1969*b*, Maloiy and Hopcraft 1971, Finch 1972*a*). Dehydrated animals tend to have lower respiratory rates and initiate panting at higher ambient temperatures than do normally hydrated animals. At night and in the early morning some species breathe slowly and deeply, extracting more oxygen per breath, therefore reducing the amount of air needed to move through the lungs, reducing respiratory water loss (Taylor 1969*a*). Another mechanism that can result in the reduction of water loss via respiratory evaporation is countercurrent heat exchange in the nasal passages. Air inspired through the nose is warmed as it passes over the nasal turbinates and is saturated with water by the time it reaches the lungs. As the air is expired through the nose, heat can transfer to the nasal mucosa as it passes back over the nasal turbinates, causing the air to become supersaturated and water to condense in the nasal passages, reducing respiratory water loss (Taylor 1969*a*, Langman et al. 1978, 1979, Schmidt-Nielsen et al. 1981). However, while breathing only through the nasal passages may conserve water, it significantly reduces heat loss from the upper respiratory tract. To maximize evaporative heat loss in the respiratory tract, air is inspired through the nose and expired through the mouth, bypassing the countercurrent heat exchanger in the nasal passage (Hales 1974, Taylor 1977).

Advantages and disadvantages exist for both panting and sweating strategies. Panting animals can maintain a lower thermal gradient between ambient and skin temperatures. By maintaining higher skin-surface temperature, panting animals minimize the net inward flow of heat from the environment, particularly when ambient temperature exceeds body temperature (Taylor 1977). Panting animals provide airflow across evaporative surfaces, whereas sweating animals must rely on the wind. Sweating animals lose significantly more electrolytes than do panting animals (Taylor 1977, Feldhamer et al. 1999). A potential disadvantage of panting is the increased energy expenditure may contribute metabolic heat to the overall heat load of the animal. The early stages of panting largely involve movement of the diaphragm, which requires relatively little energy expenditure, and the increase in metabolism of respiratory muscles can be offset by a decrease in metabolism of nonrespiratory muscles (Hales 1973). However, during the later stages of panting the increase in metabolism may not be able to be offset by decreases in metabolism in nonrespiratory muscles (Hales 1973, Taylor 1977). Ungulates also may be able to minimize energy expenditure and metabolic heat production by panting at a resonant frequency (Crawford 1962). The advantages of sweating over panting are that it requires less energy expenditure, achieves a greater maximal rate of evaporative heat loss, poses no risk of respiratory alkalosis, and animals can eat and sweat simultaneously (Taylor 1977).

**Adaptive heterothermy and selective brain cooling.**— Adaptive heterothermy has been widely cited as a mechanism

used by ungulates in arid areas to minimize water loss from evaporative cooling (i.e., sweating and panting) and to decrease inward heat flow by reducing the air to body temperature gradient (Schmidt-Nielsen et al. 1957, Schoen 1972, Taylor 1972, Taylor and Lyman 1972). 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, reducing the need to dissipate heat during the day by evaporative cooling. Normally-hydrated ungulates with access to free water typically maintain core body temperatures within a narrow range by evaporative cooling (Taylor 1970*a,b*). When dehydrated, the core body temperatures of Grant’s gazelle, Thomson’s gazelle, eland, oryx, and camel have been found to fluctuate over a wider range (Schmidt-Nielsen et al. 1957, Taylor 1969*a*, 1970*b*). The range of thermal lability in dehydrated versus hydrated animals is attributed to adaptive heterothermy and a body-water-conservation function (Schmidt-Nielsen et al. 1957, Schoen 1972, Taylor 1972, Taylor and Lyman 1972). However, we found no published studies on adaptive heterothermy in North American ungulates.

Selective brain cooling has been postulated as a mechanism for animals to maintain brain temperature below thermal critical values when body temperature increases (Brinnel et al. 1987). The carotid rete, an area of the carotid artery divided into a series of small blood vessels posterior to the brain, contacts a network of small veinules returning blood from the nasal passages. Heat is transferred from the warmer arterial blood to venous blood cooled by respiratory evaporation in the nasal passage. Blood entering the brain is  $\leq 3.9^{\circ}\text{C}$  cooler than core body temperatures (Taylor 1969*a*, 1972, Louw and Seely 1982, Wilson 1989). This observation has allowed researchers to conclude that selective brain cooling is an adaptation to protect the brain when core body temperature increases (Baker 1979, Brinnel et al. 1987).

