Review: Water stress in sheep raised under arid conditions

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[1]Department of Animal and Veterinary Sciences, Faculty of Agricultural and Food Sciences, American University of Beirut, Riad el Solh 1107-2020, Beirut, Lebanon; [2]INRA UMR 791 MoSAR, 16 rue Claude Bernard, 75005 Paris, France; and [3]AgroParisTech, UMR 791 MoSAR, 16 rue Claude Bernard, 75005 Paris, France.

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Chedid, M., Jaber, L. S., Giger-Reverdin, S., Duvaux-Ponter, C. and Hamadeh, S. K. 2014. **Review: Water stress in sheep raised under arid conditions**. Can. J. Anim. Sci. **94**: 243–257. Sheep breeds which are indigenous to arid and semi-arid regions are known for their ability to adapt to rustic environments, to climatic variations as well as to shortages in resources. Water scarcity, often combined with heat stress, is a common challenge facing these animals, causing physiological perturbations and affecting the animal's productivity. This review reports the effect of different forms of water stress on physiological indicators, blood parameters, thermoregulation and immunological status in sheep. Although the breed effect may be significant, the following are generally observed common responses: drop in feed intake and weight loss, increase in evaporative cooling through panting, production of a small volume of highly concentrated urine, haemoconcentration, high blood osmolality, and immunosuppression. Prolonged water shortage may affect lamb birth weight and survival, and lead to a decrease in milk production, especially in non-adapted breeds, which could lead to important economic losses, as reported in heat-stressed sheep husbandries. Novel stress alleviation approaches are also presented, such as vitamin C supplementation.

Key words: Arid regions, dehydration, immunosuppression, physiology, sheep, thermoregulation

Chedid, M., Jaber, L. S., Giger-Reverdin, S., Duvaux-Ponter, C. et Hamadeh, S. K. 2014. **Stress hydrique chez les moutons élevés sous conditions arides : une revue de la littérature**. Can. J. Anim. Sci. **94**: 243–257. Les races de moutons indigènes aux régions arides et semi-arides sont reconnues pour leurs habiletés à s'adapter aux environnements rustiques, aux variations climatiques ainsi qu'aux pénuries de ressources. Le manque d'eau, souvent combiné au stress thermique, est un défi commun auquel ces animaux font face, causant ainsi des perturbations physiologiques et ayant un effet sur la productivité de l'animal. Cette revue de la littérature rapporte les effets de différentes formes de stress hydrique sur les indicateurs physiologiques, les paramètres sanguins, la thermorégulation et l'état immunologique chez les moutons. Bien que l'effet de la race a un impact significatif, les suivantes sont des réponses générales communément observées : baisse de prise alimentaire et perte de poids, augmentation du refroidissement évaporatif par polypnée, production d'un petit volume d'urine fortement concentrée, hémoconcentration, forte osmolalité sanguine et l'immunosuppression. Une pénurie d'eau prolongée peut avoir un effet sur le poids à la naissance et la survie des agneaux et mène à une diminution de la production de lait, surtout chez les races non adaptées. Ceci pourrait se solder par d'importantes pertes économiques telles que celles rapportées dans les élevages de moutons qui subissent le stress thermique. De nouvelles approches pour l'allégement du stress sont aussi présentées, telles que les suppléments de vitamine C.

Mots clés: Régions arides, déshydratation, immunosuppression, physiologie, moutons, thermorégulation

Sheep production is a major economic activity in the arid and semi-arid regions of the globe. Sheep can make use of low-quality biomass in times of scarcity and transform it into useful products, such as milk, meat and wool. Native sheep breeds in arid and semi-arid areas demonstrate better performance under harsh environmental conditions than their non-native counterparts. Therefore, proper breed selection is a very valuable tool for sustaining animal production under an increasingly challenging environment (Silanikove 1992; Iňiguez 2005).

Water scarcity is a growing problem in arid and semi-arid regions with global warming and changing patterns of rainfall, which limit water resources and affect feed quality and quantity in addition to increasing heat stress. This challenging situation causes a wide array of physiological responses in sheep with a negative impact on production, immunity and welfare (Barbour et al. 2005; Jaber et al. 2011).

The objective of this review is to highlight the physiological and immunological changes in sheep when faced with water restriction, and in particular their

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Abbreviation: FFA, free fatty acid

responses during pregnancy and lactation. The additional burden of heat stress is also considered as well as the novel approach of vitamin C supplementation to alleviate water stress.

SHEEP BREEDS ADAPTED TO ARID AND SEMI-ARID REGIONS

Sheep breeds differ in their capacity to overcome water shortages; the desert bighorn sheep (*Ovis canadensis nelsoni*) can withstand water deprivation for up to 15 d (Farid et al. 1979; Turner 1979), while the Barki sheep in Egypt could not withstand 3 d without drinking (Farid et al. 1979). Reports on other breeds like the Awassi (Jaber et al. 2004), Yankasa (Aganga et al. 1989), Merino (MacFarlane 1964) and Barbarine sheep (Ben Salem et al. 2011) lie between these two extremes.

Dehydration corresponds to a negative water balance, which means that the water inputs (water drunk + water in the feed + metabolic water linked to the oxidation of carbohydrates, protein and fat) are lower than water outputs (urinary water + faecal water + water lost by evaporation from both the skin and respiratory tract). In order to avoid dehydration, sheep resort to various forms of adaptation. At the behavioural level, nocturnal feeding has been documented in bighorn sheep (Dwyer 2008); by foraging at night, sheep minimize their exposure to high thermal loads, reducing the need for evaporative cooling and thereby minimizing water loss. In the same way, sheep seek the protection of shelters and cool microclimates, when available, to hide from solar radiation during the day (Cain et al. 2005). Timing reproductive events may be affected by dehydration; water-stressed animals often decrease feed intake, which is reported to cause retardation of ovarian follicular growth (Blanc et al. 2004). In arid and semi-arid regions (in the northern hemisphere), where differences in daylight, as well as in food and water availability, are well defined, the breeding season usually spans from June to November (Amoah et al. 1996; Hamadeh et al. 1996). Consequently, lambing mostly occurs between February and April, when food and climate become more favourable for newborn survival and for dam milk production.

