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Water Stress in Small Ruminants

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1. Introduction

Small ruminants are an integral part of farming systems in the marginal arid regions of the world. These areas are characterized by water scarcity and fluctuating precipitation; under the effect of global warming and unpredictable weather, rainfall is becoming even more irregular and water availability more limited. Along with water accessibility, feed and other resources will be markedly affected by climate change. Livestock that are able, in open range, to select high quality forage to maintain a relatively similar basal diet quality from season to season, will have their intake significantly reduced in extremely dry seasons when forage biomass and its quality are low [1]. Hence, selection of adapted animal breeds is very valuable for sustaining animal production under an increasingly challenging environment [2].

Breeds of ruminants which are well adapted to arid environments demonstrate a greater capability than non-desert breeds to endure the stressful environmental effects [3]. Although small ruminants in hot arid and semi-arid regions may survive up to one week with little or even no water, water deficiency is proved to affect animals' physiological homeostasis leading to loss of body weight, low reproductive rates and a decreased resistance to diseases [4]. In addition, under natural conditions, water scarcity often occurs at times of high environmental temperature and low feed quality and availability. Therefore, the effects of these three constraints are often confounded.

In this review, the effects of various degrees and forms of dehydration on small ruminants are presented. The findings are based on previous literature on the subject as well as the results of original research by the authors on water restriction in Awassi sheep. The major changes in physiological indicators and blood parameters are presented, in addition to the interaction of dehydration with physiological status. Finally, a brief overview of new approaches for water stress alleviation, through drugs, is exposed.

2. General characteristics of small ruminants in arid and semi-arid regions

Small ruminants in the Middle East and North Africa region are mostly reared under extensive and traditional pastoral farming systems, centuries-old, relying on natural pastures and mobility to secure water and feed year round. Giger-Reverdin and Gihad (1991) [5] reported that the water requirement for maintenance of goats in temperate climates is 107ml/kg BW^{0.75}; they also indicated that the water requirements under different ambient temperatures, based on previous work, range between 3.15 kg/kg DM (at 23°C) to 4.71 kg/kg DM (at 35°C). However, the effect of ambient temperature should be viewed in combination with the particular breed origin and adaptability, since wide differences in response to heat have been reported in different breeds [6].

Sheep breeds differ in their capacity to overcome water limitation; experiments show a variety of results: Yankasa sheep survived 5 days of water restriction but with several physiological changes [7, 8]. Jaber et al. (2004) [9] concluded that Awassi females can withstand more than one month of watering every 2 days without significant changes, while a regime of watering once every five days causes important physiological perturbations. The Australian Merino sheep survived 10 days without water [10], and the desert bighorn sheep withstood water deprivation up to 15 days [11; 12], while the Barki sheep in Egypt did not endure 3 days without drinking [11].

Similarly, variations in water deprivation tolerance are observed in goat breeds. Ahmed and El Kheir (2001) [13] report that desert goats raised under traditional systems may be watered only once every 3-6 days, when water is scarce. The Black Bedouin and the Barmer goats are another example of adapted breeds that can live on a once every four days watering regime [14; 15].

Review papers are numerous on this subject, indicating differences between adapted and non-adapted sheep and goat breeds in tolerating water deprivation and the general arid conditions [6, 16].

Indigenous small ruminants are able to thrive despite extreme temperatures and limited water through their behavioral adaptations in combination with both morphological and physiological adaptations [17].

2.1. Behavioral adaptations

Feeding behavior is affected by environmental constraints. Nocturnal feeding has been documented in bighorn sheep [18] in order to avoid high temperatures during the day. Similar behavior is also reported in goats [16]. The author also indicated that feeding frequency is modified in some adapted goats which resort to more frequent and shorter meals in order to reduce heat production associated with rumen fermentation. Langhans et al. (1991) [19] further observed that feed intake is less affected by water deprivation in adapted breeds such as pygmy goats as compared to non-adapted breeds. Furthermore, Lechner-doll et al. (1995) [20] observed that adapted goats can select high quality feed

during the dry season while sheep showed less selectivity to high quality feed. Drinking behavior is also affected by water restriction whereby water deprived sheep and goats tend to drink large volumes of water in one bout upon watering. This capacity is more pronounced in goats than in sheep [5].

Timing of reproduction is another adaptive feature of sheep living in semi-arid areas: parturition is timed to a favorable period of the year to ensure offspring survival [21]. Seasonality in small ruminants is commonly observed. Reproductive cycles are thought to be regulated by environmental cues, most importantly photoperiod. Research has demonstrated that nutrition and the general body score are also important factors for normal cyclicity. Under-nutrition (below 40-60% of maintenance requirement) is reported to cause an immediate retardation in follicular growth [22]. In addition, prolonged under-nutrition induces a delay in estrous behavior that lasts for a shorter period, as compared to normally fed animals. Similarly, fasting was reported to cause major changes in the concentrations of reproductive hormones and ovulation rate [23, 24]. Since water deprivation is often accompanied by feed intake reduction, the same effects on ruminant reproductive cycles can be expected. Indigenous sheep living in the tropical and sub-tropical regions tend to breed throughout the year; however, their sexual activity may be limited, to a degree, during the summer season when the environmental temperature is elevated and feed is lacking [25]. In arid and semi-arid regions, where differences in daylight, as well as in food and water availability are well marked, the breeding season usually spans from June to November [26, 27]. Consequently, kidding and lambing mostly occur between February and April, when food and climate become more hospitable for the newborns.