Recent studies suggest the rise in core body temperature of ungulates observed in thermal studies was artificial, a result of studying animals in captive conditions in which they were prevented from employing behavioral and other thermoregulatory mechanisms (Jessen et al. 1994, Fuller et al. 1999, 2005, Mitchell et al. 2002). In thermal studies of free-ranging wildebeest, springbok, impala, and oryx, researchers 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 (Mitchell et al. 2002). Dehydration-induced hyperthermia may be adaptive in conserving water because it results in an increase in the temperature at which animals begin to thermoregulate via evaporative cooling (Fuller et al. 1999, 2005, Mitchell et al. 2002). The idea that selective brain cooling is an adaptation for protecting the brain when body temperature is allowed to rise with adaptive heterothermy has also been questioned. Fuller et al. (1999, 2005) and Mitchell et al. (2002) hypothesized that selective brain cooling is used in free-ranging animals under moderate heat loads to switch from evaporative to nonevaporative routes, and therefore has a thermoregulatory function unrelated to adaptive heterothermy (Jessen et al. 1994, Fuller et al. 1999, 2005, Mitchell et al. 2002).

## 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).

### Body Size and Shape

A major morphological characteristic that regulates heat gain and water loss in all animals is 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 (Bradley and Deavers 1980, McNab 1983, Phillips and Heath 1995). The comparatively small surface-area-to-volume ratio of large animals reduces the proportion of the animal exposed to solar radiation, reducing potential environmental heat load. Having a small surface-area-to-volume ratio also can be disadvantageous because it reduces the rate of heat loss to the environment, and shaded microclimates of sufficient size to benefit a large animal are more limited where vegetation is sparse and other types of cover are unavailable (Louw and Seely 1982). Body size is related to metabolic rate (Kleiber 1932, McNab 1988). While their overall energy requirements are higher, large animals have lower mass-specific metabolic rates than do small animals; these low metabolic rates contribute comparatively less metabolic heat to the total thermal load (Schmidt-Nielsen 1979, Louw and Seely 1982).

The shape of the body and appendages also influences the rates of heat gain and loss in animals; long and narrow appendages minimize radiant heat gain and maximize convective heat loss (Louw 1993). Desert-adapted species characteristically have longer, thinner appendages with a higher surface-area-to-volume ratio facilitating heat loss, compared with similar mesic species (Bradley and Deavers 1980, Phillips and Heath 1995).

### Pelage and Horn Characteristics

The thickness and color of the pelage affect heat transfer between the body and the environment. Pelage thickness affects the heat gain and loss of an animal from the environment; thin pelage allows more heat to reach the body, whereas thick pelage provides increased insulation from solar radiation; however, thick pelage limits the effectiveness of sweating for evaporative cooling more than thin pelage (Hofmeyr 1985). Conversely, thin pelage maximizes heat loss but provides relatively little insulation. Overall, pelage thickness tends to decrease as body size increases in desert-adapted ungulates, which may facilitate heat loss and compensate for the thermoregulatory disadvantage of large body size (Hofmeyr 1985, Hofmeyr and Louw 1987). In many species pelage thickness varies on different parts of the body. Pelage tends to be thicker on dorsal than on ventral surfaces and may be entirely lacking on the groin, axilla, scrotum, and mammary glands in some species (Feldhamer et al. 1999). These areas with little or no pelage constitute "thermal windows" where heat loss via convection and conduction can be maximized. Pelage color also affects rates of heat gain and loss. Desert-adapted ungulates typically have glossy, light-colored pelage, which reflects more radiation than dark-colored pelage (Finch 1972*b*, Hofmeyr 1985).

However, dark-colored pelage may absorb more solar radiation than light-colored pelage, reducing the amount of radiation that reaches the skin. By absorbing more solar radiation, dark-colored pelage lowers the thermal gradient between the surface of the pelage and the environment, which reduces convective heat gain from the environment (Shkolnik et al. 1972, Louw and Seely 1982, Louw 1993). While pelage coloration may perform a thermoregulatory function in some species, concealment from predators and interspecific communication may exert stronger selective pressures for pelage coloration (Stoner et al. 2003).

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, both of which would facilitate heat loss (Picard et al. 1996, 1999).

### Fat Deposition

The location of fat deposition also affects rates of heat transfer. Fat stored subcutaneously throughout the body may inhibit the loss of heat to the environment (Louw and Seely 1982). Storage of fat in localized areas may serve to reduce the impact of fat reserves on an animal's ability to lose heat to the environment by localizing the insulating effect of fat to small areas of the body, thus improving heat lost over other body surfaces. In desert ungulates the localization of fat to the rump likely is advantageous for insulating the animal from direct solar radiation, particularly when animals use body orientation to reduce heat gain (see below). Ungulates that have highly localized fat storage include camel, zebu cattle, and arid-adapted fat-tailed sheep (*Ovis aries*; Louw and Seely 1982, Wilson 1989). The deposition of fat likely influences thermoregulation in North American species; however, we did not find any published studies documenting the influence of fat deposition on thermoregulation of North American species.

