



Antelope adaptations to counteract overheating and water deficit in arid environments

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Abstract: Many arid areas have very severe climates with extremely high summer temperatures, strong solar radiation, and a lack of drinking water during the driest season. Therefore, antelopes living in arid areas are forced to solve two main problems: avoiding overheating and maintaining water balance. Generally, there are physiological, morphological, and behavioral mechanisms for antelope adaptations to arid environments. Among the mechanisms, behavioral adjustments have a minimal cost and are activated first, while physiological mechanisms are the most energetically costly and involve adaptations to high temperatures when other mechanisms are insufficient. In previous publications, some examples of the antelope behavioral adaptations have been described only rarely, while in this review, we try to clarify all available information on the adaptations of antelopes living in arid areas to their native environments, paying particular attention to behavioral adjustments. Behavioral mechanisms, especially daily activity, diet and microclimate selection, and migrations, are so important and commonly used by antelopes in natural conditions, in which physiological mechanisms are usually not involved. Antelopes adjust their behaviors according to environmental changes so successfully that purely physiological mechanisms are discovered under laboratory conditions; for example, adaptive heterothermia or selective brain cooling phenomenon is difficult to observe in their natural habitats. This review provides a better understanding of the main behavioral mechanisms of antelope adaptations to arid environments and allows for the identification of 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 are among the most austere of terrestrial environments with high air temperatures (up to 50.0°C), strong solar radiation, a lack of shaded cover, limited precipitation (<100 mm), and few sources of water (Newby et al., 2016). Therefore, solving thermoregulation problems, such as avoiding body overheating and supporting the narrow limits of body temperatures, as well as finding a solution for water deficit, are major challenges for antelopes indigenous to arid environments (Gaughan et al., 2019). Life is not possible without an adequate level of body fluids and maintaining a body temperature within a narrow range (less than $\pm 2.0^{\circ}\text{C}$) is required for effective functions in mammals, so antelopes must continuously maintain a certain amount of water in their bodies to support homeostasis. However, hot environments force arid-dwelling

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ungulates to use water for thermoregulation, making water of exclusive value, especially in deserts where water is often in short supply (Cain et al., 2006). The need for water increases with temperature rises, so animals consume more water in hot conditions, which explains 90.0%–98.0% of the changes in daily water intake (Williamson and Delima, 1991).

In conditions of elevated temperatures, heat production exceeds an ungulate's ability for dissipation, therefore all sources of endogenous heat generation have to be reduced, while the respiratory rate and surface temperatures will increase (Cain et al., 2006); that is, ungulates fed in middays have an increased respiratory rate relative to the animals fed in the morning and evening (Parker and Robbins, 2018). Increasing respiratory rate promotes more intensive respiration evaporation, adding up to 45.0% of heat loss. Dorcas gazelles (*Gazella dorcas*), for example, increase their respiratory rate with ambient temperature increases, from 45–55 breaths/min at 28°C to 50–75 breaths/min at 29°C (Yom-Tov et al., 1995). The ambient temperature is extremely important for the degree of animal comfort, and for ungulates, high temperatures can decrease the production and quality of milk in nursing mothers (Bucklin et al., 1991). High temperatures may result in heat stress for the animals; therefore, the frequency of feeding activity during the hottest hours of the day tends to be reduced (Chagas et al., 2015).

Ungulates lose or gain heat from the environments through convection, radiation, and conduction, at rates proportional to the temperature gradient between animals (their body surface area) and the environment (Taylor, 1977; Sokolov, 1982). To maintain body temperature and minimize water loss, there are three kinds of mechanisms: behavioral, morphological, and physiological mechanisms (Cain et al., 2006). Energetically, physiological mechanisms against overheating and water loss are the most expensive; therefore, this kind of mechanisms is activated as the last of the three, when the morphological and behavioral mechanisms are insufficient. On the other hand, behavioral mechanisms are the most energy-saving and 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 timing of their activity (including reproduction), increasing diet selection, changing social behaviors and body orientation, and/or migrating to the habitats with more favorable conditions (Holcomb, 2017).

In this review, we considered behavioral, morphological, and physiological mechanisms which were observed in arid-dwelling antelope species of northern Africa and Asia, paying particular attention to their behaviors. Most of these data were obtained from published articles, where the researchers described their results observed over years of field observations, although physiological adaptations were clarified predominantly in laboratory experimental work. Some phenomena documented under early laboratory conditions were not observed in natural environments, which led the researchers to believe that these phenomena did not exist at all and instead was a consequence exclusively of the laboratory environment and procedures (Mitchell et al., 2002). Later, however, it was discovered that all phenomena observed under laboratory conditions were found in natural environments as well (Strauss et al., 2016, 2017). Unlike other articles and reviews devoted to ungulate adaptations to arid environments, which provided fragmentary information and isolated examples of these adaptations in different taxonomic groups, we focus in this paper exclusively on the adaptations of arid-dwelling antelopes, trying to provide a full review of all the main published materials on this issue. Some examples of these adaptations for a few species are well known, since they are often repeated in different articles and reviews, while other species get significantly less attention and are generally unfamiliar to readers. The purpose of this study is to give a full detail review of antelope adaptations to arid environments, paying special attention to the behavioral mechanisms of antelopes.