2.2. Morphological adaptations

Ruminants are usually classified as grazers, browsers or intermediate feeders. Sheep are usually classified as grazers feeding mainly on grasses while goats are intermediate feeders which can use grasses as well as shrubs [28]. These observed preferences in feed selection have been linked to underlying morphological and physiological digestive differences. These include larger rumen and long feed passage time for grazers to allow them to digest their high fiber diet, while browsers have simple and smaller digestive system with profuse saliva production to effectively process their feed high in cell solubles [28]. However, other scientists have argued that the observed differences in feed selection are related more to body size than to actual differences in the digestive anatomy and physiology [29]. Other morphological differences are also noted in relation to the mouth anatomy with goats having a mobile upper lip, while sheep are characterized by a cleft upper lip, features that allow them to best use the available vegetation. In addition, goats have the capacity to assume a bipedal position thus they are capable of browsing higher vegetation that is beyond the reach of sheep [30]. This area of research relating morphology, diet selection and utilization and response to changes in the available vegetation is still in need of further exploration [29, 31] as it is affected by the climatic changes and drought spells that put pressure on the vegetation cover and the animals that feed on it.

Morphological characteristics such as body shape and size help reducing heat loads and minimizing water losses; it is noted that goat breeds of arid and semi-arid regions are relatively smaller than their European counterparts [6]. Smaller animals benefit from a relatively larger surface area which allows them to better dissipate heat to the environment. Fleece is another feature that plays a major role in controlling body temperature, serving as a thermal barrier that reduces the effects of the ambient temperatures through the formation of a milder microclimate within the fleece [32]. In addition, fleece and hair color of small ruminants play a role in reflecting solar radiation with light colors absorbing less heat than the darker ones thus leaving the underneath skin relatively cooler [33]. Therefore, thermostability could be maintained without directly resorting to evaporative cooling (panting) which leads to high water loss [34]. Location of body fat also affects heat dissipation rates: arid-adapted sheep exhibit highly localized fat storage [35], such as in the fat-tail, as opposed to high subcutaneous fat in non-adapted breeds; this again facilitates heat conductance to the periphery for dissipation [34]. Moreover, fat-tails are important energy reserves that help in buffering long-term dietary shortfalls to maintain survival and productivity [36, 37]. The Awassi sheep, as a representative breed adapted to arid regions, presents a medium body size, with a large fat-tail and carpet type fleece. The carpet-type wool of the Awassi allows convective heat loss from the skin to the environment [34]. Their large ears are another anatomical adaptation that is thought to help in convective heat loss [34]. Finally, as mentioned above, the localization of the fat stores in the fat-tail facilitates body heat dissipation and serves as energy reservoir for times of scarcity.

2.3. Physiological adaptations

Physiologically, ruminant breeds of arid regions show many adapted mechanisms to conserve water in times of heat and drought. Adapted breeds resort to reduction of urine volume and fecal moisture. The production of more concentrated urine is related to the length of Henlé loops located in the medulla of the kidney [38]. The thickness of the medulla is relative to kidney size, and is frequently used as an index of kidney concentrating ability [38, 39]. For instance, the desert bighorn sheep exhibits a medulla nearly twice thicker than that of other domestic sheep and thus produces highly concentrated urine of 3900 mOsm/liter H₂O [40, 41]. The Awassi sheep demonstrated a similar ability to highly concentrate urine (up to 3244 mOsm/Kg H₂O) under dehydration, and to drink large volumes upon rehydration without disrupting their homeostasis [42].

Urea renal retention is similarly increased under dehydration leading to increased urea concentration in the blood, on the other hand, urea recycling from the blood in to the gut is often observed under these conditions and is thought to contribute as a nitrogen source in times when the quality of the offered feed is low in protein [33]. The rumen is another organ that plays an important role in maintaining homeostasis under dehydration in adapted ruminants, particularly goats. Due to its relatively large volume, it acts as an important water reservoir providing most of the water lost during prolonged dehydration to maintain blood volume. It also allows the intake of large volumes of water upon rehydration which is temporarily sequestered in the rumen. Through efficient and

well-coordinated mechanisms of saliva recycling and high water and Na⁺ retention in the kidneys, slow rehydration is achieved without causing water toxicity and with minimal water losses. These processes are detailed in [15]. Small increases in body temperature are also observed during the hottest parts of the day, followed by body cooling at night through conduction and radiation. The capacity to tolerate this increase in temperature means that less water is needed for evaporative cooling [33].

3. Physiological changes in response to water stress

3.1. Effect on feed intake and body weight

Studies show a close relation between water intake and feed consumption [3, 43, 44]. Ruminant feeding behavior can be affected by the changes in osmolality of body fluids [45]. Feed intake causes hypovolemia and hyperosmolality due to the secretion of saliva and gastric juices. These mechanisms can urge ruminants, as well as other animals, to drink while eating, or alternatively not to eat when severely dehydrated [45]. Moreover, an adequate level of water intake is necessary for proper digestive functions [46]. On the other hand, Kay (1997) [33] states that drinking water is not needed for swallowing and moistening feed, since water can be circulated from the blood to maintain high salivation. However, water is needed to replace the inevitable water loss by excretion and evaporation. A possible explanation for the physiological mechanism behind the reduction in feed intake under water restriction, mainly through the reduction in meal size, may be attributed to the postprandial hyperosmolality of the ruminal fluid [19].

