Antelope adaptations to counteract overheating and water deficit in arid environments Postprint

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Abstract

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Full Text

Preamble

Antelope Adaptations to Counteract Overheating and Water Deficit in Arid Environments

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Abstract: Many arid areas have extremely severe climates characterized by exceptionally high summer temperatures, intense solar radiation, and a complete absence of drinking water during the driest season. Consequently, antelopes inhabiting these regions must solve two fundamental problems: avoiding overheating and maintaining water balance.

Generally, antelope adaptations to arid environments encompass physiological, morphological, and behavioral mechanisms. Among these, behavioral adjustments incur the minimal energetic cost and are activated first, whereas physiological mechanisms are the most energetically expensive and become engaged when other mechanisms prove insufficient. While previous publications have only rarely described examples of antelope behavioral adaptations, this review attempts to clarify all available information on the adaptations of antelopes living in arid areas to their native environments, with particular attention to behavioral adjustments. Behavioral mechanisms—especially daily activity patterns, diet and microclimate selection, and migrations—are critically important and commonly employed by antelopes under natural conditions, where physiological mechanisms are typically not engaged. Antelopes adjust their behavior so successfully in response to environmental changes that purely physiological mechanisms are often only discovered under laboratory conditions; for instance, adaptive heterothermia or selective brain cooling phenomena are difficult to observe in natural habitats. This review provides a better understanding of the principal behavioral mechanisms underlying antelope adaptations to arid environments and helps identify the key factors for successful conservation of antelopes in their natural habitats.

Keywords: antelopes; desert antelopes; behavioral mechanisms; drinking water; water loss; behaviors; arid environments

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1 Introduction

Deserts represent some of the most austere terrestrial environments on Earth, featuring high air temperatures (up to 50.0°C), intense solar radiation, scarce shaded cover, limited precipitation (<100 mm), and few water sources (Newby et al., 2016). Consequently, solving thermoregulation challenges—such as avoiding body overheating and maintaining narrow body temperature limits—and addressing water deficit represent major challenges for antelopes indigenous to arid environments (Gaughan et al., 2019). Life is impossible without adequate body fluids, and maintaining body temperature within a narrow range (less than $±$2.0°C) is required for effective mammalian physiological function. Antelopes must therefore continuously maintain sufficient water in their bodies to support homeostasis. However, hot environments compel arid-dwelling ungulates to use water for thermoregulation, making water exceptionally valuable, especially in deserts where it is often in short supply (Cain et al., 2006). Water requirements increase with rising temperatures, causing animals to consume more water under hot conditions, which explains 90.0%–98.0% of variation in daily water intake (Williamson and Delima, 1991).

Under elevated temperature conditions, heat production exceeds an ungulate's capacity for dissipation, necessitating reduction of all endogenous heat generation sources while respiratory rate and surface temperatures increase (Cain et al., 2006). Ungulates fed at midday exhibit increased respiratory rates compared to those fed in the morning and evening (Parker and Robbins, 2018). Elevated respiratory rate promotes more intensive respiratory evaporation, contributing up to 45.0% of heat loss. Dorcas gazelles (*Gazella dorcas*), for example, increase their respiratory rate with ambient temperature, from 45–55 breaths/min at 28°C to 50–75 breaths/min at 29°C (Yom-Tov et al., 1995). Ambient temperature critically affects animal comfort, and for ungulates, high temperatures can decrease both milk production and quality in nursing mothers (Bucklin et al., 1991). High temperatures may cause heat stress, leading animals to reduce feeding activity frequency during the hottest hours of the day (Chagas et al., 2015).

Ungulates lose or gain heat from the environment through convection, radiation, and conduction at rates proportional to the temperature gradient between the animal (its body surface area) and the environment (Taylor, 1977; Sokolov, 1982). To maintain body temperature and minimize water loss, three mechanisms exist: behavioral, morphological, and physiological (Cain et al., 2006). Energetically, physiological mechanisms against overheating and water loss are the most expensive and are therefore activated last, when morphological and behavioral mechanisms prove insufficient. Conversely, behavioral mechanisms are the most energy-efficient and are activated first (Fuller et al., 2005). Among such behaviors, terrestrial animals select more suitable microclimate shelters and shaded sites for protection from weather extremes, as well as adjust activity timing (including reproduction), increase diet selectivity, modify social behaviors and body orientation, and/or migrate to habitats with more favorable conditions (Holcomb, 2017).

This review examines behavioral, morphological, and physiological mechanisms observed in arid-dwelling antelope species of northern Africa and Asia, with particular attention to their behaviors. Most data were obtained from published articles describing results from years of field observations, although physiological adaptations were clarified predominantly through laboratory experimental work. Some phenomena documented under early laboratory conditions were not observed in natural environments, leading researchers to believe these phenomena did not exist in nature and were instead consequences exclusively of laboratory environments and procedures (Mitchell et al., 2002). Later, however, it was discovered that all phenomena observed under laboratory conditions also occurred in natural environments (Strauss et al., 2016, 2017). Unlike other articles and reviews devoted to ungulate adaptations to arid environments, which provided fragmentary information and isolated examples across different taxonomic groups, this paper focuses exclusively on adaptations of arid-dwelling antelopes, attempting to provide a comprehensive review of all major published materials on this topic. While some examples of these adaptations are well known for a few species because they are frequently repeated in different articles and reviews, other species receive significantly less attention and remain generally unfamiliar to readers. The purpose of this study is to provide a detailed, comprehensive review of antelope adaptations to arid environments, paying special attention to the behavioral mechanisms employed by antelopes.

2.1.1 Daily Activity Timing

Thermoregulation is achieved primarily through behavioral changes and non-evaporative heat loss when ambient temperature is moderately hot. Among behavioral mechanisms to avoid overheating, antelopes first modify their daily activity patterns, which can reduce heat loads and decrease evaporative water loss. During the hottest months, antelopes are active during cooler periods of the day: morning and evening. In hot summers, springboks (*Antidorcas marsupialis*) in the Kalahari Desert, dorcas gazelles in the Sahara region, and goitered gazelles (*Gazella subgutturosa*) in arid areas of Central Asia's northern deserts all exhibit similar behavior, showing two activity peaks in early morning and late afternoon (Blank, 1990; Yom-Tov et al., 1995). This activity pattern is found in most antelope species, particularly small-bodied antelopes, while large-bodied species are more tolerant of high midday temperatures (du Toit and Yetman, 2005). During hot hours, most antelopes remain in the shade of trees and shrubs, whereas on cool days or after rain, springboks feed throughout most of the day (Fuller et al., 2005). High temperatures lead animals to reduce daytime activity and increase twilight and nocturnal activity (Scheibe et al., 2009), switching from diurnal to nocturnal activity in summer. This pattern is observed in springboks (Fuller et al., 2005), dorcas gazelles (Yom-Tov et al., 1995), Kirk's dik-diks (*Madoqua kirkii*) (Estes, 1991), beira (*Dorcatragus megalotis*) (Giotto et al., 2008), gemsboks (*Oryx gazella*) (Boyers et al., 2019), and others. In addition to thermoregulatory benefits, antelopes feeding at night can increase water intake by up to 30.0% because their forage typically has higher moisture content from dew (Taylor, 1968; Cain et al., 2006).