Morphological adaptations are also observed in sheep adapted to arid and semi-arid regions. Fleece type (Eyal 1963) and colour (Kay 1997) contribute to protection against heat and minimize water lost due to evaporative cooling. Indigenous breeds in arid and semi-arid areas such as the Marwari (Narula et al. 2010), Omani (Mahgoub et al. 2010), Barbarine (Ben Gara 2000) and Awassi sheep (Gootwine 2011) all have carpet-type wool. This type of wool, as compared with denser wool types, seems to confer protection from solar radiation while at the same time allowing effective cutaneous evaporative cooling (Mittal and Gosh 1979; Rai et al. 1979; Cain et al. 2006). In comparison, hair-type sheep seem to be less thermoresistant under hot conditions when compared with their wool-bearing counterparts (Symington 1960). In contrast, under tropical conditions of high temperature and high humidity, McManus et al. (2009) concluded that hair-type sheep were better adapted than wool-type breeds. Moreover, a light coloured fleece allows better reflection of solar radiation thus keeping the skin underneath relatively cooler compared with darker fleeces (Cain et al. 2005; McManus et al. 2009). Another anatomical characteristic of indigenous sheep breeds from arid and semi-arid regions is the fat-tail. This external localization of the fat allows better heat dissipation from the rest of the body (Degen and Shkolnik 1978), since the body will become less insulated by the fat tissue. In addition, the fat stored in the tail represents an energy store that can be mobilized in times of dietary shortfall (Chilliard 2000; Atti et al. 2004). The concept of the fat-tail as a store of metabolic water has been questioned (Epstein 1985), and it is now believed that its main role is to supply energy whenever dietary energy intake is insufficient, which results in some metabolic water formation that could partially help in filling the animal's water requirements. The contribution to water intake that could be derived from metabolic sources was found to be around 8.5% in Yankasa sheep (Aganga 1992), while others reported a contribution of up to 15% in sheep in general (Sileshi et al. 2003). This contribution is affected by the level of reliance on the catabolic mobilization of body fat and protein tissue (Sileshi et al. 2003).

At the physiological level, water-stress-adapted sheep show a high capacity to concentrate urine. This is accomplished by the kidney, which has a thick medulla (Schmidt-Neilson and O'dell 1961) that can produce highly concentrated urine of up to 3900 mOsm L^{-1} in the bighorn desert sheep (Horst and Langworthy 1971; Turner 1973) and 3244 mOsm kg^{-1} in the Awassi sheep (Laden et al. 1987) as compared with values around 769 mOsm kg^{-1} in urine of Awassi watered ad libitum (Degen 1977). At the same time, faecal water losses are minimized, as dehydration leads to slower feed transit in the digestive tract leading to greater water reabsorption and dryer faeces (Robertshaw and Zine-Filali 1995). The rumen plays an equally important role in water conservation in arid-adapted animals whereby it can act as a water reservoir to replenish the lost volume in the blood. Rehydration of water-deprived adapted sheep activates a coordinated chain of events from the rumen, the kidneys and the salivary glands, under hypothalamic control, to preserve the water, restore homeostasis and appetite, and prevent water toxicity. These processes are described by Silanikove (1994).

Finally, arid-adapted animals may allow small increases in body temperature during the hottest parts of the day, followed by body cooling at night through conduction and radiation. The capacity to tolerate this increase in body temperature means that less water is needed for evaporative cooling (Kay 1997).

PHYSIOLOGICAL CHANGES IN RESPONSE TO WATER STRESS

Feed Intake and Body Weight

Feed consumption is highly related to water intake (Silanikove 1992). An adequate level of water intake is necessary for proper digestive function (Hadjigeorgiou et al. 2000). In contrast, Kay (1997) states that drinking water is not needed for swallowing and moistening feed, since water can be circulated from the blood to maintain high salivation; it is, however, needed to replace the inevitable water loss by excretion and evaporation. When Awassi sheep experienced a 3- to 4-d intermittent watering regimen voluntary feed intake was reduced to approximately 60% of controls (Jaber et al. 2004; Hamadeh et al. 2006). The effect of this reduction in feed intake caused by dehydration is dependent on the type of feed that is available for the animals. Van der Walt et al. (1999) observed that sheep kept on a low protein diet and subjected to water restriction showed a smaller reduction in feed intake as opposed to those given a medium protein diet, and they had better urea recycling through the digestive tract. However, the group on low protein had a slightly lower growth rate than the medium protein group. Similarly, water-restricted desert goats fed low-quality forage lost more weight than their well-fed counterparts (Ahmed Muna and El Shafei Ammar 2001). Therefore, the negative effect of water restriction is more pronounced when sheep are kept on low- versus high-quality forage (Morand-Fehr 2005). Because of this relationship, it is often difficult to differentiate the effects of water restriction, per se, from those due to low feed intake. Pulina et al. (2007) suggested that feed restriction of 50% for a period of only 3 d is enough to cause metabolic changes in lactating dairy Sarda ewes. Prolonged reduction in feed intake may eventually affect the reproductive potential of sheep (Rhind and McNeilly 1986; Maurya et al. 2004) and, consequently, reduce production.

The direct consequence of water restriction and the associated decrease in dietary intake is a reduction in body weight (Jaber et al. 2004, 2011; Hamadeh et al. 2006). Part of the reduction in weight is due to body water loss, while the other part is caused by the consequent mobilization of fat (and possibly muscle) used for energy metabolism to compensate the decrease in dietary intake (Jaber et al. 2004) and rumen fill is also reduced due to the decrease in feed intake. Furthermore, it was observed that water restriction leads to more weight loss than feed restriction alone (Ahmed Muna and El Shafei Ammar 2001; Chedid 2009; Karnib 2009). The decrease in body weight in the Awassi sheep is aggravated at peak lactation, high ambient temperature and in young animals (Hamadeh et al. 2006; Jaber et al. 2011). Moreover, dry mature Awassi ewes can tolerate a 3-d intermittent watering regimen for a month or more, although a weight loss of up to 17% would be expected (Karnib 2009).