2 Review and discussion

2.1 Behavioral mechanisms

2.1.1 Daily activity timing

Thermoregulation is achieved first of all through behavioral changes and non-evaporative heat

loss, when ambient temperature is moderately hot. Among behavioral mechanisms to avoid overheating, antelopes first change their daily activity, which can reduce heat loads and decrease evaporative water loss. During the hottest months, antelopes are active during the cooler periods of the day: morning and evening. In hot summer, springboks (*Antidorcas marsupialis*) in the Kalahari Desert, dorcas gazelles in the Sahara region, and goitered gazelles (*Gazella subgutturosa*) in arid areas of the northern deserts of Central Asia all behave similarly and show two peaks of activity, i.e., in the early morning and late afternoon (Blank, 1990; Yom-Tov et al., 1995). This activity pattern is found in most antelope species, especially small body-sized antelopes, while large body-sized species are more tolerant to the high temperatures of the midday (du Toit and Yetman, 2005). During the hot hours, most antelopes stay in the shade of trees and shrubs, while on cool days or after rain, springboks feed throughout most of the day (Fuller et al., 2005). High temperatures lead animals to reduce their activity during the day and increase their twilight and nocturnal activity (Scheibe et al., 2009), switching from daytime to nocturnal activity in summer; these animals include 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), etc. In addition to thermoregulatory benefits, antelopes feeding at night also can increase their water intake by up to 30.0%, because their forage usually has a higher moisture content from the 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 antelope 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*) live in the Farasan Islands where there is no surface water at all, but they satisfy their water demands by very selectively browsing the freshest parts of perennial shrubs and trees with high water content. In addition, in some areas, the high air humidity can condense on the leaves of hygroscopic plants, then gazelles eat these leaves to provide them not only essential food, but also water (Habibi, 1992). A similar situation is observed in gerenuks (*Litocranius walleri*) from Kenya; gerenuks do not drink in either captivity or the wild even during the rainy seasons when surface water is quite abundant, satisfying their water needs also by eaten green juicy food (Bärmann et al., 2021). The 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 of time, meeting their water needs from their succulent food (up to 67.0% of water content), or such as some antelopes who dig for juicy roots, also feed at night when the humidity is higher, increasing the water content of their food. The distinction of the second group from the first group is that these animals will drink when surface water is available. The third group of antelopes needs surface water for drinking regularly, at least every 2–4 d 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). Because of this, goitered gazelles in Iran are distributed homogenously in a radius of 5 km around water sources (Farhadinia et al., 2009). In Kazakhstan, goitered gazelles stay in areas where the juicy plants are available, usually closely to rivers, lakes, and springs or along the shores of the Aral and Caspian seas. In summer, these gazelles are found within 10–15 km from water sources, while in late autumn and winter, when water sources freeze, goitered gazelles migrate to areas with a snow cover (Zhevnerov et al., 1983). Blackbucks can be found at considerable distances from surface water, but they are not observed in areas with no drinking water at all (Jhala et al., 1992).

In the driest deserts of Central Asia, the distribution of goitered gazelles was found to be dependent on the location of watering places (Zhevnerov et al., 1983). However, during the spring rains or monsoons and the intensive vegetation growing seasons, the water content of plants increases significantly to supply the requirements of desert antelopes, i.e., 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 oryxes beisa (*Oryx gazella beisa*) (Cain et al., 2006), and 10.0% for springbucks (Estes, 1991); therefore, these antelopes can survive without drinking water for long periods of time, allowing them to travel to the most remote areas of the deserts and return to watering places only occasionally. In general, browsers are less dependent on surface water than grazers, because the roots of trees and shrubs can reach down to underground water and produce green growth even during the hottest periods when grasses are completely dry (Estes, 1991).

All year round, plants and their parts (tender shoots, leaves, buds, flowers, fruits, pods, stems, tubers, and juicy roots) containing a high percentage of water content are always preferable to desert antelopes, such as oryxes 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 mostly *Capparis spinosa*, which has a moisture content of around 70.0% (Zhevnerov et al., 1983). Moreover, many plants in arid areas have water-storage organs, such as roots, tubers, or succulent stems and leaves. Oryx beisa also assiduously digs 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*), are able to live by consuming juicy plants in the Kalahari Desert (Estes, 1991). In Iran, the distribution of goitered gazelles is highly correlated with cultivated lands, where they can always find green crops (Farhadinia et al., 2009), and in Ethiopia, common duikers (*Sylvicapra grimmia*) munch on vegetables and fruit crops (Estes, 1991). Similarly, in India, the nilgais are found in great numbers around agricultural fields and also blackbucks rely on the agricultural crops quite frequently (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 nights (Estes, 1991). In some areas of Africa, common duikers and steenboks dig roots and tubers (sweet potatoes and peanuts) in agricultural fields, if available (Estes, 1991).

When most plants start to dry out, goitered gazelles (Zhevnerov et al., 1983) and blackbucks (Jhala et al., 1992) can visit water sources up to 1–4 times per day and may drink up to 1.00 L at one time and 2.00–4.00 L per day. In India, blackbucks live in arid areas, but they need water at least once a day. In contrast, the chinkara (*Gazella benetti*) eats moisture-laden leaves and flowers instead of drinking water, allowing it to inhabit all dry areas of the Thar Desert. Blackbucks can be found only in the border regions of this desert, where they can find surface water throughout the year. However, blackbucks are now appearing in newly irrigated areas of the desert, where these antelopes were previously absent (Rahmani and Sankaran, 1991).