2.1.2 Diet Selection Under Water Deficit Conditions

Surface water is a key resource for antelopes in arid areas because most species require drinking water to maintain body fluid homeostasis (Kihwele et al., 2020). Only a few antelope species in arid areas can survive without surface water. For example, Farasan gazelles (*Gazella gazella farasani*) inhabit the Farasan Islands where no surface water exists, yet they satisfy their water demands by selectively browsing the freshest parts of perennial shrubs and trees with high water content. Additionally, in some areas, high air humidity can condense on hygroscopic plant leaves, which gazelles then consume, providing both essential food and water (Habibi, 1992). A similar situation occurs in gerenuks (*Litocranius walleri*) from Kenya, which do not drink in either captivity or the wild, even during rainy seasons when surface water is abundant, satisfying their water needs instead through consumption of green, juicy food (Bärmann et al., 2021).

A second group of ruminants in arid areas, such as springboks (Cain et al., 2004) and steenboks (*Raphicerus campestris*) (Estes, 1991), can survive without drinking water for long periods, meeting their water needs from succulent food (up to 67.0% water content). Some antelopes also dig for juicy roots or feed at night when humidity is higher, increasing the water content of their food. The distinction between this second group and the first is that these animals will drink when surface water is available. A third group of antelopes requires surface water for drinking regularly—at least every 2–4 days in summer when ambient temperature is high and food is dry—such as goitered gazelles (Zhevnerov et al., 1983), blackbucks (*Antilope cervicapra*) (Jhala et al., 1992), and nilgais (*Bocelaphus tragocamelus*) (Bohra et al., 1992). Consequently, goitered gazelles in Iran are distributed homogeneously within a 5 km radius around water sources (Farhadinia et al., 2009). In Kazakhstan, goitered gazelles remain in areas where juicy plants are available, typically near rivers, lakes, and springs or along the shores of the Aral and Caspian seas. In summer, these gazelles are found within 10–15 km of water sources, while in late autumn and winter, when water sources freeze, goitered gazelles migrate to areas with snow cover (Zhevnerov et al., 1983). Blackbucks can be found considerable distances from surface water but are not observed in areas lacking drinking water entirely (Jhala et al., 1992).

In the driest deserts of Central Asia, goitered gazelle distribution depends on the location of watering places (Zhevnerov et al., 1983). However, during spring rains or monsoons and intensive vegetation growth seasons, plant water content increases significantly to supply desert antelope requirements: 70.0%–80.0% for goitered gazelles (Zhevnerov et al., 1983), 60.0% for elands (*Taurotragus oryx*) (Cain et al., 2006), 50.0% for Arabian oryxes (*Oryx leucoryx*) (Stanley-Price, 1989), over 30.0% for blackbucks (Jhala et al., 1992), Grant's gazelles (*Nanger granti*), and oryx beisa (*Oryx gazella beisa*) (Cain et al., 2006), and 10.0% for springboks (Estes, 1991). This allows these antelopes to survive without drinking water for long periods, enabling them to travel to the most remote desert areas and return to watering places only occasionally. In general, browsers are less dependent on surface water than grazers because tree and shrub roots can reach underground water and produce green growth even during the hottest periods when grasses are completely dry (Estes, 1991).

Throughout the year, plants and their parts (tender shoots, leaves, buds, flowers, fruits, pods, stems, tubers, and juicy roots) containing high water percentages are always preferable to desert antelopes, such as oryx beisa (*Oryx gazella beisa*) (Estes, 1991), blackbucks (Bohra et al., 1992), goitered gazelles (Kingswood and Blank, 1996), and springboks (Cain et al., 2004). During summer in Kazakhstan, goitered gazelles eat primarily *Capparis spinosa*, which has a moisture content of approximately 70.0% (Zhevnerov et al., 1983). Moreover, many plants in arid areas possess water-storage organs such as roots, tubers, or succulent stems and leaves. Oryx beisa diligently digs for roots, bulbs, and tubers, which along with wild melons and cucumbers, supply sufficient water for this species (Estes, 1991). Even water-dependent grazers such as black wildebeests (*Connochaetes gnou*) and hartebeests (*Alcelaphus buselaphus*) can survive by consuming juicy plants in the Kalahari Desert (Estes, 1991). In Iran, goitered gazelle distribution is highly correlated with cultivated lands where they can always find green crops (Farhadinia et al., 2009). In Ethiopia, common duikers (*Sylvicapra grimmia*) feed on vegetables and fruit crops (Estes, 1991). Similarly, in India, nilgais are found in large numbers around agricultural fields, and blackbucks also frequently rely on agricultural crops (Bohra et al., 1992).

In Namibia, Kirk's dik-diks are cultivation followers, staying in the shelter of prickly pears (*Opuntia*) around villages and feeding on crops and orchards at night (Estes, 1991). In some African areas, common duikers and steenboks dig for roots and tubers (sweet potatoes and peanuts) in agricultural fields when available (Estes, 1991).

When most plants begin to dry out, goitered gazelles (Zhevnerov et al., 1983) and blackbucks (Jhala et al., 1992) may visit water sources 1–4 times per day, drinking up to 1.00 L at one time and 2.00–4.00 L per day. In India, blackbucks living in arid areas need water at least once daily. In contrast, chinkara (*Gazella benetti*) consumes moisture-laden leaves and flowers instead of drinking water, enabling it to inhabit all dry areas of the Thar Desert. Blackbucks are found only in border regions of this desert where surface water is available year-round; however, blackbucks are now appearing in newly irrigated areas of the desert where they were previously absent (Rahmani and Sankaran, 1991).