The co-occurrence of decrease in feed intake along with water restriction renders the differentiation between water versus feed shortage related effects difficult. Previous work has shown that Awassi sheep under 3-4 days intermittent watering regime reduced their voluntary feed intake to approximately 60% of the control [9, 47]. Similar rates are reported in [48] in different domestic ruminants subjected to dehydration, especially when combined with heat stress. The drop in feed intake under dehydration is also dependent on the type of feed that is available to the animals. Water restricted goats reduced their feed intake by 18.8% when offered legume hay compared to 21.21% when offered grass hay with lower crude protein content [49]. Therefore the negative effect of water restriction is more pronounced on low versus high quality forage [16]. This reduction in feed intake is partially compensated for by a slower feed movement and longer retention time in the digestive tract [46, 50, 51]. This is thought to lead to an increase in digestibility and nutrient utilization, as longer time is available for the microflora in the digestive tract to act on the feed [49, 52]. However, this hypothesis needs further research as reports seem inconclusive. Further drop in feed intake was recorded with increasing the degree of water restriction in South African indigenous goats [52]; but an improved nutrient utilization was also reported by the same author. Concomitantly, Ahmed Muna and El Shafei Ammar (2001) [49] reported an improvement in digestibility of Lucerne hay under water restriction in desert goats, and similarly, higher organic matter digesti-

bility was observed in water-restricted dairy cows [53]. These adaptations allow the exploitation of grazing areas which are distant from water sources, and prevent erosion especially in regions where water is scarce and grazing pressure is high. In contrast, others [46, 48, 54] found no changes in feed digestibility in water-restricted sheep and goats. It was suggested that the elevated digestibilities usually observed are rather the result of dry matter accumulation rather than “a real increase in fermentation or digestion” [50].

The drop in feed intake puts an additional burden on the water stressed animal. In fact, in order to survive such regimes, adapted ruminants are thought to resort to lowering their metabolic rate in order to reach a new body condition with lower maintenance requirements [55]. Consequently, the effects of this decrease in dietary intake should be considered along with the effects of dehydration. Feed restriction of 50% for only a 3-day period is enough to cause metabolic changes in lactating dairy Sarda ewes [56]. It has also been reported that the depleted body condition during periods of energy deficiency reduces heat tolerance [57], which in turn affects the reproductive potential of sheep [58, 59].

As reported in [9, 47, 60-64] the most obvious physiological consequence of water restriction with the concomitant reduction in feed intake is weight loss. Many trials on dry and lactating Awassi ewes recorded a drop in weight ranging between 0.84% and 26% (Table 1). Besides the effect of the water regimen, other factors contribute to body weight variation such as the physiological status of the animal (lactating or dry), its age, and the prevailing climatic conditions during the experiment (ambient temperature). It is clear in Table 1 that watering every two days did not cause a mentionable weight loss in Awassi ewes even if the temperature reached up to 32°C. The highest weight loss (26.2%) was recorded in young sheep (2-year-old ewes) and in lactating animals. Reported results lead to one conclusion that dry Awassi have a high adaptation to dehydration, and can tolerate 3-day water restriction regime, up to one month with losing only 16.8% of their body weight (Chedid et al., unpublished).

Significant weight loss is documented in other breeds of sheep and goats subjected to feed and water stress [6, 65]. Part of this weight reduction is due to body water losses [9] 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 [9, 66]. Furthermore it was observed that water restriction leads to more weight loss as compared to feed restriction alone [49, 62-63] although the difference was not always statistically significant.

The following table (Table 2) presents the effect of water and feed restriction on body weight of adult dry Awassi ewes [62, 63].

Results in both studies are in compliance: water restricted animals lost more weight (approximately two fold) than those drinking every day but receiving less feed; however, large individual variations were recorded within each of the experimental groups (N=8). Therefore, further research is needed for conclusive results on the difference between water and feed restriction impact on weight loss.

Physiological status	Water restriction regime	Drop in weight (%)	Age	Ambient temp. (°C)	Reference
Non-lactating	2-day-restriction	0.84	mature	15-32	[9]
	3-day-restriction	9.98	mature	27-30	[62]
		16.8	mature	23-28	[63]
		16.7	mature	27-31	[47]
		26.2	2 years	30-31	[64]
		10.4	mature	18-21	
	4-day-restriction	3.32	mature	15-32	[9]
	1L on day 4 and 3L on day 8 of 12-day water restriction	22.13	mature	25-35	[61]
1L on day 4 of 7-day water restriction	16.8	mature	23-33	Chedid et al. (unpublished)	
Lactating	3-day-restriction	26.2	mature	27-31	[47]

Table 1. Effect of water restriction on body weight of Awassi sheep.