Blood Chemistry

Dehydration in warm weather leads to haemoconcentration as highlighted by increased haemoglobin and packed cell volume levels (Li et al. 2000; Ghanem 2008), although some authors reported no variation in these parameters in water-restricted sheep (Igbokwe 1993; Jaber et al. 2004). More consistently, serum protein and albumin are reported to increase (Jaber et al. 2004; Alamer 2005; Casamassina et al. 2008; Ghanem et al. 2008; Hamadeh et al. 2009) due to the decreased blood volume (Cork and Halliwell 2002). However, albumin and protein levels tend to decrease after prolonged water restriction (Hamadeh et al. 2006; Ghanem et al. 2008), which reflects dietary deficiency. Serum albumin serves as a labile protein reservoir providing a readily available source of amino acids until an alternative source is secured through diet or by mobilizing body sources such as skeletal muscle (Moorby et al. 2002). Albumin also plays an important role in osmoregulation and fluid movement control between different body compartments since it is a major contributor to blood colloid osmotic pressure; for this reason the rates of albumin breakdown and synthesis are regulated in response to dehydration to maintain normal colloid osmotic pressure and fluid distribution (Burton 1988).

Water stress causes a decrease in urine output and the production of dry faeces controlled, respectively, by vasopressin and increased water reabsorption from the gastro-intestinal tract (Olsson et al. 1997). Under these conditions, the transfer function of the kidney is altered (Kataria et al. 2007) with slower glomerular filtration and higher urea reabsorption (Silanikove 2000). Consequently, the levels of urea and creatinine in blood are increased (MacFarlane et al. 1964; Laden et al. 1987; Igbokwe 1993; Jaber et al. 2004). However, upon prolonged water restriction and reduced feed intake, urea levels may start to decline reflecting an increase in urea recycling into the gut (Igbokwe et al. 1993; Marini et al. 2004), so it can be used as a nitrogen source by rumen microflora.

Another consequence of decreased blood volume and increased renal retention is hyperosmolality as well as an increase in electrolyte concentrations (Qinisa et al. 2011), mainly sodium, Na^+, and chloride, Cl^- (Rawda 2003; Ghanem 2005; Hanna 2006). The chain of events activated under dehydration, in order to preserve homeostasis, is described by Silanikove (1994): renal water and Na^+ retention is increased, while saliva production is reduced; to compensate for lost water, the animals mobilize the water from the rumen and the digestive tract; water movement is achieved through active transport of Na^+ across the rumen wall; this ruminal fluid is hyperosmotic therefore the excess Na^+ is reabsorbed by the kidneys and recycled through saliva, to preserve the blood Na^+ levels. Rehydration in water-deprived sheep is equally challenging since they can drink a large volume of water in one bout, therefore risking haemolysis. However, adapted animals respond by producing large volumes of hypotonic saliva (Dahlborn and Holtenius 1990; Silanikove 1994) that channels the excess water in the blood back to the rumen. At the same time it is important that the animal minimizes the loss of this water, since the next watering may be days away; therefore kidney water retention is maintained immediately after rehydration. Finally, in order to keep body fluids at the correct tonicity, appetite is activated to ensure that Na^+ and energy requirements are met to restore normal transport of water and electrolytes across different body compartments.

Fat Mobilization

As previously mentioned, along with restricted water intake comes a reduction in feed consumption, leading to undernutrition. In order to compensate for the energy shortfall, sheep mobilize body reserves. Subcutaneous fat is mobilized first, but when energy deficiency is lengthy, native breeds turn to their specialized fat depots such as the fat-tail. The fat-tail adipocytes deposit fat when feed is available and fat mobilization was demonstrated in energy deficient Barbarine (Atti et al. 2004) as well as the Awassi sheep (Jaber et al. 2011), thus buffering fluctuations in dietary intake.

Increased cholesterol levels are another indicator of fat mobilization in water-restricted sheep such as the Awassi (Jaber et al. 2004; Hamadeh et al. 2006) and Yankasa ewes (Igbokwe 1993). This reflects a deficit in dietary energy intake leading to body fat mobilization. Similarly, free fatty acid (FFA) levels were reported to increase in Awassi (Ghanem et al. 2008; Jaber et al. 2011) and the Sudanese desert sheep (Abdelatif and Ahmed 1994) indicating that fat is being mobilized from adipocytes to be used as fuel (Varady et al. 2007). Results of different experiments describing the effect of intermittent watering supply on changes in fat mobilization parameters in Awassi ewes are summarized in Table 1. These findings show the significant increase in cholesterol and FFA, while glucose levels remained practically the same between water-restricted and control groups.

Interestingly, the variations in energy intake following water restriction do not appear to be consistently mirrored by changes in glucose levels. Most reports indicated no significant variation in glucose levels in water-restricted sheep (Igbokwe 1993; Jaber et al. 2004; Casamassima 2008; Ghanem et al. 2008). Moreover, Ahmed and Abdelatif (1994) observed a direct relationship between plasma glucose and dry matter intake in feed- and water-restricted sheep. In ruminants, diet-derived volatile fatty acids are the main source of energy; however, glucose is needed for key processes in the body, hence the importance of maintaining blood glucose at a constant level (McDowell 1983).

Additionally, insulin and leptin concentrations, key hormones in energy metabolism, tended to decrease in water-restricted Awassi ewes (Jaber et al. 2011). Low insulin levels are thought to facilitate lipolysis (Vernon 1992) needed to compensate the dietary energy shortfall. Leptin levels are usually related to animal fatness; indeed, fat-tail adipocyte diameter is strongly correlated to leptin in water-restricted Awassi sheep (Jaber et al. 2011). According to Chilliard et al. (2000, 2005), the decrease in leptin activates a mechanism that will eventually control lipolysis to prevent FFA from reaching toxic levels; at the same time, this will ensure the preservation of fat stores for longer survival under conditions of fluctuating feed availability.