Dorcas gazelles are extreme habitat generalists among gazelle species and inhabit a great variety of dry habits (Kingswood and Mallon, 2001). Nevertheless, these gazelles require a continuous supply of water 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 in summer, they face a daily shortage of about 0.12 L (per 10 kg of body weight). Dorcas gazelles can withstand a lack of surface water for 9–12 d in winter and 3–4 d in summer, with a body mass loss of 14.0%–20.0% (Yom-Tov et al., 1995). With the scarcity of water, dorcas gazelles decrease their amount of food intake and stop eating on the 4th day. An animal discovered in the 1990s, after a long period without water, could hardly chew or swallow the food, and looked dry and emaciated (Yom-Tov et al., 1995). To reduce the dependence on surface water, dorcas gazelles are highly selective in diet choices and change their diet according to seasons, but they never eat halophytic plants, requiring 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 the leaves, twigs, and fruits of *Ziziphus* and other shrubs (Yom-Tov et al., 1995). These gazelles also stay in areas after rains, where leaves of *Acacia* have a higher water content (Yom-Tov et al., 1995). In addition, dorcas gazelles are very selective in choosing plant parts, foraging on roots and flowers of lilies in the sand dunes, and selecting the

parts with a maximal water content (Henley et al., 2007). Though dorcas gazelles do not eat grasses, they spend much time digging and turning the soil in search of the roots of grasses and other plants; they also eat dates, both green and ripe (Yom-Tov et al., 1995). The occurrence of dorcas gazelles in the Negev Desert is positively associated with access to perennial water sources, especially when the water content of the plants they eat is low (Henley et al., 2007). The same is true for goitered gazelles who prefer to nibble the tips of plants, such as *Calligonum* ssp., which is the most edible species with the highest water content in summer, i.e., 90.0%–95.0% in May and June, and 55.0%–65.0% in July (Zhevnerov et al., 1983).

The indigenous Kalahari antelopes generally are able to survive without drinking water due to their behavioral diet adaptations (Williamson, 1987). Springboks living in the Kalahari Desert are unable to survive without water, since their diet contains a minimum of water by mass (Greenwald 1967). Therefore, in the Etosha National Park in Namibia, springboks go to drink at all times of the day almost all year round, but they will stop after rain and during cold weather (Bigalke, 1972); the ambient temperature was confirmed to have a significant effect on the frequency of drinking of springboks in the Kalahari Desert. Springboks can also drink highly mineralized water from boreholes in the river-bed (Child et al., 1971). In addition, they select succulent plant parts, such as flowers, fruits, and tubers, allowing them to survive without drinking water while grazing in the coastal fynbos of South Africa (Hofmeyr and Louw, 1987). Some desert plants grown in the habitat of springboks (Louw and Seely, 1982) and oryxes (Cain et al, 2006) can absorb moisture during cool, humid conditions, so grazing at night and morning can probably increase water content from the air or the dew (Taylor, 1968). A similar case was observed in Grant's gazelles, which mainly eat *Disperma* sp. in the Kenyan Desert. This plant species is very dry (1.0% of water content) during the hot days, but overnight it absorbs water from the night air to raise its water content to 30.0%–40.0%, 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 they can survive without surface water; there is even a Somali legend that a Guenther dik-dik will die if it drinks (Kingswood and Kumamoto, 1996). The Kirks's dik-diks (*Madoqua kirkii*), on the other hand, have been observed drinking from rainwater puddles in natural conditions (Tinley, 1969), while some, like Günther's dik-diks (*Madoqua guentheri*), have been observed to lick 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 a high moisture content to compensate for a scarcity of drinking water (Williamson and Delima, 1991). Precisely, how long ruminants can remain without drinking depends on several factors: meteorology, water quantity and quality, water content of the food ingested, and the age of animals and their stage in the biological cycle. In summer, not only are the midday maximum temperatures important but the night temperatures are also of great significance. Sudden climatic changes (occasional rainfall or cooler nights) modify drinking behavior significantly and animals can satisfy their need for water with moisture in their food and do not need to drink, even on very hot days (Gauthier-Pilters, 1984).

Under experimental conditions, antelopes restricted from drinking water typically lose body mass and reduce their evaporative water loss by up to 55.0% (Taylor, 1970a). In natural conditions, blackbucks lose 13.0% of their body weight over 3 d when they are deprived of drinking water (Jhala et al., 1992). Experiments with long-term restrictions of food and water for Arabian sand gazelles (*Gazella marica*) over a 4-month period demonstrated that they adjust their body physiology by slightly decreasing their body mass, but the sizes of the liver, heart, muscles, and metabolic rate decline significantly. As a result, their oxygen demands decrease, and the gazelles lose less amounts of evaporative water through their breath (Ostrowski et al., 2006).