	Treatment*		Reference
	Water restriction	Feed restriction	
Weight loss (%)	9.98	5.7	[62]
	17.9	8.2	[63]

*Water restricted animals received water every 3 days;

Feed restricted animals had free access to water but received 60% feed of the ad libitum intake.

Table 2. Effect of water restriction versus feed restriction on body weight in Awassi ewes.

3.2. Fat metabolism: Fat cell diameter, cholesterol, glucose, fatty acids, leptin and insulin

The fat deposited during the periods of pasture abundance is mobilized and utilized for maintaining the body and sustaining production during periods of scarcity [67, 68]. The specialized fat depot represented in the fat-tail of many indigenous sheep, serves as a readily available source of energy to circumvent variation in dietary energy intake. This was well described in the Barbarine sheep subjected to long periods of undernutrition [37] as well as in the Awassi which showed a reduction in the fat-tail adipocyte diameter following an intermittent watering regime [64]. Ermias et al. (2002) [68] highlighted the importance of the location of fat depots as adaptive features to periodic fluctuations in nutrition. They noted that the rump and fat-tail depots are the most responsive under such conditions. On the other hand, Atti et al. (2004) [37] noted that subcutaneous fat is the first energy depot to be mo-

bilized when energy intake is deficient. This is true for the fat-tailed sheep such as the Barbarine on which they conducted their study, as well as other ruminants. However, the fat-tail provided an adaptive advantage by being slowly mobilized when undernutrition is extended over a long period thus allowing long-term survival by using up this important energy store.

Fat mobilization under water restriction is further denoted by high levels of cholesterol [69] and Free Fatty Acids (FFA) in the blood [61, 64]. The increase in plasma cholesterol following water scarcity is attributed to the decrease in energy intake, along with fat metabolism [70]. These results were recorded in different ruminant species submitted to water deprivation such as Awassi [9, 47] and Yankasa ewes [8]. Furthermore, the high level of FFA outlined in water restricted Awassi [61, 64] and the Sudanese desert sheep [71] reflects lipid mobilization within the adipocyte, thus permitting lipid stores to be used as fuel when feed intake is limited [72]. Similarly, FFA levels in the blood of lactating goats correlated positively with fat mobilization in times of under nutrition [73].

Reports about the changes in glucose levels in water restricted sheep are contradicting: while no significant change was recorded by some authors [8, 9, 61, 74], a decrease in plasma glucose level was observed in Merino sheep after 24 and 48 hours of fasting [75], and in intermittently watered Awassi, although the change was not significant [47]. Glucose metabolism decreases due to the decline of propionate (the major precursor for gluconeogenesis) production in the rumen caused by low feed intake [76]. Although ruminants derive most of their energy requirements from volatile fatty acids resulting from rumen fermentation of carbohydrates, they still have an absolute need for glucose, necessitating a good homeostatic control of this compound [77].

Fat mobilization seems to be coordinated by underlying changes in the levels of key hormones. In dry Awassi ewes, subjected to an intermittent watering once every four days, FFA were negatively correlated with insulin and leptin as highlighted in [64]. The decrease in plasma insulin is probably caused by the decline in feed intake, insulin secretion being accelerated by feeding [78]. Insulin levels are thought to remain low during fasting periods in order to facilitate lipolysis [79]. Similarly, the decrease in leptin levels in dehydrated and undernourished ruminants is well documented and explained by the decrease of the metabolic status which inhibits the adipose tissue from secreting leptin [80]. Moreover, a strong correlation between leptin concentration and fat-tail adipocyte diameter was noted in [64] highlighting the relation between the secretion of leptin by the adipose tissue and body fatness [81]. Chilliard et al. (2000) [36] proposed a model whereby insulin, cortisol and leptin interact in the process of adaptation to underfeeding and re-feeding in ruminants such as experienced also under intermittent watering. The drop in leptin following undernutrition leads to a chain of events that includes stimulation of re-feeding and decrease of energy expenditure and insulin-sensitivity, that serves to re-establish homeostasis by preventing excessive lipolysis that would yield toxic levels of fatty acids, and preserve body stores to prolong survival [36, 81].

3.3. Hematology: PCV and hemoglobin

Dehydration in warm weather conditions reduces plasma volume as water is taken up by the tissue [82]. Although some authors reported and agreed that increased PCV and Hb concentration are good indicators of dehydration [42, 61, 71, 83, 84] results on these two parameters have been inconclusive. Even though levels of hematocrit were found to increase in Awassi [42, 60] and Merinos [61] subjected to water stress in some experiments, no variation was remarked in Yankasa [7, 8], Awassi [9] and Australian whether sheep [85] under similar watering conditions. Similar contradictory results were reported regarding hemoglobin: whilst an elevation of hemoglobin level was attributed to a decrease in plasma volume due to water loss [47, 61, 85] others did not report any variation [7-9]. These undetermined results may be an indication that adapted sheep can maintain plasma volume [86] and redistribute body water after a long water deprivation period [87].