Thermoregulation

Thermoregulation under water restriction is of particular importance since, in sheep, evaporation is the

Table 1. Effect of different water restriction regimens on fat mobilization in non-lactating Awassi ewes

		Fat mobilization parameters			
Water regimen	Age of animals	Free fatty acid	Cholesterol	Glucose	Reference
2-d restriction	Mature	–	No change	No change	Jaber et al. (2004)
3-d restriction	Mature	–	Increase*	No change	Hamadeh et al. (2006)
	1–2 yr	–	Increase*	Increase*	Karnib (2009)
	Mature	–	Increase*	–	Karnib (2009)[z]
	Mature	Increase*	Increase*	–	Chedid (2009)[z]
	2 yr	Increase*	No change	–	Jaber et al. (2011)
	Mature	No change	No change	–	Jaber et al. (2011)
4-d restriction	Mature	–	Increase*	No change	Jaber et al. (2004)
1L on day 4 and 3L on day 8 of 12-d water restriction	Mature	Increase*	Increase*	No change	Ghanem et al. (2008)

[z] Comparisons were made between the initial values of day 0 before the initiation of the experiment (Control) and the means of values obtained under water restriction (water restricted). For all other experiments, the comparison was between separate water restricted and control groups that were included in the experiment.

*Indicates significant differences at $P < 0.05$.

major route of heat dissipation, at a time when the animal is challenged to maximize water preservation. It is estimated that 60% of heat is lost by respiratory evaporation and 40% through cutaneous evaporation (Brockway et al. 1965; Jenkinson 1972). The thermoregulatory aptitude of sheep to react to different environmental conditions varies according to the breed and its capacity to tolerate heat or cold (Degen and Shkolnik 1978; Srikandakumar et al. 2003). Thermoregulation traits include respiration rate, rectal (core) temperature, thyroid activity and water and feed consumption (Bhattacharya and Hussain 1974), which will be discussed in the following sections.

Evaporative Cooling

Sheep in semi-arid regions need to adopt special physiological functions to sustain thermal equilibrium (Maurya et al. 2004). Under neutral environmental temperature (12°C), sheep lose about 20% of their total body heat through respiratory moisture; this rate increases to about 60% at an ambient temperature of 35°C (Thompson 1985), which sometimes leads to respiratory alkalosis due to increased respiratory rate (Cain et al. 2006). Hales (1973) observed that sheep could maintain normal respiratory and cardiovascular functions when subjected to mild heat stress, while severe hyperthermia greatly affected the respiratory function, although cardiovascular activity remained mildly altered.

When dehydrated, arid-adapted sheep (and goats) tend to reduce their thermoregulatory evaporative cooling mechanisms (panting and sweating) in order to maintain their body water and prevent further dehydration (Baker 1989; McKinley et al. 2009). McKinley et al. (2009) reported that water-deprived sheep have a slow panting rate that increases twofold after rehydration. Different breeds demonstrate different panting and sweating rates reflecting different adaptive potential to tolerate heat stress. Alamer and Al-hozab (2004) observed that the Awassi and Najdi sheep could tolerate water deprivation, with the Awassi demonstrating a better capacity at water conservation under heat stress, through a lower sweating rate, than Najdi sheep. In a comparative study, Rai et al. (1979) found that breeds with denser fleece, such as the Rambouillet, were less effective in heat dissipation through cutaneous evaporative cooling and had to rely more on respiratory cooling; furthermore, in this breed, sweating started at lower environmental temperatures than in adapted breeds such as the Chokla, leading to higher water losses. Unlike the camel (Schmidt-Neilsen et al. 1956), dehydrated sheep and goats shift to preferential heat dissipation through the respiratory path rather than by sweating (Hales and Brown 1974; Baker 1989; Robertshaw 2006). It was suggested that this may be a way of obtaining evaporative cooling of the brain area while minimizing total water losses in dehydrated animals (Robertshaw and Dmi'el 1983). In fact, Fuller et al. (2007) concluded that dehydration leads to selective brain cooling, which is usually followed by inhibition of evaporative heat loss thus preserving body water. Selective brain cooling is probably achieved by transferring heat from arterial blood in the carotid to the venous blood cooled by respiratory evaporation in the nasal passages (Taylor and Lyman 1972; Cain et al. 2006; Fuller et al. 2007). Brain cooling maybe also responsible for the observed temporary hyperthermia that is often reported in dehydrated sheep, activated by the hyperosmolality observed in dehydrated animals (Fuller et al. 2007). This could allow for temporary heat storage at peak day temperatures, followed by passive body cooling at night when ambient temperatures drop (Alamer and Al-hozab 2004). This adaptive feature, allows the maintenance of homeothermy while minimizing water loss (Silanikove 1992) by increasing the core temperature threshold and delaying the time at which evaporative cooling mechanisms are activated (Cain et al. 2006).

As observed in desert-adapted goats (Ahmed and El-Kheir 2004), water lost through panting for evaporative cooling is compensated for by an increased capacity to conserve water through the production of small volumes of highly concentrated urine. To achieve this, sheep resort to high Na^+ and water retention in the kidneys. More and Sahni (1978) reported that dehydrated sheep maintained positive balances for cations, particularly K^+, based on the comparison of electrolytes input through feed and water and their output through faeces and urine. The highly positive K^+ balance led them to conclude that it is being lost through sweating, since it cannot be stored in the body, in order to maintain osmotic pressure and acid-base balance within different body fluid compartments. Therefore, cutaneous evaporative cooling also plays a role in maintaining electrolyte and acid-base balance under arid conditions.