## Behavioral Mechanisms

Behaviors of desert ungulates that aid thermoregulation and the maintenance of water balance include timing of activity, diet selection, use of microhabitats, social behaviors, body orientation, migration, and timing of reproduction (Berry et al. 1984, Skinner and van Jaarsveld 1987, Fryxell and Sinclair 1988*a*, Sargeant et al. 1994). Use of more than one of these behaviors may reduce heat loads and water loss.

### Timing of Activity

Changes in the duration or timing of daily activities can reduce daily heat loads and minimize evaporative water loss. During the hottest, driest periods of the year, desert ungulates tend to spend a smaller proportion of the day being active and display crepuscular activity patterns, foraging and moving during the cooler periods of the day (Jarman 1977, Alderman et al. 1989, Vrahimis and Kok 1992, Sargeant et al. 1994). Nocturnal activities, including feeding, have been documented for pronghorn, oryx, eland, African buffalo (*Syncerus caffer*), desert bighorn sheep, and desert mule deer (Ellis and Travis 1975, Lewis 1977, Miller et al. 1984, 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 water in forage by feeding at night. In areas where relative humidity increases at

night, as ambient temperatures decrease and the air loses its capacity to hold water, condensation (dew) forms on vegetation, increasing water content up to 30% (Taylor 1968, 1972, Burke 1988). Furthermore, the general behavior of foraging on succulent plants (e.g., cacti), underground storage organs (e.g., tubers), and browse species with higher moisture content, regardless of time of day, provides a means to reduce the amount of free water needed to maintain water balance (Taylor 1969a, Jarman 1973, Williamson 1987, Warrick and Krausman 1989).

### **Use of Microclimates**

The use of cooler microclimates also reduces heat loads, helps maintain a temperature gradient between the body and the environment that results in convective heat loss, and reduces the need for evaporative cooling. Also, by bedding down on cool substrates ungulates can increase conductive heat loss. Use of shaded, lower-temperature microhabitat is a common behavior during midday when temperatures are highest and has been observed in a variety of ungulates, including desert bighorn sheep, desert mule deer, collared peccary (*Pecari tajacu*), dorcas gazelle, eland, oryx, and springbok (Taylor and Lyman 1967, Bigalke 1972, Sowls 1997, Tull et al. 2001).

### **Body Orientation**

Ungulates that are active during the hotter periods of the day and those that inhabit areas where shade is unavailable are able to reduce the amount of solar radiation absorbed or to increase convective heat loss by adjusting body position relative to the location of the sun and wind (Berry et al. 1984, Hofmeyr and Louw 1987, Vrahimis and Kok 1992). To minimize heat gain from solar radiation or to maximize convective heat loss, animals stand with the long axis of the body parallel to the direction of the sun or wind with the rump pointed towards the sun or wind or lie down in this position with head down, shaded by their body (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. By bedding down in small groups, animals create shade for each other and reduce the amount of surface area exposed to solar radiation (Wilson 1990, Sowls 1997).

### **Migration**

Some species avoid high temperatures, limited water availability, and poor forage conditions by migrating (Western 1975, Sinclair and Fryxell 1985, Fryxell and Sinclair 1988b). Ungulate species that exhibit migratory behavior include eland, gazelles, gemsbok, springbok, wildebeest, elephant (*Loxodonta africana*), and zebra (*Equus* spp.) in Africa; elk (*Cervus elaphus*), pronghorn, bison (*Bison bison*), mule deer, and caribou (*Rangifer tarandus*) 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 1961, Talbot and Talbot 1978, Fryxell and Sinclair 1988a). Regardless of the pattern of migration (e.g., longitudinal vs. altitudinal migration), common causes of migration include quantity and quality of forage resources, avoidance of predation,

and availability of drinking water (Fryxell and Sinclair 1988a, Rautenstrauch and Krausman 1989).

### **Timing of Reproduction**

Reproduction in ungulates typically is timed to ensure that parturition occurs at a favorable time of year to maximize offspring survival (Thompson and Turner 1982, Witham 1983, 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). Species that inhabit arid and semiarid areas with unpredictable environmental conditions display more opportunistic breeding patterns, with young born over a more extended time period (Skinner and van Jaarsveld 1987). The young of springbok, gemsbok, and eland in Africa and desert bighorn sheep in North America tend to be born over a more extended period of time (Thompson and Turner 1982, Witham 1983, Skinner and van Jaarsveld 1987, Skinner and Louw 1996).