2.1.3 Endurance to salty water

Goitered gazelles on the Barsa-Kelmes Island drink water mostly from the Aral Sea; in the western Kazakhstan, they willingly drink salty water along the coast of the Caspian Sea, which

has a salt content of 9–15 g/L (Zhevnerov et al., 1983). They can consume water with a salt content of up to 20 g/L, but a liter of drinking water with more than 20 g of salts is unsuitable and gazelles will die, especially the young ones (Gorelov, 1972). More salty water (salt content of 35 g/L) is intolerable, so most likely there are no goitered gazelles on the shores of the Persian Gulf and the Arabian Sea (Zhevnerov et al., 1983). Experiments with dorcas gazelles were done to observe if they can drink sea water from the Red Sea (salt content of 36–41 g/L) when no fresh water is available. The results showed that they cannot utilize this sea water, because drinking such a high percentage of salty water will lead to a loss in body weight of as much as 15.0% of their original weight in just three days. Dorcas gazelles can maintain their original weight but only when the seawater is diluted by 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). Blackbuck also have the ability to drink salty and sea water (Jhala et al., 1992). Springboks also can drink highly mineralized water from boreholes (Skinner and Louw, 1996). Along the Caspian and Aral seas, goitered gazelles are able to 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 better quality foods to satisfy their water and energy demands, which is a very important behavioral adaptation for large ungulates (Knight et al., 1988). Arid environments, with their unpredictability of water and forage resources, drive the ungulates to a nomadic lifestyle (Nandintsetseg et al., 2019). Migrations of antelopes are observed commonly 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 cause of these migrations is not only forage quality but also the availability of drinking water (Cain et al., 2006). Saiga antelopes are always continuously on the move, migrating from the steppes to the 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) every day. In hot summer, they often migrate along rivers and concentrate around permanent water sources. Saiga antelopes also move quickly through waterless areas and appear in some areas even after a small rain (Fadeev and Sludskiy, 1982). The most typical feature of the oryx is that it is one of the most desert-adapted antelopes specialized for a nomadic lifestyle (Estes, 1974), since this antelope species requires just 4.85 mL/d drinking water or 4.0% of its body weight (Yom-Tov et al., 1995). During the dry periods in Kazakhstan, goitered gazelles stay in interior desert areas until they have temporary water sources and juicy vegetation, but when everything dries up, they become nomadic and start to 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 the natural water sources are dry in summer and the moisture gained from vegetation is not enough, dorcas gazelles migrate far west towards the Nile Valley due to the shortage of water in their native range; further, dorcas gazelles living in the Red Sea hill areas migrate to the Red Sea coastal plain in winter for the 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 the 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 and 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 from shrubs, trees, or inside hollows during the hot summer days and searching for more comfortable places by using features of the micro-relief are very useful behaviors for ungulates (Holcomb, 2017). There is a strong linear relationship of the use of shade by antelopes with both ambient temperature and the incidence of solar radiation (Dunbar, 1979). The temperature of the skin of antelopes exposed to solar radiation is on average up to 6.4°C higher than that in the shade (Parker and Robbins, 2018); air temperature may be lower by up to 12.0°C in the shade compared to the open areas (Hetem et al., 2011). In hot environments, small body-sized 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), are easily able to find shade under Acacia trees or near large stones and steep slopes or even next to tuft grasses and medium-sized and small shrubs. Goitered gazelles stay in the shade under the crowns of shrubs and trees. Sometimes several depressions can be found located in a circle under a single bush as the gazelle changes its location with the movement of the shadow (Zhevnerov et al., 1983; Blank, 2020). The larger antelopes, such as the elands, also can find shady places around large trees or in rock shelters in spite of the fact that they have a lower possibility of finding complete shade for total refuge from sunlight (Fuller et al., 1999).

The distribution of dorcas gazelles in the Negev Desert is related not only to forage quality and water content in food, but also to access to shelter from solar insolation under the canopy of Acacia trees (Baharav, 1980, 1982). Adult males of goitered gazelles prefer to use elevated lands and less shade from vegetation, while females and especially fawns utilize the 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 the herd clusters tightly together until the late afternoon (Cain et al., 2004).

Blackbucks, especially adult males, prefer to stay in the open sun all throughout the day, even during the peak of summer, at the expense of their effective physiology (Bohra et al., 1992). Similar behavior of staying under the sun during the heat of the day is observed in the oryx, because they can conserve body water through a flexible body temperature (Cain et al., 2006). During the hottest summer days, goitered gazelles stand on hilltops or plateaus, where the wind blows almost constantly, helping the body thermoregulation (Blank, 2020). Goitered gazelles prefer salt marshes and depressions between dunes, where the wind blows well and the soil cools overnight; as the air temperature increases, the animals move to the edges of dunes, the places that are closer to the seashore where the 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 surface of the body can be provided by wetting the fur with saliva by the animal itself. Günther's dik-diks demonstrate this behavior, spreading saliva over their body flanks due to increasing evaporation. This method requires a lot of water and can be used by animals for only a short time because of the permanent water deficit in arid environments (Cain et al., 2006).

2.1.6 Body orientation

When shade is not available, ungulates adjust their body position relative to the sun and wind (Berry et al., 1982; Hofmeyr and Louw, 1987). To reduce solar radiation, animals stand with the long axis of their body parallel to the direction of the sun or the rump pointed towards the sun or wind or lie down in a position with their head down and shaded by their body (Cain et al., 2006). Springboks can reduce their solar radiation load by 62.0% through changing their body orientation (Hofmeyr and Louw, 1987).

During the cold periods, wildebeests orient their bodies in a "tail-to-wind" posture, and then change their positions to face into the wind with a rise in temperature (Berry et al., 1982; Maloney et al., 2005). In the absence of shade, the elands, black wildebeests, impalas (*Aepyceros*

melampus), and springboks stand in the positions parallel to the solar radiation, reducing their heat loads (Hetem et al., 2011). When shade is not available, springboks orient their hindquarters toward the sun or in the direction of the solar beam. This behavior significantly reduces exposure to the direct solar radiation and the higher solar load (Hofmeyr and Louw, 1987).