Rectal Temperature

Sheep are homeotherms (MacFarlane 1964; Degen 1977); they try to maintain their body temperature within a fixed range even under harsh climatic conditions. Normal rectal temperatures range between 38.3 and 39.9°C under thermo-neutral conditions, but when exposed to heat stress (33–38.5°C), the rectal temperature increases significantly and when surrounding temperatures exceed 42°C, it becomes life threatening to the sheep (Marai et al. 2007). A high variation (increase) in rectal temperature indicates lack of thermal equilibrium and increased water ingestion in order to replace evaporative losses (Mohamed and Johnson 1985); it also involves a marked reduction in feed intake and will negatively influence reproductive function of the sheep (Eltawill and Narendran 1990).

Reports on the effect of water restriction on rectal temperature in sheep are not consistent. While some

(Ghanem et al. 2005, 2008; Sevi et al. 2009) reported that dehydration was found to cause an increase in rectal temperature in sheep, others (MacFarlane 1964; Degen 1977; Jaber et al. 2004; Hamadeh et al. 2006; Chedid 2009) found that sheep, such as the Awassi, retain thermostability even under water suppression. On the other hand, Ahmed and Abdelatif (1994) pointed out that dehydration causes a slight decrease in rectal temperature, while reduced feed intake considerably reduces it, especially when combined with a reduction in water intake. When studying the effect of water deprivation on unshorn sheep, McKinley et al. (2009) found that the core temperature was maintained during the first day (24 h) of dehydration, but a significant increase was noted on the second day without water.

Table 2 shows that Awassi sheep can maintain their core temperature under different water restriction regimens. However, when subjected to water limitation combined with high ambient temperatures, this breed displayed a significant increase in its rectal temperature supporting the hyperthermia hypothesis mentioned above.

Thyroid Activity

Thyroid hormones, T3 and T4, play a major role in thermoregulation and metabolic homeostasis of energy and proteins, as well as in the metabolic response of animals to different nutritional and environmental conditions (Huszenicza et al. 2002; Latimer et al. 2003; Thrall 2004). Levels of T3 and T4 were found to decrease in water-limited healthy Marwari, non-lactating Awassi ewes and Butana desert rams (Abdelatif and Ahmed 1994; Kataria and Kataria 2006; Jaber et al. 2011); this effect was reversed upon rehydration in Marwari sheep (Kataria and Kataria 2006). The reduction in thyroid hormone activity under dehydration is associated with the animal's attempt to minimize water losses by reducing general metabolism (Nazifi et al. 2003; Kataria and Kataria 2007). It also reflects the reduction in feed intake since T3 and T4 were reported to decrease in feed-restricted pregnant Whiteface Western ewes (Ward et al. 2008), while T4 increased following the afternoon meal in water-restricted Butana rams (Abdelatif and Ahmed 1994). The decrease in thyroid activity is further reinforced under heat stress (Hamadeh et al. 1994; Khalifa et al. 2002). In arid adapted animals, changes in thyroid activity may be affected more by the physiological activity (pregnancy or lactation) of the animals than by seasonal changes in temperature as has been noted in Awassi and Finn × Texel × Awassi sheep (Hamadeh et al. 1994). Furthermore, the authors noted the importance of the production system under which the animals are raised, whereby extensively raised animals of both breeds were shown to be less sensitive to ambient heat than their intensively raised counterparts due to better adaptation to the environmental conditions. Bernabucci et al. (2010) further described the importance of metabolic and hormonal acclimation to heat stress in order to limit its negative consequences.

Many aspects of thermoregulation in situations of dehydration remain to be studied. In a recent review, Alamer (2011) noted that prolactin is a hormone that is found to be increased in blood in response to heat stress. In this review, the author summarizes the role of prolactin in thermoregulation including its possible effects on fluid balance and distribution in hydrated and dehydrated animals, modulation of sweat gland activity, regulation of seasonal pelage growth, etc. Research on this topic will be valuable in understanding how different sheep cope with the combined effects of heat and dehydration.

Immunosuppression

In general, immune response and stress are negatively correlated. Exposure to stressful environmental conditions can modify a host's resistance by affecting its immune system, mainly through the mediation of immunosuppressant hormones such as glucocorticoids (Ewing et al. 1999). Although it is obvious that water stress, as any other form of stress, would cause perturbations in the

Table 2. Effect of water restriction on rectal temperature of Awassi sheep

	Average rectal temp. (°C)				
Water restriction regime	Water restricted	Control	Age	Ambient temp. (°C)	Reference
2-d-restriction	39.4 ± 0.06	39.4 ± 0.06	Mature	15–32	Jaber et al. (2004)
3-d-restriction	39.4 ± 0.14	39.2 ± 0.14	Mature	27–30	Chedid (2009)[z]
	38.6 ± 0.15	38.6 ± 0.15	Mature	23–28	Karnib (2009)[z]
	39.5* ± 0.05	39.4 ± 0.05	Mature	27–31	Hamadeh et al. (2006)
4-d-restriction	39.5 ± 0.06	39.4 ± 0.06	Mature	15–32	Jaber et al. (2004)
1L on day 4 and 3L on day 8 of 12-d water restriction	40.0* ± 0.25	39.4 ± 0.10	Mature	25–35	Ghanem (2005)
1L on day 4 of 7-day water restriction	39.8* ± 0.10	39.5 ± 0.10	Mature	23–33	Chedid et al. (unpublished)

*Means within a same experiment with (z) are significantly different $P < 0.05$.

[z] Comparisons were made between the initial values of day 0 before the initiation of the experiment (Control) and the means of values obtained under water restriction (water restricted). For all other experiments, the comparison was between separate water restricted and control groups that were included in the experiment.

general health status and welfare of the animal, research dealing with the effect of dehydration and immunity is very limited. This might be due to the fact that sheep native to arid regions, where occasional water shortages are most common, are known to be well-adapted to dehydration, thus directing scientists' attention to other research topics.