3.4. Blood chemistry

3.4.1. Total protein, globulin and albumin

According to Caldeira et al. (2007a, b) [88, 89], serum total protein, globulin and particularly albumin are good indicators for predicting the animal's protein status. A drop in serum albumin concentration is observed in ruminants with low dietary protein intake [88, 90], followed by a decrease in globulin concentration when this dietary insufficiency is prolonged [88]. Many authors reported an increase in blood albumin and globulin in sheep under water restriction [9, 61, 74, 91, 92]. The high protein concentration is explained by the reduced plasma volume due to dehydration [93]. However, reduction in total protein and albumin was noticed after 3 days of water deprivation in Awassi [47] and in Barki sheep under water stress [94] suggesting that low feed intake is behind this reduction and that circulating proteins are being used in order to compensate for the dietary shortfall. Accordingly, maximum values of total serum protein were recorded on the 8th day of water restriction in Awassi followed by a decline at the end of the experiment (12 days) [61]. Serum albumin is a major labile protein reservoir, but it is also very important in the maintenance of body osmoregulation. Consequently, some variations in serum albumin levels can occur, but the maintenance of normal levels has to be re-established as soon as amino acids from other sources like the skeletal muscle are available [95].

3.4.2. Creatinine and urea

Urea is mainly synthesized in the liver using NH_4^+ , the end product of protein catabolism, and is released to the blood [96]. Urea is excreted by the kidneys to rid the body of the excess N intake that was not used for maintenance or production [90], or it is recycled through saliva or by reabsorption into the rumen to be utilized by rumen microflora [96, 97]. Creatinine is produced in the muscles and excreted by the kidneys in proportion to the muscle mass and the rate of proteolysis [88, 97]. The transfer function of the kidney is altered under water stress [98] with slower glomerular filtration and higher urea re-absorption [6, 8, 99]. Water stress induces a decrease in urine output and the production of dry faeces under the

action of vasopressin, and increased water reabsorption from the gastro-intestinal tract [100]. Urine volume dropped by 75% and fecal water output was 37% lower in desert sheep subjected to 5 days of water restriction [101]. Consequently, urea reabsorption by the kidney is also expected to increase as reflected by increased concentration in the blood [102], which was confirmed by several trials on Merinos [65], Yankasa [7, 8] and Awassi sheep [9, 42]. When Yankasa sheep were submitted to two consecutive periods of five-day water stress, an increase in urea and creatinine concentration was observed after the first period but only creatinine levels remained high after the second [8]. Thus the author suggested that urea is being re-circulated from the blood system into the digestive tract. This is consistent with the observations that urea conservation at the level of the kidneys and recycling into the gut is increased when dietary nitrogen intake is low [102].

On the other hand, creatinine levels in lambs were not affected by 48-hour water restriction [103], while others observed an increase of this parameter in water restricted animals [47, 91]. The creatinine concentration is influenced by the level of reliance on proteolysis and endogenous N sources [88, 98] as well as by higher kidney retention due to decreased glomerular filtration rate. In turn, these factors are related to the degree of protein/N intake deficiency that the animal is experiencing as well as the level of dehydration.

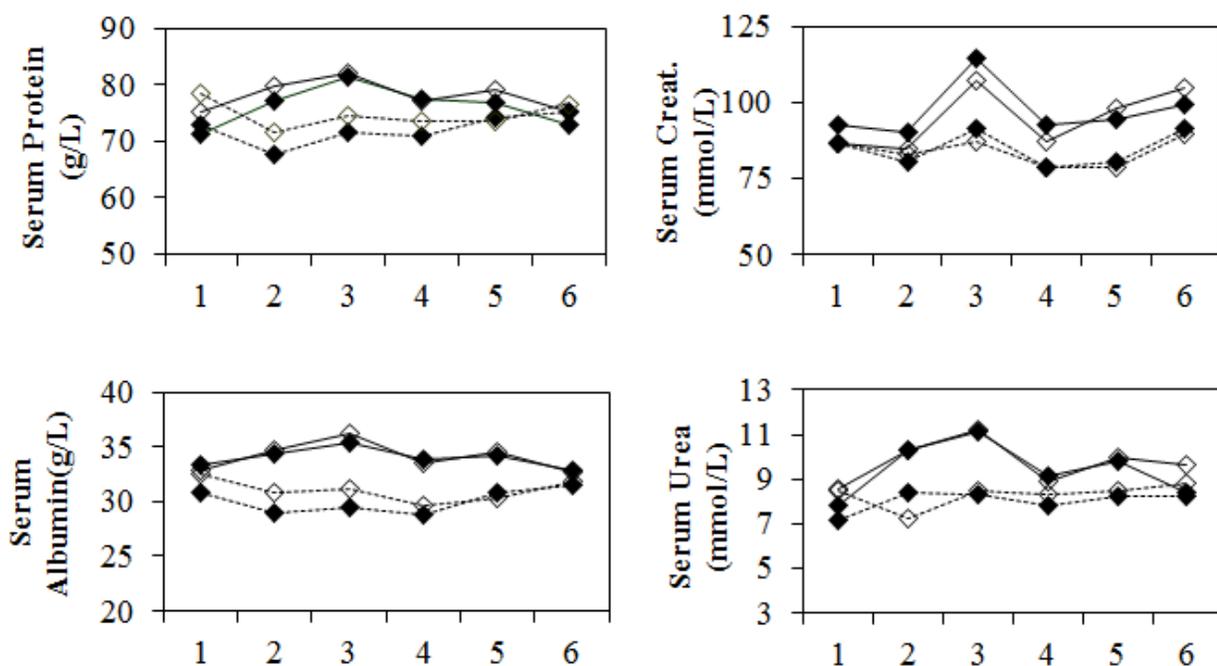


Figure 1. Changes in some serum chemistry indicators of dry (◊) and lactating (◆) Awassi ewes subjected to daily watering (—) or to water restriction (- - -). (Adapted from [47])