Dorcas gazelles are extreme habitat generalists among gazelle species, inhabiting a wide variety of dry habitats (Kingswood and Mallon, 2001). Nevertheless, these gazelles require a continuous water supply in winter (0.47–0.59 L/d) and summer (0.72–0.84 L/d). Dorcas gazelles are partly independent from drinking water in winter but face a daily shortage of approximately 0.12 L (per 10 kg body weight) in summer. They can withstand a lack of surface water for 9–12 days in winter and 3–4 days in summer, with a body mass loss of 14.0%–20.0% (Yom-Tov et al., 1995). With water scarcity, dorcas gazelles decrease food intake and stop eating by the fourth day. An animal discovered in the 1990s after a long period without water could hardly chew or swallow food and appeared dry and emaciated (Yom-Tov et al., 1995). To reduce dependence on surface water, dorcas gazelles are highly selective in diet choices and change their diet seasonally, but they never eat halophytic plants that would require extra drinking water (Yom-Tov et al., 1995). They eat only green grasses during the wet season and no grasses during the dry season, when they prefer exclusively fresh tree leaves, flowers, and pods (*Acacia* and *Balanites*), as well as leaves, twigs, and fruits of *Ziziphus* and other shrubs (Yom-Tov et al., 1995). These gazelles also remain in areas after rains where *Acacia* leaves have higher water content (Yom-Tov et al., 1995). Additionally, dorcas gazelles are very selective in choosing plant parts, foraging on lily roots and flowers in sand dunes and selecting parts with maximal water content (Henley et al., 2007). Although dorcas gazelles do not eat grasses, they spend considerable time digging and turning soil in search of grass roots and other plants; they also eat dates, both green and ripe (Yom-Tov et al., 1995). Dorcas gazelle occurrence in the Negev Desert is positively associated with access to perennial water sources, especially when the water content of their food is low (Henley et al., 2007). The same is true for goitered gazelles, which prefer to nibble plant tips such as *Calligomun* spp., the most edible species with the highest water content in summer (90.0%–95.0% in May and June, and 55.0%–65.0% in July) (Zhevnerov et al., 1983).

Indigenous Kalahari antelopes can generally survive without drinking water due to their behavioral diet adaptations (Williamson, 1987). Springboks living in the Kalahari Desert cannot survive without water since their diet contains a minimum water content by mass (Greenwald, 1967). Therefore, in Etosha National Park, Namibia, springboks drink at all times of day almost year-round, but stop after rain and during cold weather (Bigalke, 1972). Ambient temperature significantly affects springbok drinking frequency in the Kalahari Desert. Springboks can also drink highly mineralized water from boreholes in riverbeds (Child et al., 1971). Additionally, they select succulent plant parts such as flowers, fruits, and tubers, enabling them to survive without drinking water while grazing in the coastal fynbos of South Africa (Hofmeyr and Louw, 1987).

Some desert plants in springbok (Louw and Seely, 1982) and oryx habitats (Cain et al., 2006) can absorb moisture during cool, humid conditions, so grazing at night and morning probably increases water content from air or dew (Taylor, 1968). A similar case was observed in Grant's gazelles, which primarily eat *Disperma* sp. in the Kenyan Desert. This plant species is very dry (1.0% water content) during hot days but absorbs water from night air overnight, raising its water content to 30.0%–40.0%, thereby compensating for the daily water deficit of Grant's gazelles (Taylor, 1972). Dik-diks prefer to eat juicy vegetation and obtain water from food and dew, and apparently can survive without surface water; there is even a Somali legend that a Günther's dik-dik will die if it drinks (Kingswood and Kumamoto, 1996). Kirks's dik-diks (*Madoqua kirkii*) have been observed drinking from rainwater puddles in natural conditions (Tinley, 1969), while some, like Günther's dik-diks (*Madoqua guentheri*), have been observed licking condensation droplets that formed on their noses.

Arabian gazelles (*Gazella gazella* and *Gazella marica*) have adapted to extremely harsh conditions on the Arabian Peninsula by selecting foods with high moisture content to compensate for scarce drinking water (Williamson and Delima, 1991). The duration that ruminants can survive without drinking depends on several factors: meteorological conditions, water quantity and quality, water content of ingested food, and animal age and biological cycle stage. In summer, not only are midday maximum temperatures important, but night temperatures are also significant. Sudden climatic changes (occasional rainfall or cooler nights) modify drinking behavior considerably, and animals can satisfy their water needs with moisture in their food without drinking, even on very hot days (Gauthier-Pilters, 1984).

Under experimental conditions, antelopes restricted from drinking water typically lose body mass and reduce evaporative water loss by up to 55.0% (Taylor, 1970a). In natural conditions, blackbucks lose 13.0% of their body weight over three days when deprived of drinking water (Jhala et al., 1992). Experiments with long-term food and water restriction in Arabian sand gazelles (*Gazella marica*) over a four-month period demonstrated that they adjust their body physiology by slightly decreasing body mass, but liver, heart, and muscle sizes and metabolic rate decline significantly. As a result, their oxygen demands decrease, and the gazelles lose smaller amounts of evaporative water through respiration (Ostrowski et al., 2006).

2.1.3 Endurance to Salty Water

Goitered gazelles on Barsa-Kelmes Island drink water mostly from the Aral Sea; in western Kazakhstan, they willingly drink salty water along the Caspian Sea coast, which has a salt content of 9–15 g/L (Zhevnerov et al., 1983). They can consume water with salt content up to 20 g/L, but one liter of drinking water with more than 20 g of salts is unsuitable and will kill gazelles, especially young ones (Gorelov, 1972). More salty water (salt content of 35 g/L) is intolerable, so most likely no goitered gazelles inhabit the shores of the Persian Gulf and Arabian Sea (Zhevnerov et al., 1983). Experiments with dorcas gazelles tested whether they could drink seawater from the Red Sea (salt content of 36–41 g/L) when no fresh water was available. Results showed they cannot utilize this seawater because drinking such highly saline water leads to body weight loss of as much as 15.0% of original weight in just three days. Dorcas gazelles can maintain their original weight only when seawater is diluted 2–4-fold (Yom-Tov et al., 1995). In Central Asia, goitered gazelles can drink not only salty water but also bitter-salty water (with sodium chloride) found in some springs (Savinov and Bekenov, 1983). Blackbucks can also drink salty and seawater (Jhala et al., 1992). Springboks can drink highly mineralized water from boreholes (Skinner and Louw, 1996). Along the Caspian and Aral seas, goitered gazelles can eat seaweeds (*Zostera*) and naiads (*Najas*) cast ashore by waves, which are saturated with salty water (Zhevnerov et al., 1983).