The effect of heat stress on sheep immunity, milk production as well as udder health was reviewed by Sevi and Caroprese (2012): heat stress reduced cellular immunity by decreasing cellular proliferation. The mechanism of action is unclear and may involve heat shock proteins, altered cytokines profiles as wells as changing cortisol levels. Sevi et al. (2009) reported a severe drop in immunity in ewes exposed to high ambient temperatures; this immuno-reduction was accompanied by a significant mineral imbalance and an increase in milk neutrophil levels, and higher counts of *Staphylococci*, coliforms and *Pseudomonas*, thus showing how heat stress can negatively influence both an animal's health and milk quality.

In 2004, Barbour et al. studied the effect of water restriction on the humoral antibody response of Awassi ewes to *Salmonella* Enteritidis; they found that immunity in the dehydrated animals was significantly lower than in Awassi receiving water 24 h a day. Moreover, the study showed that the humoral antibody response to *Salmonella* Enteritidis fimbriae and other polypeptides decreased by 38.5% in the water-restricted sheep as compared with their daily watered counterparts. Marked immunosuppression was also observed in water-deprived lactating Awassi ewes, which showed a significant drop in their immunity to polypeptides >21 kDa as compared with non-lactating ewes (Barbour et al. 2005).

Differential leukocyte counts are sometimes used as a combined indicator of the immune status and stress level of animals. Kannan et al. (2007) reported that a leukogram is a good indicator of prolonged stress in transported goats. Glucocorticoid levels have been linked to leukocyte profiles of the immune system where high ratios of heterophils or neutrophils to lymphocytes in blood samples indicate high concentrations of glucocorticoids and therefore high levels of stress (Dhabhar et al. 1995; Kannan et al. 2007; Davis et al. 2008). However, it was also observed that glucocorticoids may not always suppress leukocytes but rather induce a redistribution of the immune cells to certain organs such as the skin, thought to be the first line of defence against pathogen entry (Dhabhar 2006; Martin, 2009).

In a review about the mechanisms of stress-induced immunity modulation, Moynihan (2003) summarized the possible routes for immune suppression and even stimulation following stress. The author describes four main compounds that can modulate stress: corticotropin-releasing hormone, endogenous opioids, catecholamines and glucocorticoids, with glucocorticoids being the most widely studied. He further notes the complex relationship between stress and immunity, highlighting differences in the response based on the nature, duration and severity of the stressor on one hand and on the immune function or organ that is being assessed on the other. To these factors, Salak-Johnson and McGlone (2006) add the effects of social status and genetics, which also play an important role in determining how an animal's immune system responds to a certain stressor.

The specific effects of water stress, particularly in sheep, are poorly understood. This line of research would be of great interest to determine the consequences of short-term and long-term water shortages on sheep defence systems during different critical production and reproductive periods.

CHANGES IN RELATION TO PHYSIOLOGICAL STATUS

Pregnant and lactating animals have 40–50% higher water turnover rates than non-lactating animals (Cain et al. 2005) with a greater need for feed, water and electrolytes in order to meet the requirements of the foetus and the mammary gland (Olsson 2005).

Pregnancy

The reported changes in pregnant water-restricted sheep are usually similar to those observed in non-pregnant animals, including haemoconcentration (More and Sahni 1980), which denotes a reduction in the extracellular fluid space. However, in contrast to non-pregnant sheep, pregnancy seems to reduce the urine concentrating capacity of animals in response to dehydration, probably due to the high concentrations of circulating prostaglandins, which cause a reduction in sensitivity to arginine-vasopressin (Benlamlih et al. 1985; Rodriguez et al. 1996).

The effect of water restriction during pregnancy on lamb weight and survival is an important aspect to consider, since it affects productivity and sustainability of the farm operation. The desert-adapted Magra and Marwari sheep could sustain a twice weekly watering regimen imposed for an extended period with no effects on lamb birth weight (Mittal and Gosh 1986). Furthermore, pregnant Chokla ewes watered once every 4 d gave birth to lambs of lower weight compared with ewes that were watered daily or once every 3 d; however, after birth at 12 wk of age, lamb weights were similar between the different groups (More and Sahni 1980). Further studies to assess the long-term consequences of water restriction during gestation on the growth and later performance of offspring are necessary.

Lactation

Water restriction in lactating Awassi (Hamadeh et al. 2006) and Comisana ewes (Casamassima et al. 2008) led to a greater weight loss than in non-lactating animals since they have higher metabolic requirements necessitating greater mobilization of fat deposits (Sevi et al. 2002). Lactating sheep have a relatively higher blood volume due to the high water demand by the mammary gland (El-Nouty et al. 1991). Consequently, water restriction led to lower haemoglobin levels in lactating Awassi sheep when compared with their non-lactating counterparts (Hamadeh et al. 2006). Reports indicate that blood chemistry indicators such as glucose, cholesterol, protein, albumin and globulin, show little variation between lactating and non-lactating sheep beyond the first month of lactation (Hamadeh et al. 2006). When subjected to water restriction, the changes in blood indicators of lactating sheep were similar to those of non-lactating animals including significant increases in serum concentrations of triglycerides, albumin, total proteins and cholesterol, urea and creatinine (Rodriguez et al. 1996; Hamadeh et al. 2006; Casamassima et al. 2008). Lactation did not seem to modify the response to water restriction. Moreover, differences in pH and electrolyte levels were observed between water-restricted lactating and non-lactating Awassi ewes. An increase in pH was noted in water-restricted lactating Awassi sheep; it was related to a drop in Ca^{++} and K^{+} needed for milk production and a corresponding increase in Na^{+} and Cl^{-} needed for nutrient transport (Fig. 1) (Hamadeh et al. 2006). Dehydration usually causes a decrease in milk production due to reduced blood flow to the mammary gland (Hossaini-Hilali et al. 1994; Dahlborn et al. 1997; Mengistu et al. 2007). In contrast, milk osmolality, density and lactose content appear to increase under water restriction (Dahlborn 1987; Hossaini-Hilali et al. 1994). Lactose is the major osmotic component of milk, and its concentration is strictly controlled to keep milk isotonic with the blood (Dahlborn 1987).