2.1.7 Standing position during the hottest hours

During the hot midday, goitered gazelles occasionally rest in standing positions to protect their bodies from overheating, since the air temperature at a standing height is lower by several degrees than that at the ground level. For goitered gazelles in Kazakhstan, this temperature difference is 7.0°C in the plump salt marsh and 18.0°C in the sands of the seashore (Zhevnerov et al., 1983). It was found that animals decrease their body temperatures more while standing still in the shade during the hottest hours (Estes, 1991). Klipspringers (*Oreotragus oreotragus*) and dik-diks (*Madoqua* spp.) mostly stand rather than lay in the shade during the hottest hours, which is also likely related to the necessity to dissipate body heat more efficiently (Estes, 1991).

2.1.8 Wallowing (rolling in dust and mud)

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*)). The functional sweat glands are underdeveloped in these animals and wallowing in the mud serves as a compensation mechanism for cooling and sunburn protection in support of thermoregulation (Bracke, 2011). Therefore, in hot weather, all Suidae species seek water and wallow in mud to lower their body temperatures. However, most of 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 the Central Asian deserts

Male goitered gazelles establish individual territories during the rutting season (November and December) and prefer to not leave their territories during the entire breeding season (Blank, 1998). These territories are found often in the submontane dry plains with a lack of water. During the rutting season, male goitered gazelles need a high level of energy and water while the only source for water is snow. The snow cover, however, is unstable and usually melts or is blown away within several days. Territorial males can survive without water for a few days until the next snowfall, but in some warmer and snowless years, the breeding area gets no snow for long periods of time (more than a week); therefore, even though they prefer not to, these males have to leave their territories for 1–2 h to drink water, running all the way to the watering place and then come back (Blank, 1998). The 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 longer after chasing females during the warm sunny days than during the cold and cloudy days. Based on these observations, it is clear that the snow cover is a necessary part of the rutting season and plays an exceptional role in the reproduction of goitered gazelles (Blank, 1998).

Goitered gazelles experience great difficulty during the early, snowless frosts, when water sources freeze but there is no snow cover. These gazelles graze more intensively for a longer time in the morning after a frosty night, when the frost falls on the plants and the grasses remain moist for a longer time. During the periods of low snow, the occurrence of gazelles significantly increases in the pastures with sharply crossed terrain, where snow accumulates under the influence of the wind and is available longer. For goitered gazelles, the autumn migration is often caused not by a lack of food, but by the freezing of available water sources in the absence of snow cover. In snowless, frosty winters, gazelles are quickly exhausted because of water drought, sometimes resulting in death (Zhevnerov et al., 1983). Other ungulate species in Central Asia 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 the desert mountains also eats snow and is not interested in other water sources (Fedosenko, 2000); and saiga antelope rarely visits water sources in winter, instead getting water

from the snow to meet its needs (Fadeev and Sludskiy, 1982).

2.2 Morphological features against overheating and water loss

For ungulates, the important morphological features regulating heat gain and water loss are body size and shape. Large ungulates obtain heat at a slower rate than small ungulates because of a lower ratio of surface to volume and a higher thermal inertia. The disadvantage of large ungulates is the slow reduction of heat and a limited number of available shaded places. While large animals have larger energy requirements, they have relatively lower metabolic rates than smaller species. In addition, ungulates adapted to arid environments have longer and thinner appendages (ears and legs) with a higher ratio of surface to volume, providing more intensive heat loss (Cain et al., 2006). For example, the vasodilation of the blood vessels supplying long ears increases heat loss from radiation and convection, e.g., springboks (Skinner and Louw, 1996). Many desert dwarf antelopes (*Dorcatragus*, *Madoqua*, and *Raphicerus*), staying in areas with a deficit of drinking water, prefer to feed on mainly green shoots and fruits with a considerable water content. With an extremely narrow muzzle and row of incisors, dik-diks select the smallest food items, which are the most nutritious and juicy parts of plants. This forage is too sparse, but dik-diks have small body size and can survive within a minimal space, while these food amounts could not support larger browsers (Estes, 1991). The dik-diks' flexible upper lips and tongues are also useful to pluck foliage or juicy shoots, extending their reach by standing on their hind legs (Estes, 1991).

The pelage of antelope provides a barrier between the animal and its environment. The physical characteristics of the pelage can feature prominently in thermal adaptations of animals to specific climatic zones. The most important thermal features of the pelage are thickness, density, and color (Hofmeyr, 1985). The thickness and color of an animal's pelage have an impact on the heat transfer between the body and the environment. Thin pelage provides better heat loss and gain, but thick pelage can better protect the animals from sun insolation while constraining the cooling effect of sweating. In general, the thickness of the pelage decreases with body size for the desert ungulates, enhancing heat loss and compensating for the disadvantages of a large body size (Cain et al., 2006). The pelage varies in different parts of the body, tending to be thicker in the dorsal parts and maybe thinner or even lacking in the ventral surfaces, which act like "thermal windows" with maximal convection and conduction (Feldhamer et al., 1999). The pelage and its color are the most conspicuous adaptations to life in a desert. Desert-adapted ungulates usually have a glossy, light pelage for reflecting more radiation than dark-colored pelage, although the latter can better protect the skin from the direct sun radiation and reduces convective heat gain from the environment (Cain et al., 2006). Roberts (1977) asserted that the light-colored pelage of gazelles is an important part of their overall adaptive strategy, decreasing heat absorption during the hot summer days. A reduction of conductivity of 2–3-fold for water vapor is observed in the pelage of goitered gazelles, as well, 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 ungulate species, such as springbok, have a thinner pelage with a higher conductance than expected for antelopes of similar sizes, which provides a rapid heat loss if the ambient temperature is lower than the skin temperature at the cessation of exercise. This situation would appear after sprinting away from predators at top speed (Hofmeyr and Louw, 1987). Klipspringers have special insulating coats that are able to withstand extreme cold and heat environments, up to 40.0°C in the shade (Estes, 1991). Hartebeests use shade rarely (Ben-Shahar and Fairall, 1987), because they have thicker pelage and lower pelt absorption rate, which reduce the heat load and allow them to survive on the open grass plains in the more arid areas (Hofmeyr, 1985). For springboks, the white color of the rump and face increase reflectivity and enhance the benefits of a parallel orientation to the sun; therefore, these animals prefer a rump oriented to the sun when grazing (Skinner and Louw, 1996).