2.1.4 Migrations

In arid environments, unpredictable changes in water and forage resources are known drivers of nomadic movements (Nandintsetseg et al., 2019). Desert ungulates roam widely to search for higher-quality foods to satisfy their water and energy demands, representing a very important behavioral adaptation for large ungulates (Knight et al., 1988). The unpredictability of water and forage resources in arid environments drives ungulates toward a nomadic lifestyle (Nandintsetseg et al., 2019). Antelope migrations are commonly observed in Africa (Thomson's gazelles (*Eudorcas thomsoni*), Grant's gazelles, and wildebeests (*Connochaetes taurinus*)), Asia (goitered gazelles, Tibetan antelopes (*Pantholops hodgsonii*), and saiga antelopes (*Saiga tatarica*)), and North America (pronghorns (*Antilocapra americana*)). The main drivers of these migrations include both forage quality and drinking water availability (Cain et al., 2006). Saiga antelopes are continuously on the move, migrating from steppes to desert areas, staying for several days in areas with rich pastures and abundant water sources because they need to drink water (or eat snow in winter) daily. In hot summers, they often migrate along rivers and concentrate around permanent water sources. Saiga antelopes also move quickly through waterless areas and appear in some locations even after small rain events (Fadeev and Sludskiy, 1982). The oryx is one of the most desert-adapted antelopes, specialized for a nomadic lifestyle

(Estes, 1974), requiring just 4.85 mL/d drinking water or 4.0% of its body weight (Yom-Tov et al., 1995). During dry periods in Kazakhstan, goitered gazelles remain in interior desert areas while temporary water sources and juicy vegetation persist, but when everything dries up, they become nomadic and search for water, migrating to large rivers and lakes (Zhevnerov et al., 1983). Sand gazelles used to migrate between northern Saudi Arabia and Syria in spring to give birth in the moister conditions of the Euphrates Valley (Kingswood and Blank, 1996). In Sudan, when all natural water sources dry up in summer and moisture from vegetation is insufficient, dorcas gazelles migrate far west toward the Nile Valley due to water shortages in their native range; additionally, dorcas gazelles living in Red Sea hill areas migrate to the Red Sea coastal plain in winter for winter rains (Yom-Tov et al., 1995).

Many gazelle species move seasonally to subdeserts or even desert areas to feed on nutrient-rich forage during the short rainy season, then return to moister savannas during the prolonged dry season. Thomson's gazelles, Grant's gazelles, Soemmerring's gazelles (*Nanger soemmerringii*), and dama gazelles (*Nanger dama*) were also migratory in the past, aggregating and moving in herds of hundreds or thousands that concentrated in areas with green vegetation growth produced by localized rainfall. The same species and even the same individuals may be nomadic, migratory, or resident in turn, depending on the distribution and condition of their food supply (Estes, 1991).

2.1.5 Microclimate Selection for Resting

Staying in the shade of shrubs, trees, or inside hollows during hot summer days and searching for more comfortable places using micro-relief features are very useful behaviors for ungulates (Holcomb, 2017). A strong linear relationship exists between antelope shade use and both ambient temperature and solar radiation incidence (Dunbar, 1979). The skin temperature of antelopes exposed to solar radiation averages up to 6.4°C higher than that in shade (Parker and Robbins, 2018), while air temperature may be lower by up to 12.0°C in shade compared to open areas (Hetem et al., 2011). In hot environments, small-bodied antelopes such as Günther's dik-diks (Kingswood and Kimamoto, 1996), beira (Giotto et al., 2008, 2010), steenboks (Hofmeyr, 1985), springboks (Hofmeyr and Louw, 1987), and chinkara (Bohra et al., 1992) can easily find shade under *Acacia* trees, near large stones and steep slopes, or even next to tuft grasses and medium to small shrubs. Goitered gazelles stay in the shade under shrub and tree crowns. Sometimes several depressions can be found in a circle under a single bush as the gazelle changes its location with the moving shadow (Zhevnerov et al., 1983; Blank, 2020). Larger antelopes such as elands can also find shady places around large trees or in rock shelters, despite having fewer opportunities for complete refuge from sunlight (Fuller et al., 1999).

Dorcas gazelle distribution in the Negev Desert relates not only to forage quality and water content in food but also to access to shelter from solar insolation under *Acacia* tree canopies (Baharav, 1980, 1982). Adult male goitered gazelles prefer to use elevated lands and less vegetation shade, while females and especially fawns utilize shade from shrubs and trees more frequently (Blank, 2020). During hot summer days, springboks cease grazing early and stand or lie down in the shade of trees and bushes, where herds cluster tightly together until late afternoon (Cain et al., 2004).

Blackbucks, especially adult males, prefer to stay in open sun throughout the day, even during summer peaks, at the expense of their physiological efficiency (Bohra et al., 1992). Similar sun-exposure behavior during midday heat is observed in oryx, which can conserve body water through flexible body temperature regulation (Cain et al., 2006). During the hottest summer days, goitered gazelles stand on hilltops or plateaus where wind blows almost constantly, aiding body thermoregulation (Blank, 2020). Goitered gazelles prefer salt marshes and depressions between dunes where wind blows well and soil cools overnight; as air temperature increases, the animals move to dune edges closer to the seashore where wind blows (Zhevnerov et al., 1983). Moderate wind speeds can reduce skin temperatures by up to 8.5°C compared to windless conditions (Parker and Robbins, 2018). Heat transfer through evaporation from the body surface can be enhanced by wetting fur with saliva. Günther's dik-diks demonstrate this behavior, spreading saliva over their body flanks to increase evaporation. This method requires substantial water and can only be used briefly due to permanent water deficit in arid environments (Cain et al., 2006).

2.1.6 Body Orientation

When shade is unavailable, ungulates adjust their body position relative to sun and wind (Berry et al., 1982; Hofmeyr and Louw, 1987). To reduce solar radiation, animals stand with their body's long axis parallel to the sun's direction, point their rump toward the sun or wind, or lie down with their head lowered and shaded by their body (Cain et al., 2006). Springboks can reduce their solar radiation load by 62.0% through changing body orientation (Hofmeyr and Louw, 1987).

During cold periods, wildebeests orient their bodies in a "tail-to-wind" posture, then change positions to face into the wind as temperature rises (Berry et al., 1982; Maloney et al., 2005). In the absence of shade, elands, black wildebeests, impalas (*Aepyceros melampus*), and springboks stand in positions parallel to solar radiation, reducing their heat loads (Hetem et al., 2011). When shade is unavailable, springboks orient their hindquarters toward the sun or in the direction of the solar beam. This behavior significantly reduces exposure to direct solar radiation and higher solar loads (Hofmeyr and Louw, 1987).