### **Conclusions**

Ungulates adapted to desert areas are able to survive and reproduce despite extreme temperatures and limited water availability using a variety of physiological, morphological, and behavioral mechanisms to either avoid or tolerate environmental conditions that can result in heat stress and dehydration (Schmidt-Nielsen 1979, Louw and Seely 1982). The mechanisms used by ungulates for thermoregulation and maintenance of water balance have been the subject of numerous studies, including studies on domestic goats, sheep, horses (*Equus caballus*), feral donkey, cattle, camels, guanacos (*Lama guanicoe*), llamas (*Llama glama*), deer, elk, pronghorn, desert bighorn sheep, and a wide range of African gazelles and other bovids (Schmidt-Nielsen et al. 1957, Robertshaw and Taylor 1969, Wesley et al. 1970, Turner 1973, Parker and Robbins 1984).

In the southwestern United States, water often is assumed to be one of the primary factors limiting the distribution, productivity, and recruitment of desert ungulates, including desert mule deer, Sonoran pronghorn (*A. a. sonoriensis*), and desert bighorn sheep (Leslie and Douglas 1979, Sánchez-Rojas and Gallina 2000, deVos and Miller 2005). Thus, wildlife management agencies have invested significant resources in construction and maintenance of perennial water sources (Rosenstock et al. 1999). Despite these efforts, the efficacy of these water sources has been questioned and their continued construction and maintenance has become controversial (Broyles and Cutler 1999, Czech and Krausman 1999, Rosenstock et al. 2001).

Much of this controversy is because of the lack of experimental studies specifically designed to assess the influence of these water sources on ungulate populations and the conflicting results of observational studies involving use of water catchments, and animal distribution and habitat use relative to these water sources (Leslie and Douglas 1979, Krausman and Leopold 1986, Deblinger and Alldredge 1991, Krausman and Etchberger 1995). In addition, some populations of desert ungulates occupy areas without perennial water sources and it has been suggested that these animals can obtain sufficient water from forage

(Mendoza 1976, Watts 1979, Alderman et al. 1989, Warrick and Krausman 1989).

Given the current controversy over building water catchments to provide water for desert ungulates in the arid southwestern United States (Broyles and Cutler 1999, Rosenstock et al. 2001), more information is needed regarding the efficacy of water catchments, the physiological responses of North American ungulates (e.g., desert bighorn sheep and desert mule deer) to dehydration, and the population-level consequences resulting from the presence or absence of these water sources. Further studies of the water turnover, minimum water requirements, and physiological responses of desert ungulates to dehydration will be needed.

We argue more studies are needed that determine the amount of water obtained from forage, the minimum forage-moisture content needed to maintain water balance in the absence of free-standing water, and the effect of dehydration on milk production, milk composition, and the influence on survival of

young, particularly for the management of desert ungulates such as desert bighorn sheep. Other specific areas in need of study include determining the physiological responses (e.g., water flux, blood chemistry, electrolyte balance, water loss through feces, urine, and evaporation) of ungulates to dehydration under varying environmental (e.g., hot, dry vs. hot, wet conditions) and forage conditions, the influence of diet quality on water balance dynamics and dehydration tolerance, and the effect of water availability on forage intake and dry matter digestibility with diets of varying quality. These types of studies will provide much needed information with more applicability for wildlife managers trying to maintain viable and productive populations.

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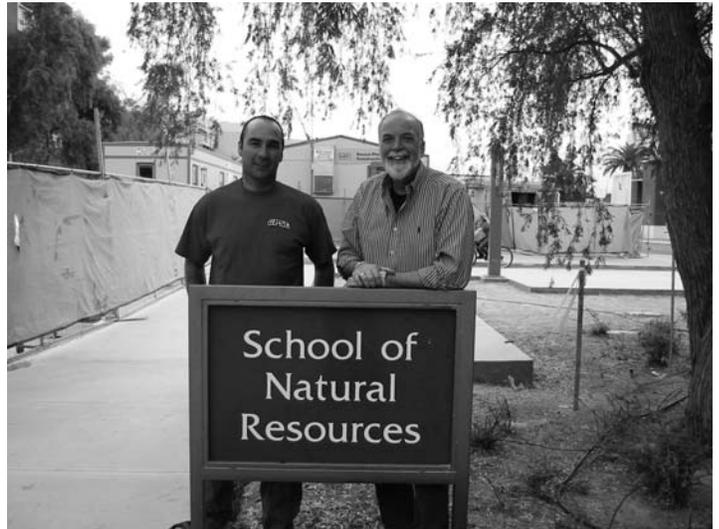
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