Bovoid horns also may have a thermoregulatory function as well. Arid-dwelling bovuids 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 has the capability to maintain water balance in two ways. The rumen of hydrated ungulates contains great amounts of water (20.0% of body weight), compensating ungulates during short periods of water deprivation in the first few days of dehydration. In addition, the rumen in some species prevents hemolysis and osmotic shock during rapid rehydration in dehydrated individuals. The function of the rumen or foregut is ingesting large volumes of water over a short time and then passing it to the blood and tissues until osmotic homeostasis is restored (Cain et al., 2006).

The location of fat accumulation also influences heat transfer and subcutaneous fat may retain heat. Therefore, arid-dwelling ungulates need to store fat in small, localized parts of the body, improving heat transfer from other body surfaces. Many desert ungulates store their fat in the rump part, leaving most free surfaces of the body and supplying protection to the rump against the direct sun light, 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 to allow them to lose heat rapidly through their unusually thin pelage. This is a great advantage during the hot seasons, but it turns into a disadvantage in cold weather, leading to a high mortality rate (Skinner and Louw, 1996).

Many ungulate species have a blood vessel system in the nose, which cools blood that first flows to the brain. This is a form of selective brain cooling in which the brain cools down before the rest of the body, sometimes resulting in the temperature of a brain significantly lower ($\leq 3.9^{\circ}\text{C}$) than the body temperature. This cooling mechanism is found in a number of 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 a relatively large surface area and are more vulnerable to dehydration and overheating in hot environments than large body-sized animals. In addition, small antelopes need to save their limited water and cannot afford to sweat. So, they developed an effective way to lower body temperature by evaporative cooling of the blood through 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 to enlarge and extend 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 a bellows to increase the rate of air flow through the nostrils, allowing an increase in the blood cooling. The nasal cavities have a moist, black mucosa that aids in evaporative cooling and helps to minimize water loss (Estes, 1991). The cooled blood then flows to the brain, making it cooler than the core of the body, which is necessary because the overheating of the brain is the greatest danger to survival (Kingswood and Kimamoto, 1996). Among the five species of dik-diks, the Gunther'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 the prevention of overheating of the brain during chase, escape, or high ambient temperature, and can also promote water conservation through a countercurrent heat exchange in the nasal passages (Frey and Hofmann, 1996). Inhaled air passes over the nasal turbinate and is then saturated with water when reaching the lungs. Exhaled air transfers heat to the nasal mucosa over the nasal turbinate on its way back out and becomes supersaturated by water that condenses in the nasal passages, reducing respiratory water loss. During nights, the nasal cavities of Kirks's dik-diks condense water from exhaled air, saving more than 58.0% of the water (Kingswood and Kimamoto, 1996); Kirks's dik-dik and Gunther's dik-dik have been observed to lick drops of condensed water from their noses (Fray and Hofmann, 1996). In addition, 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, the flat, dense, short, smooth, and light pelage can reflect sun light and protect the skin. There are adaptations of the nose that first cool the brain and promote the conservation of water. Further, localized fat storage can prevent overheating.

2.3 Physiological adaptations to high temperatures and water shortage

Evaporative cooling with water from the body is the main way of heat transfer in terrestrial vertebrates to maintain body temperature within acceptable limits when the air temperature exceeds the body temperature. The maximal rate of cutaneous evaporation is higher than the 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 the mean daily water intake; gazelles, for example, could not lose their metabolic heat without evaporation (Taylor, 1972). When the ambient air temperature rises to 40.0°C and the skin temperature increases to more than 39.5°C, sweating and external water loss increases by 2.0–2.5 times for goitered gazelles (Soldatova and Grazhdankin, 1989). A similar phenomenon has been observed in other ungulates, such as Kirk's dik-dik and suni (*Nesotragus moschatus*) (Estes, 1991). Dorcas gazelles start to sweat when the air temperature rises to 25.0°C, and water loss from sweat increases 40-fold when the temperature rises from 20.0°C to 30.0°C (Yom-Tov et al., 1995). The total water loss of a dorcas gazelle during a summer day is about 0.30–0.40 L/12 h, while during the night it decreases by 3–4-fold (Yom-Tov et al., 1995). Water released through the skin by sweating is a very effective way for maintaining body temperature within acceptable limits, but ungulates lose a great amount of water during this process and this kind of thermoregulation is acceptable only when drinking water is available. However, surface water is typically a scarce resource in arid areas, creating another thermoregulation challenge in minimizing water loss. Thus, panting is a better process of saving water than sweating (Cain et al., 2006).