2.1.7 Standing Position During the Hottest Hours

During hot midday periods, goitered gazelles occasionally rest in standing positions to protect their bodies from overheating, since air temperature at standing height is several degrees lower than at ground level. For goitered gazelles in

Kazakhstan, this temperature difference is 7.0°C in plump salt marshes and 18.0°C in seashore sands (Zhevnerov et al., 1983). Animals decrease their body temperatures more while standing still in shade during the hottest hours (Estes, 1991). Klipspringers (*Oreotragus oreotragus*) and dik-diks (*Madoqua* spp.) mostly stand rather than lie in shade during the hottest hours, likely related to the necessity of dissipating body heat more efficiently (Estes, 1991).

2.1.8 Wallowing

Wallowing is observed in several non-ruminant species (Perissodactyls and Tylopoda), and only a few artiodactyls are known to do it, such as red deer (*Cervus elaphus*) and bison (*Bison bison*). It is especially inherent in water-loving ungulates (wild boars (*Sus scrofa*)). Functional sweat glands are underdeveloped in these animals, and wallowing in mud serves as a compensation mechanism for cooling and sunburn protection to support thermoregulation (Bracke, 2011). Therefore, in hot weather, all Suidae species seek water and wallow in mud to lower body temperature. However, most cervid and bovid species do not wallow. This behavior is not typical for antelopes either, and only wildebeests have been observed wallowing (Estes, 1991).

2.1.9 Snow Eating Instead of Water Drinking in Central Asian Deserts

Male goitered gazelles establish individual territories during the rutting season (November and December) and prefer not to leave their territories throughout the entire breeding season (Blank, 1998). These territories are often found in submontane dry plains lacking water. During the rutting season, male goitered gazelles need high levels of energy and water while the only water source is snow. However, snow cover is unstable and usually melts or blows away within several days. Territorial males can survive without water for a few days until the next snowfall, but in some warmer, snowless years, breeding areas may have no snow for long periods (more than a week). Therefore, even though they prefer not to, these males must leave their territories for 1–2 hours to drink water, running all the way to the watering place and then returning (Blank, 1998). Snow cover is so important for rutting males because they can increase the intensity of their rutting activity when snow is available as a water source. Territorial males eat snow more often and for longer periods after chasing females during warm sunny days than during cold, cloudy days. Based on these observations, snow cover is a necessary component of the rutting season and plays an exceptional role in goitered gazelle reproduction (Blank, 1998).

Goitered gazelles experience great difficulty during early, snowless frosts when water sources freeze but no snow cover exists. These gazelles graze more intensively for longer periods in the morning after frosty nights when frost falls on plants and grasses remain moist for extended periods. During periods of low snow, gazelle occurrence significantly increases in pastures with sharply crossed terrain, where snow accumulates under wind influence and remains available longer. For goitered gazelles, autumn migration is often caused not by food shortage but by freezing of available water sources in the absence of snow cover. In snowless, frosty winters, gazelles quickly become exhausted due to water drought, sometimes resulting in death (Zhevnerov et al., 1983). Other Central Asian ungulate species also use snow as drinking water in winter. For example, Transcaspian urial (*Ovis vignei arcal*) eats snow found in chinks, preferring melting snow cover (Savinov and Bekenov, 1983); argali (*Ovis ammon*) living in desert mountains also eats snow and shows no interest in other water sources (Fedosenko, 2000); and saiga antelope rarely visits water sources in winter, instead obtaining water from snow to meet its needs (Fadeev and Sludskiy, 1982).

2.2 Morphological Features Against Overheating and Water Loss

For ungulates, important morphological features regulating heat gain and water loss include body size and shape. Large ungulates obtain heat at slower rates than small ungulates due to a lower surface-to-volume ratio and higher thermal inertia. The disadvantage of large ungulates is slow heat reduction and limited availability of shaded places. While large animals have greater energy requirements, they have relatively lower metabolic rates than smaller species.

Additionally, ungulates adapted to arid environments have longer, thinner appendages (ears and legs) with a higher surface-to-volume ratio, providing more intensive heat loss (Cain et al., 2006). For example, vasodilation of blood vessels supplying long ears increases heat loss through radiation and convection in springboks (Skinner and Louw, 1996). Many desert dwarf antelopes (*Dorcatragus*, *Madoqua*, and *Raphicerus*), inhabiting areas with drinking water deficits, prefer to feed mainly on green shoots and fruits with considerable water content. With extremely narrow muzzles and rows of incisors, dik-diks select the smallest food items—the most nutritious and juicy plant parts. This forage is too sparse for larger animals, but dik-diks' small body size allows them to survive in minimal spaces where these food amounts could not support larger browsers (Estes, 1991). Dik-diks' flexible upper lips and tongues are also useful for plucking foliage or juicy shoots, extending their reach by standing on their hind legs (Estes, 1991).

Antelope pelage provides a barrier between the animal and its environment. The physical characteristics of pelage feature prominently in thermal adaptations to specific climatic zones, with thickness, density, and color being the most important thermal properties (Hofmeyr, 1985). Pelage thickness and color impact heat transfer between the body and environment. Thin pelage provides better heat loss and gain, but thick pelage better protects animals from solar insolation while constraining the cooling effect of sweating. Generally, pelage thickness decreases with body size in desert ungulates, enhancing heat loss and compensating for disadvantages of large body size (Cain et al., 2006). Pelage varies across body parts, tending to be thicker on dorsal surfaces and thinner or even absent on ventral surfaces, which act as “thermal windows” with maximal convection and conduction (Feldhamer et al., 1999). Pelage and its color are the most conspicuous adaptations to desert life. Desert-adapted ungulates usually have glossy, light pelage that reflects more radiation than dark-colored pelage, although the latter can better protect skin from direct solar radiation and reduce convective heat gain from the environment (Cain et al., 2006). Roberts (1977) asserted that the light-colored pelage of gazelles is an important component of their overall adaptive strategy, decreasing heat absorption during hot summer days. A 2–3-fold reduction in water vapor conductivity is observed in goitered gazelle pelage when a layer of still air appears between hairs, restraining evaporation. Further, the more developed the hair layer, the greater the obstacle to evaporation and the lower the overall conductivity of the outer hair coating (Soldatova and Grazhdankin, 1989). Other species such as springbok have thinner pelage with higher conductance than expected for antelopes of similar size, providing rapid heat loss if ambient temperature is lower than skin temperature at the cessation of exercise, such as after sprinting away from predators at top speed (Hofmeyr and Louw, 1987). Klipspringers have special insulating coats that can withstand extreme cold and heat environments up to 40.0°C in shade (Estes, 1991). Hartebeests rarely use shade (Ben-Shahar and Fairall, 1987) because they have thicker pelage and lower pelt absorption rates, which reduce heat load and allow them to survive on open grass plains in more arid areas (Hofmeyr, 1985). For springboks, the white color of the rump and face increases reflectivity and enhances benefits of parallel orientation to the sun; therefore, these animals prefer rump orientation toward the sun when grazing (Skinner and Louw, 1996).