Figure 1, adapted from [47], illustrates the changes over repeated cycles of three days water restriction on major blood chemistry parameters of dry Awassi ewes. This figure shows that the response to the watering regime tends to decrease over time after it reaches a certain peak. This underlines the adaptation mechanisms that the animals activate in order to ach-

ieve homeostasis under the imposed treatment. The observed return to normal values in protein and albumin concentrations could indicate that these compounds are being used up from the blood in replacement of the deficient dietary intake, or this could also denote the mobilization of water from the extracellular fluid and the rumen into the blood stream [47]. Similarly, the decline in urea at the end of the treatment could be related to the above mentioned urea recycling mechanism, while creatinine concentrations remained relatively high as previously observed in [8]. The figure also illustrates that lactating and dry animals had similar responses to water restriction with no effect of lactation (2-3 months in lactation) on these blood parameters.

3.4.3. *Electrolytes and osmolality*

Analyzing osmolality is a good approach for monitoring the hydration status. It has been proved that osmolality and electrolytes levels are largely affected by water deprivation: the reduced plasma volume causes hyperosmolality inducing consequently an increase in electrolytes concentration [104] mainly sodium Na^+ and chloride Cl^- [60, 105, 106]. These results were reported in different breeds of sheep and goats [10, 63, 71, 91, 103, 107].

Increased renal retention of Na^+ is a physiological response to water restriction in different small ruminant breeds, which allows the maintenance of sodium balance in the body. Ashour and Benlemlih (2001) [87] attributed the increased renal retention to the influence of aldosterone, whereas McKinley et al. (2000) [107] added the effect of vasopressin secretion. Dehydration causes an increase in plasma vasopressin levels in both lactating goats [108-110] and non-lactating ones [108, 111]. According to Yesberg et al. (1970) [112] urinary vasopressin excretion rate is directly related to urinary osmolality and inversely related to urine flow rate. This explains why dehydrated goats and sheep decrease their urine volume while the osmolality and vasopressin levels augment. Olsson (2005) [113] noted that thermoregulation and fluid balance, as regulated by thirst control, vasopressin secretion, sodium balance and other osmotic and cardiovascular signals, seem to be centrally regulated at the hypothalamic level, particularly the preoptic and anterior hypothalamic neurons. Silanikove (1994) [15] presents a detailed account of the dynamics of major electrolytes under dehydration in connection with water conservation and homeostatic mechanisms in ruminants. In addition to the increased renal retention of water and Na^+ , saliva secretion is decreased in dehydrated animals but its osmolality is increased. In parallel, the ruminants resort to utilize the large volume of water present in the gut through active transport of Na^+ across the rumen wall. This transport necessitates the presence of a minimal amount of volatile fatty acids in the rumen, hence the importance of sustaining some feed intake during dehydration. The hyperosmotic fluid absorbed from the rumen needs to be desalted the salivary flow to the rumen has to be maintained in order to preserve homeostasis.

Rehydration is an equally challenging situation for ruminants that can lead to hemolysis in non-adapted or severely dehydrated animals. Many studies reported the slow return to normal levels of blood volume, osmolality and other blood components after the rehydration of ruminants, although the animals drank large amounts of water at once [42, 92, 114]. The mechanisms allowing the slow release of the ingested water from the rumen into the blood

stream are not fully understood. The production of hypotonic saliva is dramatically increased following rehydration [15] thus allowing the recycling of absorbed water and Na^+ from the blood back into the rumen to prevent a sudden drop in blood osmolality. In parallel, the kidney sustains its water/ Na^+ conservation activity to prevent the loss of the ingested water which is vitally needed in anticipation of a future dehydration cycle. Rehydration also activates appetite and thermoregulatory mechanisms that allow the final restoration of homeostasis and normal functioning in up to 24 hours after rehydration or more.

Studies on different sheep breeds [115, 116] showed a negative correlation between Na^+ and K^+ in plasma. Concurrently, blood K^+ was reported to decrease in water-deprived sheep [9, 65] probably due to the intra-erythrocytic diffusion of K^+ or loss of these ions in urine in exchange of Na^+ re-absorption [8]. However, others observed an elevation in plasma K^+ under water restriction [7, 117], while [8, 47, 61] did not report a variation in K^+ levels in Yankasa and Awassi sheep, respectively. These inconclusive results about K^+ alteration under water restriction do not make of potassium a reliable indicator of the hydration status; on the contrary they warrant further studies about the role played by this blood parameter during dehydration.

Chloride Cl^- is the major anion in extra cellular fluids (ECF). It functions primarily in transport processes integral to cation and water balance and as a conjugate anion in acid-base metabolism. Several findings reported that dehydration leads to an increase in plasma chloride levels in parallel to sodium levels [8, 9, 47, 74] as Cl^- is passively distributed in relation to the electrical gradients established by active Na^+ transport [118]. This increase may be attributed to many phenomena such as the hemoconcentration resulting from a lower blood water level [74], and the increase in aldosterone and vasopressin concentrations [87] leading to increased renal retention.