Many small African antelopes spend hot days in the shade of trees and shrubs and pant to cool down with their mouths partly open and their tongues protruding slightly (Estes, 1991). Under high ambient temperatures and restrained drinking conditions, springboks that could not avoid the direct solar radiation sweat profusely and show extremely open mouth panting because of the marked rise in body temperature (Hofmeyr and Louw, 1987). Blackbucks pant when the ambient temperature rises above 44.0°C; however, they do not pant when they have access to drinking water (Jhala et al., 1992). Dik-diks can regulate their cutaneous evaporation, minimizing it for thermal panting instead of sweating (Kingswood and Kimamoto, 1996). Thomson's gazelle and Grant's gazelle both 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 surface of the body due to the release of sweat. Both increased frequency of open-mouth breathing (panting) and sweating increase water loss compared to normal water loss and contribute to intensive heat dissipation from the body. As air temperature rises from 22.0°C to 40.0°C, the respirations of Thomson's gazelles and Grant's gazelles increase from 15 to 200 breaths/min (Taylor, 1972). Long and thick pelage of some mammals complicates the heat transfer through skin evaporation, so mammals resort to the intensification of respiratory moisture (Cain et al., 2006). Sweating is a more effective way of heat transfer compared to panting, but with a lack of water, the intensity of water loss by sweating and panting decreases (Taylor, 1972). Since sweating requires a large flow of water with an increase in temperature, the effectiveness of sweating decreases in comparison with panting and hyperthermia should occur faster in animals that sweat. Probably for this reason, panting, rather than sweating, is more common in desert mammals with a lack of water and a high ambient temperature (Taylor, 1972). In general, advantages and disadvantages exist for both sweating and panting strategies. Panting provides airflow over the evaporative surfaces, which can maintain a higher skin temperature and minimizes the inward flow of heat from the environment, but it can also increase energy expenditure and contribute to metabolic heat. In

contrast, sweating does not need additional energy and achieves a greater rate of heat loss than panting, but it is dependent on the wind to decrease the skin temperature, increasing the 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 body-sized ungulates (Cain et al., 2006). Dik-diks also can lower their metabolic rate and, as a result, can save 3.5–5.0 mL of water per kilogram of body weight per day; under heat stress conditions, their body temperatures can increase by 4.1°C above normal (Kingswood and Kimamoto, 1996). The lower metabolic rates of ungulates (eland and steenbok) in arid areas are associated with lesser water turnover rates, which are lower in ungulates of arid areas than in species of more mesophilic conditions (Cain et al., 2006). Moreover, water turnover rates increase from 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 their urine output from 2-fold (for blackbucks) up to 3–4-fold (for dorcas gazelles), and by doubling the concentration of urine; however, in winter, when water is more available, the amount of urea for dorcas gazelles increases by 70.0% while the concentration of urea decreases (Yom-Tov et al., 1995). Many ruminants in arid areas can increase urine concentration and decrease its amounts. The eland, for example, can excrete 637 mmol/L urea compared to 136 mmol/L urea from domestic cattle (Lindsay, 2002). Similarly, springboks possess efficient kidneys with the ability to minimize water loss in the urine: the maximal urine concentration in this species maybe up to 3000 mOsm/L, though it usually does not exceed 1620 mOsm/L in tested individuals (Hofmeyr and Louw, 1987). This is a 3-fold increase over the concentration ability of the human kidney (500–800 mOsm/L), but lower than that of most desert rodents (4000–6000 mOsm/L) (Skinner and Louw, 1996). Among all species of desert ungulates, dik-diks can reach the highest urine concentration (up to 4762 mOsm/L), which is the second highest kidney concentration ability among mammalian species next to desert rodents (Kingswood and Kimamoto, 1996). In summer, the output of urine and feces decreases about 30.0% for blackbucks and 50.0% for dorcas gazelles, and water content is reduced by 3-fold (Yom-Tov et al., 1995). This ability of desert ungulates' kidneys to produce concentrated urine is related to the longer length of the loop of Henlé (or nephron loop), compared to other species (Cain et al., 2006).

During the hot months, fresh pellets are very dry, wasting little water through defecation. The daily production of feces in the dorcas gazelles is 0.3% of body mass with a water content of 52.0% in winter; while in summer, this rate decreases to about 50.0% (Yom-Tov et al., 1995). The water content of pellets for dorcas gazelles drops to 48.0% of water weight in winter and 43.0% in summer when they are deprived of free water (Yom-Tov et al., 1995). The content of water in feces ranges from 40.0% to 50.0% in desert species (e.g., springbok), while it can reach up to 70.0%–80.0% in mesophilic ungulates (e.g., domestic cattle). Some hydrated ungulate species (dorcas gazelles and impala) are able to decrease fecal water content by up to 17.0%–50.0%; blackbucks can produce feces with a low water content of 43.3% (Jhala et al., 1992). Dik-diks have the ability to reabsorb water from feces (lowest water content among ungulates) and concentrate and restrict the output of urine (Kingswood and Kimamoto, 1996). Water reabsorption occurs in the colon, and species having longer intestines with more surface area and smaller circumference of the proximal and distal colon are able to 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, and release heat at night when the ambient temperature decreases below the body temperatures, reducing the need to use evaporative cooling during the day (Taylor, 1970a, b). Elands have a low respiratory water loss compared to oxygen consumption at night. Each night, the body temperatures of elands are very low, and as the temperatures drop, their respiratory rate decreases while the amount of oxygen extracted from the

air increases (Cain et al., 2006). Springboks exhibit an expected diurnal rhythm in body temperatures, with the highest values recorded in the hottest hours of midday. Body temperatures at the higher range of ambient temperature (30.0°C–40.0°C) are significantly greater than that at the lower range of ambient temperature (20.0°C–30.0°C), indicating that springboks are able to store some heat by means of mild adaptive hyperthermia. During a full gallop, the body temperatures of springboks can increase from 39.6°C up to 41.4°C within minutes (Skinner and Louw, 1996). The dik-diks, like camels and some other ruminants in arid habitats, can raise their body temperatures during the day and store heat to maintain a small temperature gradient based on the environment; the dik-diks' nose can prevent the overheating of the brain at high body temperatures (Frey and Hofmann, 1996).