Bovid horns may also have thermoregulatory functions. Arid-dwelling bovids have relatively larger horn cores and thinner keratin covers than mesic-dwelling antelopes, both of which can aid in heat loss (Picard et al., 1996, 1999).

The rumen of ruminants can maintain water balance in two ways. The rumen of hydrated ungulates contains large amounts of water (20.0% of body weight), compensating during short periods of water deprivation in the first few days of dehydration. Additionally, the rumen in some species prevents hemolysis and osmotic shock during rapid rehydration in dehydrated individuals. The rumen or foregut functions by ingesting large volumes of water over short periods, then passing it to blood and tissues until osmotic homeostasis is restored (Cain et al., 2006).

Fat accumulation location also influences heat transfer, as subcutaneous fat may retain heat. Therefore, arid-dwelling ungulates need to store fat in small, localized body parts to improve heat transfer from other body surfaces. Many desert ungulates store fat in the rump, leaving most body surfaces free and providing protection to the rump against direct sunlight when the rump is oriented toward the sun (Cain et al., 2006). Some desert antelopes living in relatively warm habitats, such as springbok, seldom have significant fat reserves, allowing them to lose heat rapidly through their unusually thin pelage. This is advantageous during hot seasons but becomes disadvantageous in cold weather, leading to high mortality rates (Skinner and Louw, 1996).

Many ungulate species have a blood vessel system in the nose that cools blood flowing to the brain. This represents a form of selective brain cooling in which the brain cools before the rest of the body, sometimes resulting in brain temperatures significantly lower ($ $3.9°C) than body temperature. This cooling mechanism occurs in several species, such as wildebeest (Jessen et al., 1994) and springbok (Mitchell et al., 2002), although low activity attenuates selective brain cooling and high activity eliminates this mechanism (Jessen et al., 1994; Mitchell et al., 2002). Small African desert antelopes (*Dorcatragus*, *Madoqua*, and *Raphicerus*) have relatively large surface areas and are more vulnerable to dehydration and overheating in hot environments than large-bodied animals. Additionally, small antelopes must conserve their limited water and cannot afford to sweat, so they have developed an effective way to lower body temperature through evaporative cooling of blood via nasal panting (Estes, 1991).

For Günther's dik-diks, the most distinctive adaptation against heat stress and an especially effective mechanism for nasal panting is the enlargement and extension of the nose, expanding the nasal cavity. This effectively turns the nose into a flexible trunk with tiny nostrils and a hairy muffle that operates like bellows to increase airflow rate through the nostrils, allowing increased blood cooling. The nasal cavities have a moist, black mucosa that aids evaporative cooling and helps minimize water loss (Estes, 1991). The cooled blood then flows to the brain, making it cooler than the body core, which is necessary because brain overheating poses the greatest danger to survival (Kingswood and Kimamoto, 1996). Among the five dik-dik species, Günther's dik-dik has the largest nose and lives in the most arid habitat. Fuller et al. (1999) and Mitchell et al. (2002) hypothesized that selective cooling in free-living ungulates works only under moderate heat loads, switching from evaporative cooling, and its function is independent of adaptive heterothermy.

For some ruminants and carnivores, the nose aids in preventing brain overheating during chase, escape, or high ambient temperature, and can also promote water conservation through countercurrent heat exchange in nasal passages. Inhaled air passes over nasal turbinates and becomes saturated with water when reaching the lungs. Exhaled air transfers heat to nasal mucosa over nasal turbinates on its way out and becomes supersaturated with water that condenses in nasal passages, reducing respiratory water loss. During nights, nasal cavities of Kirks's dik-diks condense water from exhaled air, saving more than 58.0% of water (Kingswood and Kimamoto, 1996). Kirks's dik-dik and Günther's dik-dik have been observed licking condensed water drops from their noses (Fray and Hofmann, 1996). Additionally, the nose can reduce heat loss from the upper respiratory tract when air is inhaled through the nose and exhaled through the mouth, bypassing the countercurrent heat exchanger in the nasal passage (Taylor, 1977).

Thus, flat, dense, short, smooth, and light pelage can reflect sunlight and protect the skin. Nasal adaptations first cool the brain and promote water conservation. Furthermore, localized fat storage can prevent overheating.

2.3 Physiological Adaptations to High Temperatures and Water Shortage

Evaporative cooling using water from the body is the main heat transfer mechanism in terrestrial vertebrates to maintain body temperature within acceptable limits when air temperature exceeds body temperature. The maximal rate of cutaneous evaporation is higher than respiratory evaporation (Taylor, 1977), and all ungulate species have sweat glands, with the exception of musk deer (genus *Moschus*) (Sokolov, 1982). Temperature explains 90.0%–98.0% of mean daily water intake; gazelles, for example, could not lose metabolic heat without evaporation (Taylor, 1972). When ambient air temperature rises to 40.0°C and skin temperature increases above 39.5°C, sweating and external water loss increase 2.0–2.5 times in goitered gazelles (Soldatova and Grazhdankin, 1989). Similar phenomena have been observed in other ungulates such as Kirk's dik-dik and suni (*Nesotragus moschatus*) (Estes, 1991). Dorcas gazelles begin sweating when air temperature rises to 25.0°C, and water loss from sweat increases 40-fold when temperature rises from 20.0°C to 30.0°C (Yom-Tov et al., 1995). Total water loss for a dorcas gazelle during a summer day is about 0.30–0.40 L/12 h, while at night it decreases 3–4-fold (Yom-Tov et al., 1995). Water released through skin by sweating is very effective for maintaining body temperature within acceptable limits, but ungulates lose substantial water during this process, making this thermoregulation method acceptable only when drinking water is available. However, surface water is typically scarce in arid areas, creating another thermoregulation challenge: minimizing water loss. Thus, panting is a better water-saving process than sweating (Cain et al., 2006).