Calcium plays an important role in regulating ion gating and as a co-factor for intermediary metabolism reactions. However, studies did not report variation in Ca^{++} under water deprivation in the Awassi [9, 47] nor in Comisana sheep [74].

Finally, blood pH, a critical parameter for normal enzymatic and metabolic functions, seems to be well maintained in intermittently watered Awassi [9, 47, 61]. Increase in pH was only recorded in highly restricted Awassi following a once in a five days intermittent watering regime [9], this could be related to a combination of the high dehydration state and environmental heat which leads to hyperventilation and consequently to respiratory alkalosis as observed in other heat stressed animals due to the increased elimination of CO_2 [119].

Figure 2 is an illustration of the effect of a 12 days water restriction episode on Awassi dry ewes. The animals were offered 1 liter of water on day 4 and 3 liters on day 8 only. In this trial, the treatment had no significant effect on blood pH and K^+ concentration, while Na^+ and Cl^- were significantly increased under the restriction regime. The trial also included a group of water restricted animals that received 2.5g/d of vitamin C, the effect of which is discussed below (vitamin C section). It is worth noting here that the levels of Na^+ and Cl^- seem to have reached a peak after which they started to show a slight decline. This observation reinforces the previously proposed idea of adaptation to the restriction regime to reach

a new homeostasis by activating water mobilization and conservation mechanisms to restore the blood volume and composition.

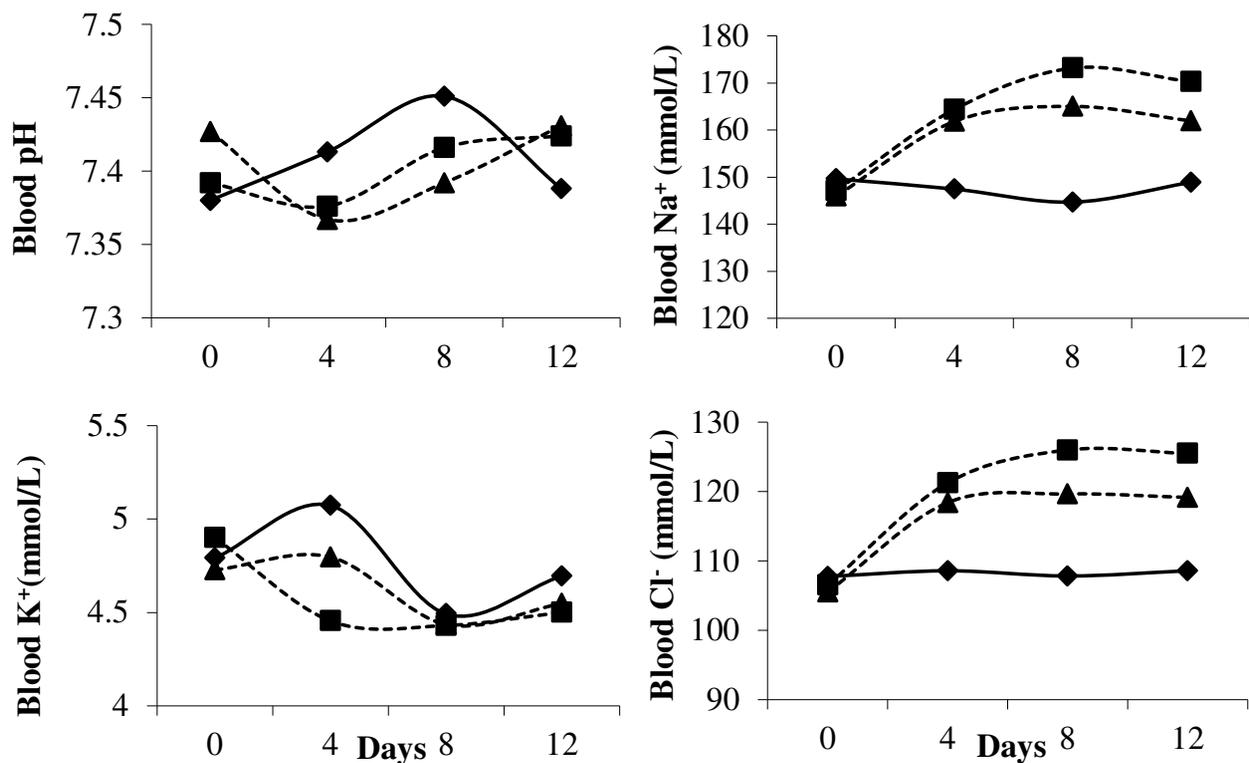


Figure 2. Effect of water restriction (---) on dry Awassi ewes with (▲) and without (■) vitamin C supplementation (Ghanem et al., 2008, unpublished data)

3.5. Cortisol and other hormones

Cortisol is a hormone secreted in order to deal with stress. It is released due to the activation of the hypothalamo-pituitary-adrenal axis by stress. Although it plays a major role in maintaining the balance of water and electrolytes [120, 121], its mechanism is not very clear yet [122]. Dehydration had no effect on serum cortisol levels of Awassi [9, 61] and Clun forest sheep [123] which is consistent with the results obtained under laboratory conditions in sheep deprived of feed and water for 48h [124]. On the other hand, Kataria and Kataria (2004) [98] suggested that the increase in cortisol levels in dehydrated Marwari sheep (for 6 days) is a sign that the animals are under stress; they also reported that cortisol levels did not return to normal even after 72 hours of rehydration. Working on the same subject, Li et al. (2000) [85] reported plasma cortisol variation with fasting while water restriction had no additional effect on this parameter. A decline in serum cortisol was recorded in intermittently watered Awassi along the experimental period [47]. Concurring with [125], it is suggested that cortisol could be a good parameter in assessing acute stress response in small ruminants but not chronic stress such as dehydration.