Similarly, with restrictions in water intake, Thomson's gazelles and Grant's gazelles also abandon evaporative cooling and decrease the loss of water through sweating (31.0%–63.0%); they also raise their body temperatures above the air temperature, in thermal balance with their surroundings without panting (up to 41.0°C). During the cool desert nights (air temperature around 22.0°C), their body temperatures fall again to a normal level (37.0°C–38.0°C) (Taylor, 1972). Other researchers have denied this adaptive heterothermic phenomenon, because it is found only in captivity where ungulates are unable to use behavioral and other thermoregulatory mechanisms; while 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 fail 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) were found to show this heterothermic mechanism of reducing evaporative water loss (up to 21.0%–29.0%) and, similar to animals in captivity, they increase their body temperatures, store heat during the hot days, and dissipate the extra heating during the cool nights. Later, the selective brain cooling is found in many antelope species and other bovids (Strauss et al., 2016, 2017), and the original denial of this physiological mechanism is apparently related to the fact that in natural environments, behavioral adaptations are almost always in action in most cases while physiological adaptations are only involved in extreme cases.

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

2.4 Conservation challenges

The anthropogenic factors affecting the distribution and abundance of wildlife is currently a major concern especially for antelope populations in arid areas (Yom-Tov et al., 1995; Kingswood and Blank, 1996). In general, gazelles avoid direct contact with humans and livestock (Chammem et al., 2008). Virtually, all antelope species in arid areas are declining and populations everywhere are increasingly fragmented and isolated, with some close to the extinction threshold and the disappear huge numbers of other local populations having already (Kingswood and Mallon, 2001). North Africa once had the most diverse antelope wildlife among other arid areas of Africa and Asia. Hunting has been the principal factor in the decrease of all species of gazelles and the total elimination from the region of large antelopes, such as addax (*Addax nasomaculatus*), bubal hartebeest (*Alcelaphus buselaphus buselaphus*), and scimitar-horned oryx (*Oryx dammah*) (Kingswood and Mallon, 2001). Poaching with vehicles and firearms has had the greatest effect on gazelle populations (Kingswood and Mallon, 2001). Dorcas gazelles, for example, having the greatest distribution over all arid areas of the African continent, are now in danger in most of their ranges due to overhunting; they have been largely extinct in the Atlas area, Arabian Peninsula, and the Near East (Yom-Tov et al., 1995). A survey in Egypt revealed that hunting and habitat destruction caused the disappearance of dorcas gazelles from much of their habitats. Moreover, in Sudan, hunters take advantage of the concentration of gazelles during migration and kill them in large numbers (Yom-Tov et al., 1995).

Overhunting decreases population density significantly, while gazelles tend to avoid areas with

agricultural development completely, though they are more tolerant to the disturbances from livestock. An indicative example is the fate of Acacia gazelles (*Gazella gazella acaciae*) in southern Israel, where the development of crop cultivation and the usage of underground water for growing vegetables has lowered the underground water table to a depth of 13 m. As a result, all springs and the rich near-water vegetation around them disappeared completely. The entire landscape changed drastically, turning oases into extremely arid areas. As a consequence, Acacia gazelles are now extinct around two large springs in the Arava Valley and the last herd is close to extinction at the location of the last spring in Yotvata with an artificial water source for gazelles to drink (Blank, 1996). It has since been learned that Acacia gazelles inhabit areas only around springs and related water sources and cannot live in pure arid conditions. In contrast, dorcas gazelles, which are a real desert species, are able to increase their numbers considerably in the same habitat (Blank, 2005).

Thus, the occurrence probability of many gazelle species is mainly dependent on the presence of human beings and their impact on land use, rather than specific habitat characteristics. The recent intensification of agriculture in more remote areas of arid regions constitute a serious threat to the conservation of endangered populations of many gazelle species (Yom-Tov et al., 1995). In most North African countries, feeding livestock is related to the disappearance, for example, the loss of Acacia tree leaves and their pods, not allowing to antelopes to survive, because of the absence of any possible forage. In addition, 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 areas of the deserts, they are dominating all water sources. From this review, it is clear that most antelope species cannot survive without drinking water, therefore, they are doomed for complete extinction due to a lack of resources.

3 Conclusions

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

Most populations of antelopes that live in arid areas decrease their numbers, while others go totally extinct. In addition to poaching, the main cause of this process is the faster economic development of arid areas, causing the 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. Various surveys have uncovered many details of this adaptation in desert antelopes in the lowlands of Africa and Asia, while we have negligible information on adaptations of antelopes living in the vast areas of the cold, dry highlands of Tibetan Plateau, Pamirs, and Tianshan Mountains. This work remains for future investigations.

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