Many small African antelopes spend hot days in the shade of trees and shrubs, panting to cool down with mouths partly open and tongues slightly protruding (Estes, 1991). Under high ambient temperatures and restricted drinking conditions, springboks that cannot avoid direct solar radiation sweat profusely and exhibit extreme open-mouth panting due to marked body temperature increases (Hofmeyr and Louw, 1987). Blackbucks pant when ambient temperature rises above 44.0°C but do not pant when they have access to drinking water (Jhala et al., 1992). Dik-diks can regulate cutaneous evaporation, minimizing it in favor of thermal panting instead of sweating (Kingswood and Kimamoto, 1996). Thomson's gazelle and Grant's gazelle dissipate heat primarily through panting (Taylor, 1972). In contrast to dogs, ruminants often pant through their noses, thereby reducing water loss (Taylor et al., 1969a, b).

Water loss can occur through the respiratory tract and from the body surface due to sweat release. Both increased open-mouth breathing frequency (panting) and sweating increase water loss compared to normal levels and contribute to intensive heat dissipation from the body. As air temperature rises from 22.0°C to 40.0°C, respiration rates in Thomson's gazelles and Grant's gazelles increase from 15 to 200 breaths/min (Taylor, 1972). Long, thick pelage in some mammals complicates heat transfer through skin evaporation, so mammals resort to intensified respiratory moisture loss (Cain et al., 2006). Sweating is more effective for heat transfer than panting, but with water shortage, the intensity of water loss through both sweating and panting decreases (Taylor, 1972). Since sweating requires large water flow with increasing temperature, its effectiveness decreases compared to panting, and hyperthermia should occur faster in animals that sweat. Probably for this reason, panting rather than sweating is more common in desert mammals facing water scarcity and high ambient temperature (Taylor, 1972). In general, both sweating and panting strategies have advantages and disadvantages. Panting provides airflow over evaporative surfaces, which can maintain higher skin temperature and minimize inward heat flow from the environment, but it can also increase energy expenditure and contribute to metabolic heat. In contrast, sweating does not require additional energy and achieves a greater rate of heat loss than panting, but it depends on wind to decrease skin temperature, increasing heat inflow to the body from outside (Taylor, 1977).

Reduction in metabolic rate can minimize heat production and reduce water loss for ungulates. Desert-adapted ungulates have lower metabolic rates than other similar-sized ungulates (Cain et al., 2006). Dik-diks can also lower their metabolic rate, saving 3.5–5.0 mL of water per kilogram of body weight per day; under heat stress conditions, their body temperatures can increase 4.1°C above normal (Kingswood and Kimamoto, 1996). Lower metabolic rates of ungulates (eland and steenbok) in arid areas are associated with lower water turnover rates, which are lower in arid-area ungulates than in species from more mesophilic conditions (Cain et al., 2006). Moreover, water turnover rates increase 40.0%–50.0% in pregnant and lactating females compared to non-lactating individuals and decrease in dehydrated ungulates at any ambient temperature (Cain et al., 2006).

Blackbucks concentrate their urine to minimize water loss (Jhala et al., 1992). When blackbucks and dorcas gazelles are deprived of drinking water or receive only very salty water, they reduce water loss by lowering urine output 2-fold (for blackbucks) to 3–4-fold (for dorcas gazelles) and by doubling urine concentration. In winter, when water is more available, urea amount for dorcas gazelles increases 70.0% while urea concentration decreases (Yom-Tov et al., 1995). Many ruminants in arid areas can increase urine concentration and decrease urine volume. The eland, for example, can excrete 637 mmol/L urea compared to 136 mmol/L from domestic cattle (Lindsay, 2002). Similarly, springboks possess efficient kidneys that minimize water loss in urine: maximal urine concentration in this species may reach 3000 mOsm/L, though it usually does not exceed 1620 mOsm/L in tested individuals (Hofmeyr and Louw, 1987). This represents a 3-fold increase over human kidney concentration ability (500–800 mOsm/L) but is lower than most desert rodents (4000–6000 mOsm/L) (Skinner and Louw, 1996). Among all desert ungulate species, dik-diks can achieve the highest urine concentration (up to 4762 mOsm/L), the second highest kidney concentration ability among mammalian species after desert rodents (Kingswood and Kimamoto, 1996). In summer, urine and feces output decreases about 30.0% for blackbucks and 50.0% for dorcas gazelles, and water content is reduced 3-fold (Yom-Tov et al., 1995). This ability of desert ungulate kidneys to produce concentrated urine is related to longer loop of Henle (or nephron loop) length compared to other species (Cain et al., 2006).

During hot months, fresh pellets are very dry, wasting little water through defecation. Daily feces production in dorcas gazelles is 0.3% of body mass with 52.0% water content in winter, while in summer this rate decreases to about 50.0% (Yom-Tov et al., 1995). Dorcas gazelle pellet water content drops to 48.0% of water weight in winter and 43.0% in summer when deprived of free water (Yom-Tov et al., 1995). Water content in feces ranges from 40.0% to 50.0% in desert species (e.g., springbok), while reaching up to 70.0%–80.0% in mesophilic ungulates (e.g., domestic cattle). Some hydrated ungulate species (dorcas gazelles and impala) can decrease fecal water content by up to 17.0%–50.0%; blackbucks can produce feces with low water content of 43.3% (Jhala et al., 1992). Dik-diks can reabsorb water from feces (lowest water content among ungulates) and concentrate and restrict urine output (Kingswood and Kimamoto, 1996). Water reabsorption occurs in the colon, and species with longer intestines having more surface area and smaller proximal and distal colon circumference can produce drier feces (Cain et al., 2006).

Elands can survive in hot semi-deserts without drinking water because they can raise their body temperatures and "store" heat during the day, then release heat at night when ambient temperature decreases below body temperature, reducing the need for evaporative cooling during the day (Taylor, 1970a, b). Elands have low respiratory water loss relative to oxygen consumption at night. Each night, eland body temperatures are very low, and as temperatures drop, their respiratory rate decreases while the amount of oxygen extracted from air increases (Cain et al., 2006). Springboks exhibit an expected diurnal rhythm in body temperature, with highest values recorded during the hottest midday hours. Body temperatures at higher ambient temperature ranges (30.0°C–40.0°C) are significantly greater than at lower ranges (20.0°C–30.0°C), indicating that springboks can store some heat through mild adaptive hyperthermia. During a full gallop, springbok body temperatures can increase from 39.6°C to 41.4°C within minutes (Skinner and Louw, 1996). Dik-diks, like camels and some other arid-habitat ruminants, can raise their body temperatures during the day and store heat to maintain a small temperature gradient with the environment; the dik-dik nose can prevent brain overheating at high body temperatures (Frey and Hofmann, 1996).