ECONOMIC IMPACT OF HEAT STRESS ON SHEEP PRODUCTION

Loss in production due to water stress is similar to that observed under heat stress, especially since the two occur together under arid and semi-arid environments; heat stress leads to decreases in milk production, reproduction and feed intake, causes infertility and increases the risks of lameness and culling (Alhidary et al. 2012; De Vries 2012; Lucy 2012). Heat stress in cattle causes loss of appetite and weight gain (Sackett et al. 2006), it negatively affects the oestrus cycle and hence reduces reproduction (Monty and Wolf 1974; Hansen et al. 2001) leading ultimately to economic losses.

Most of the literature investigates the economic impact of heat stress on dairy and beef cattle production. According to Sackett et al. (2006) economic losses in feedlot beef cattle in Australia is estimated around 16.5 million AUD when 30% of the cattle is subjected to heat stress during summer, whereas losses in dairy and beef cattle in the United states is estimated to be $897–1500 million and $370 million, respectively (St-Pierre et al. 2003). While St-Pierre et al. (2003) attribute these losses to welfare expenses, such as infrastructure and shading, others (Sackett et al. 2006; Lucy 2012) suggest that heat stress problems can be solved by investing in heat reduction systems, modifying animals' genetics and intensifying the reproductive management in heat stress periods.

A decade ago, although heat was acknowledged as a source of stress in sheep, the economic impact of this stress was not well studied, perhaps because sheep are mainly raised in extensive systems rather than in feedlots (that exhibit high rates of respiratory diseases under hot

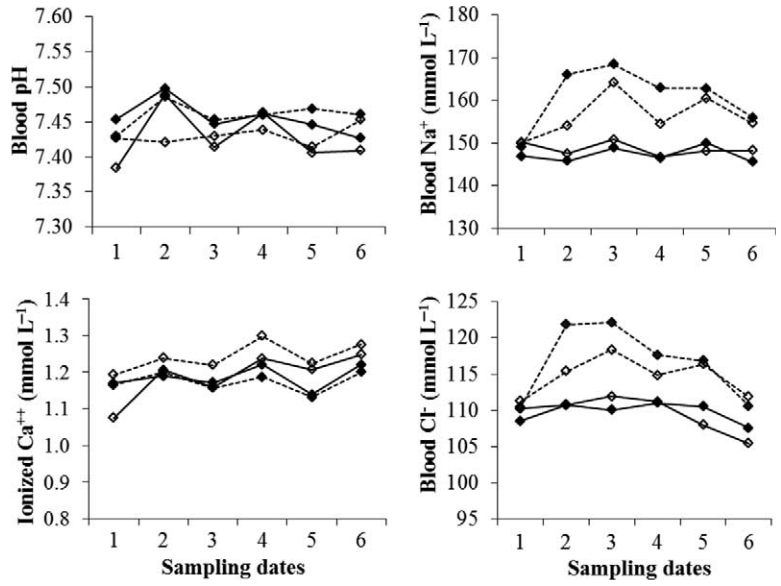

Fig. 1. Changes in electrolytes of non-lactating (◇) and lactating (◆) Awassi ewes watered daily (–) or subjected to a 3-d-restriction regimen (---) (Hamadeh et al. 2006).

and humid climatic conditions) or because sheep are bred in a variety of environmental conditions and are considered to be rustic animals that can withstand high ambient temperatures (Silanikove 2000). Literature on the economic impact of heat stress on sheep production is still scarce; nonetheless, recent works reported that thermal stress can lead to severe economic losses in sheep husbandry (Pluske et al. 2010; Wojtas et al. 2013). Kandemir et al. (2012) reported that lamb production is seriously affected when pregnant ewes are exposed to heat stress during mid and late gestation: the total of embryo cell number and the placentome size are significantly decreased; lamb birth weight, growth rate and the total body solids and daily solids gain are also reduced.

Economic losses caused by high temperatures could be reduced by protecting ewes from heat waves during the breeding season (Kandemir et al. 2012), and by the addition of shelters and the implementation of fleece length strategies in commercial feeding lots (Pluske et al. 2010). Moreover, the integration of a preventive health program, feed optimization and basic selection of the animals has proven efficacy in improving the economic sustainability of sheep production in semi-arid regions (Tami et al. 2005). The economic impact of water and/or heat stress on sheep production in arid and semi-arid regions warrants further research, especially since it reflects on the livelihoods of the majority of the rural population in these areas.

VITAMIN C: STRESS ALLEVIATOR

Vitamin C administration is not a common practice in adult livestock nutrition (McDowell 2000) since it is normally biosynthesized in ruminants (National Research Council 2007). It is an important antioxidant that helps in the scavenging of free radicals (Jariwalla and Harakech 1996). It also plays a role in modulating the immune response by enhancing neutrophil function and in minimizing free radical damage (Politis et al. 1995) and by improving antibody response to antigens (Cummins and Brunner 1990).

Administration of vitamin C to stressed animals such as weaned pigs (de Rodas et al. 1998), heat stressed Japanese quails (Avci et al. 2005), aluminum intoxicated rabbits (Yousef 2004) and heat stressed broilers subjected to feed restriction (McKee et al. 1997) yielded positive results such as improving performance under stressful conditions, enhancing feed intake, protecting from toxicity and improving body energy storage. Similarly, stress alleviation was reported in vitamin C supplemented goats in hot and dry conditions (Minka and Ayo 2007).

Several studies were performed to assess the effect of vitamin C supplementation on water-stressed Awassi sheep: supplementation tended to decrease weight loss (Ghanem et al. 2008; Karnib 2009) and was linked to improved feed intake (Hamadeh et al. 2009). Similar results were obtained in goats during stressful transportation conditions accompanied by dehydration (Kannan et al. 2000; Minka and Ayo 2007). The effect of vitamin C on weight reduction after water restriction is shown in Table 3. It is clearly seen that vitamin C administration reduces weight loss regardless of the dose given and the water limitation regimen. The reduction in weight loss could have economic significance in large farming operations, warranting further studies.