Similarly, with restricted water intake, Thomson's gazelles and Grant's gazelles abandon evaporative cooling and reduce water loss through sweating (31.0%–63.0%); they also raise their body temperatures above air temperature, achieving thermal balance with their surroundings without panting (up to 41.0°C). During cool desert nights (air temperature around 22.0°C), their body temperatures fall again to normal levels (37.0°C–38.0°C) (Taylor, 1972). Other researchers have denied this adaptive heterothermic phenomenon, arguing it occurs only in captivity where ungulates cannot use behavioral and other thermoregulatory mechanisms. For free-ranging ungulates such as wildebeest (Jessen et al., 1994), springbok (Fuller et al., 2005), impala (Mitchell et al., 2002), and oryx (Fuller et al., 1999), they failed to find adaptive heterothermy. However, investigations of free-living Arabian sand gazelles (Ostrowski and Williams, 2006) and Arabian white oryx (*Oryx leucoryx*) (Ostrowski et al., 2003; Hetem et al., 2010) found they exhibit this heterothermic mechanism, reducing evaporative water loss (up to 21.0%–29.0%) and, similar to captive animals, increasing body temperature, storing heat during hot days, and dissipating extra heat during cool nights. Later, selective brain cooling was found in many antelope species and other bovids (Strauss et al., 2016, 2017), and the original denial of this physiological mechanism apparently relates to the fact that in natural environments, behavioral adaptations are almost always active while physiological adaptations are engaged only in extreme cases.

Thus, physiological adaptations to arid environments include: (i) sweating and nasal panting; (ii) urine concentration and moisture extraction from feces; (iii) metabolic rate reduction with dehydration; (iv) body temperature elevation during hot days; and (v) selective brain cooling.

2.4 Conservation Challenges

Anthropogenic factors affecting wildlife distribution and abundance are currently a major concern, especially for antelope populations in arid areas (Yom-Tov et al., 1995; Kingswood and Blank, 1996). Generally, gazelles avoid direct contact with humans and livestock (Chammem et al., 2008). Virtually all antelope species in arid areas are declining, with populations increasingly fragmented and isolated, some approaching extinction thresholds and many local populations having already disappeared (Kingswood and Mallon, 2001). North Africa once had the most diverse antelope wildlife among arid areas of Africa and Asia. Hunting has been the principal factor in decreasing all gazelle species and completely eliminating large antelopes such as addax (*Addax nasomaculatus*), bubal hartebeest (*Alcelaphus buselaphus buselaphus*), and scimitar-horned oryx (*Oryx dammah*) from the region (Kingswood and Mallon, 2001). Poaching with vehicles and firearms has had the greatest effect on gazelle populations (Kingswood and Mallon, 2001). Dorcas gazelles, having the widest distribution across all arid areas of the African continent, are now endangered throughout most of their range due to overhunting; they have been largely extirpated from the Atlas area, Arabian Peninsula, and Near East (Yom-Tov et al., 1995). A survey in Egypt revealed that hunting and habitat destruction caused dorcas gazelle disappearance from much of their habitat. Moreover, in Sudan, hunters take advantage of gazelle concentrations during migration and kill them in large numbers (Yom-Tov et al., 1995).

Overhunting significantly decreases population density, while gazelles tend to completely avoid areas with agricultural development, though they are more tolerant of livestock disturbances. An illustrative example is the fate of Acacia gazelles (*Gazella gazella acaciae*) in southern Israel, where crop cultivation development and underground water use for vegetable growing lowered the water table to 13 m depth. As a result, all springs and rich near-water vegetation around them disappeared completely. The entire landscape changed drastically, transforming oases into extremely arid areas. Consequently, Acacia gazelles are now extinct around two large springs in the Arava Valley, and the last herd is near extinction at the last spring in Yotvata, which has an artificial water source for gazelles (Blank, 1996). It has since been learned that Acacia gazelles inhabit only areas around springs and related water sources and cannot survive in pure arid conditions. In contrast, dorcas gazelles, which are true desert species, can increase their numbers considerably in the same habitat (Blank, 2005).

Thus, the occurrence probability of many gazelle species depends mainly on human presence and land use impacts rather than specific habitat characteristics. Recent agricultural intensification in more remote arid regions constitutes a serious threat to conservation of endangered populations of many gazelle species (Yom-Tov et al., 1995). In most North African countries, livestock feeding relates to disappearance of *Acacia* tree leaves and pods, preventing antelope survival due to absence of possible forage. Additionally, surface water is a key resource for both antelopes and livestock (Kihwele et al., 2020), and with livestock now occupying the most remote and arid desert areas, they dominate all water sources. From this review, it is clear that most antelope species cannot survive without drinking water and are therefore doomed to complete extinction due to resource scarcity.

3 Conclusions

Most arid-dwelling ungulate species need surface water to maintain body fluid balance. Water-independent species consume more water through their food than ungulates that drink frequently. In adapting to arid conditions, antelope species tend to reduce dependency on drinking water during evolution to the point that some do not drink water at all, though such species are very rare. Some thermoregulation and water loss reduction mechanisms work simultaneously, but ungulates use them in a specific sequence: behavioral changes and morphological features that consume the least energy are activated first, followed by physiological mechanisms that demand more energy resources. Even among physiological processes, not all mechanisms work simultaneously. Under moderate climate conditions, apart from behavioral mechanisms, only evaporative mechanisms are activated, while kidneys and colon do not support water reabsorption. During dry seasons, when surface water is lacking, these physiological mechanisms cause animals to excrete more concentrated urine and drier feces.

Most antelope populations in arid areas are decreasing, while others have gone completely extinct. In addition to poaching, the main cause of this process is rapid economic development of arid areas, causing loss of natural habitats and forcing antelopes into waterless areas where they cannot survive without drinking water.

This review demonstrates that arid-dwelling antelopes have various mechanisms for adaptation to arid environments. Many surveys have uncovered numerous details of these adaptations in desert antelopes of African and Asian lowlands, while we have negligible information on adaptations of antelopes living in the vast cold, dry highlands of the Tibetan Plateau, Pamirs, and Tianshan Mountains. This work remains for future investigations.

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Note: Figure translations are in progress. See original paper for figures.