When assessing haematological effects, packed cell volume levels were reported to decrease in vitamin C supplemented dehydrated Awassi sheep (Ghanem et al. 2008) and transported Red Sokoto goats (Minka and Ayo 2007). In contrast, conflicting observations were reported regarding the haemoglobin concentrations: in transport-stressed goats vitamin C administration decreased haemoglobin (Minka and Ayo 2007), while in water-stressed Awassi sheep there was no effect (Ghanem et al. 2008).

The effects of vitamin C administration on serum protein, globulin and albumin in water-stressed Awassi sheep are not consistent (Hamadeh et al. 2006, 2009; Ghanem et al. 2008). It is worth noting that the water restriction regimen and the amount of vitamin C used in these experiments were not identical. This may explain the variable results. Additionally, it was observed that daily supplementation of water-restricted Awassi sheep with 5 g of vitamin C led to an increase in serum creatinine and urea, while lower levels had no effect (Hamadeh et al. 2009; Karnib 2009).

Vitamin C has an indirect impact on fat mobilization through its role in norepinephrine and carnitine formation, which helps fat mobilization and fatty acid transport, respectively (Ghanem et al. 2005). However, vitamin C administration to water-restricted Awassi sheep did not lead to significant changes in adipocyte diameter and other fat mobilization indicators (Jaber et al. 2011), while cholesterol levels tended to be higher in other experiments (Ghanem et al. 2005; 2008; Karnib 2009).

Blood osmolality and electrolytes are greatly affected by water restriction. However, their response to vitamin C supplementation in water-stressed Awassi ewes is not consistent (Hanna 2006; Ghanem et al. 2008; Hamadeh et al. 2009; Karnib 2009). Cortisol levels, used as indicators of water stress, did not show any differences between vitamin C supplemented and non-supplemented animals (Parrot et al. 1996; Parker et al. 2003; Ghanem et al. 2008), although others demonstrated that vitamin C played a role in decreasing cortisol secretion (Civen et al. 1980; Sivakumar et al. 2010).

In conclusion, more research is needed to fully explore the role of vitamin C in stress alleviation and determine the correct level to be supplied to sheep in various stress situations, particularly since supplemented animals lost less weight.

CONCLUSION

This review highlights the adaptive mechanisms observed during dehydration of sheep reared mainly in arid and semi-arid regions. Regardless of their physio-

Table 3. Effect of different regimes of water restriction (WR) and vitamin C (Vit C) administration on percent weight change in dry Awassi ewes[z]

Water regimen	Average ambient temperature (°C)	Age of animals	Vit C administration	Control[y]	WR	WR + Vit C	Reference
3-d restriction	28.5	2 yr	3 g Vit C ewe^{-1} d^{-1}	+3.1*a*±9.85	−26.2*b*±3.77	−22.5*b*±1.85	Jaber et al. (2011)
3-d restriction	28.5	2 yr	5 g Vit C ewe^{-1} d^{-1}	+3.1*a*±9.85	−26.2*b*±3.77	−23.0*b*±1.00	Jaber et al. (2011)
3-d restriction	17.5	3 yr	3 g Vit C ewe^{-1} d^{-1}	+6.2*a*±3.16	−10.4*b*±1.6	−7.7*b*±0.74	Jaber et al. (2011)
3-d restriction	17.5	3 yr	10 g Vit C ewe^{-1} at the beginning and in the middle of the experiment	+6.2*a*±3.16	−10.4*b*±1.6	−7.8*b*±3.15	Jaber et al. (2011)
3-d restriction	25	2–3 yr	3 g Vit C ewe^{-1} d^{-1}	–	−16.8*a*±1.14	−12.7*b*±1.27	Karnib (2009)
1 L on day 4 and 3 L on day 8 of 12-d water restriction	30	2–3 yr	2.5 g Vit C ewe^{-1} d^{-1}	+0.7*a*±2.00	−13.7*b*±2.00	−6.0*b*±2.00	Ghanem et al. (2005)
1 L on day 4 and 3 L on day 8 of 12-d water restriction	30	2–3 yr	2.5 g Vit C ewe^{-1} d^{-1}	+1.2*a*	−22.1*c*	−6.9*b*	Ghanem et al. (2008)

[z] All animals were weighed at day zero before the initiation of the experiment and at the end of the experiment.

[y] Control animals were watered daily.

a–c Different letters in the same row indicate significant differences ($P < 0.05$).

logical statuses, sheep subjected to water stress decreased their feed intake, which consequently resulted in a reduction in weight caused by water and body mass loss. Changes are also observed in blood parameters, thermoregulatory mechanisms and immunity.

Adapted breeds under water restriction during hot and dry seasons mobilize their fat stores in order to overcome dietary deficiency. This is clearly seen in the high levels of FFA and cholesterol in blood. Moreover, water conservation is mirrored by water retention by the kidneys as reflected by small volumes of urine and high blood Na^+, urea and osmolality. Non-lactating ewes of highly adapted breeds are able to survive severe water shortages on short intermittent watering regimens without displaying serious physiological damage, thus enabling pastoralists to roam during the hot summer months with their flock when water resources are scarce. However, young, lactating and gestating animals are affected by dehydration, which may reduce milk production (during peak production), reproduction, lamb weight and resistance to disease. The Awassi sheep is presented as an example of adapted indigenous breeds.

This review also highlights the promising use of vitamin C, an antioxidant nutrient supplement, in attenuating the negative effect of water stress.

Determining the adaptability of sheep to water restriction is crucial in order to take the proper measures to sustain the extensive production systems in arid regions where water scarcity is becoming more common. Future research is needed to study the overlapping effects of water stress, feed limitation and high ambient temperatures. Testing new management approaches and drugs for stress alleviation is also important, while giving special attention to animal welfare and the practical use of these procedures in the field.

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