Thyroid hormones (Triiodothyronine T3 and Thyroxine T4) play a major role in many physiological events such as thermoregulation and metabolic homeostasis of energy and proteins [126-128]. T3 and T4 concentration is affected by many factors like reproductive status, climatic conditions [127, 129] nutrition, age and gender [130, 131]. Water restriction [64] and nutrient limitation [132] were found to lower the levels of T3 and T4 in dry Awassi ewes and pregnant Whiteface Western ewes, respectively. Similarly, Caldeira et al. (2007a) [88] noticed a decrease in these hormones with decreasing body score of ewes. They concluded that T3 is a good indicator of the metabolic state of the animal. On the other hand, variable T3 and T4 responses to seasonal variations and/or dehydration were reported in literature from various ruminants [133]. The concentrations of these two hormones were found to be strongly correlated ($R^2=0.568$; $P=0.000$) [64]. The authors suggested that this decline in T3 under water restriction reflected the declining metabolic state due to dehydration and decreased feed intake while the declining T4 concentration was probably a response to the thermal stress experienced by the animals in that experiment. Similarly, T4 concentrations were reported to vary with the season while T3 is affected by both the season and the physiological status of the sheep [134]. The reduction of thyroid hormone activity under dehydration is associated with the animal's attempt to minimize water losses by reducing general metabolism [135].

4. Changes in relation with physiological status

As seen above, small ruminants in arid and semi-arid regions face many constraints related to fluctuating temperatures as well as shortages in feed and water sources. Pregnancy and lactation increase the needs for adaptive mechanisms due to the greater need for food, water and electrolytes in order to meet the requirements of the fetus and the mammary glands [113]. Water requirements could increase up to 50% by late pregnancy (around 160 ml/kg $BW^{0.75}$) while the requirement for milk production is stated as 165 ml/kg $BW^{0.75}$ for a milk production level of 148g milk/kg^{0.75} [5]. Pregnant and lactating animals have 40-50% higher water turnover rates than dry animals [17]. However, Degen (1977) [35] recorded a small difference in water turnover between control and pregnant Awassi and Merinos sheep.

4.1. Pregnancy

The reported physiological changes vary according to the degree of water restriction and stage of pregnancy. Chokla pregnant ewes submitted to intermittent watering (every 72 and 96 hours) under semi-arid conditions showed significant hemoconcentration and reduction in extracellular fluid space as compared to pregnant Chokla receiving water daily [136]. Similarly, Olsson et al. (1982) [137] reported increases in plasma osmolality and Na^+ concentration in pregnant goats dehydrated for 30h accompanied by a decrease in glomerular filtration rate, while plasma protein and hematocrit did not change with dehydration. Interestingly, it was observed that pregnant goats [137] and sheep [138] have a lower capacity to concentrate urine in response to dehydration. Authors in both studies suggested that the apparent reason for this observation is a decreased sensitivity to Arginin-Vasopressin (AVP) which in turn, could be partially due to the effects of high prostaglandin concentrations

which increase during late gestation. Research on the Matebele goat showed that a low nutrition level during late pregnancy had little effect on kid birth weight [139]. Similarly, a twice weekly watering regime imposed for a prolonged period had no effect on birth weight of desert adapted Magra and Marwari sheep [140]. On the other hand, pregnant Chokla ewes watered every 4 days gave birth to lambs of lower weight compared to ewes that were watered daily or every three day; however, at 12 weeks of age, lambs' weight were similar between the differently watered groups [136]. Working on goats, Mellado et al. (2006) [141] highlighted the importance of goat birth weight and weight gain at 25 days of age on their future reproductive performance under intensive conditions in hot arid environments. On the other hand, in a recent study prenatal feed restriction in the last trimester resulted in lower male offspring weight in goats, but had no effects on later behavior and growth [142]. Further studies are needed to assess the long term consequences of dehydration and/or intermittent watering during gestation on the growth and later performance of the offspring.

4.2. Lactation

Significant weight loss was recorded in lactating water-stressed Awassi [47] and Comisana ewes [74] as compared to control animals. Weight loss during lactation is due to body water loss caused by less water and feed intake combined with energy deficit that drives lactating animals to strongly depend on their body reserves [143].

Physiologically, lactating animals show lower hemoglobin concentration than dry ones [47]. According to [120], the decrease in hemoglobin concentration in lactating ewes is explained by the high water content and plasma volumes due to increased water mobilization to the mammary glands. It was found in [47] that lactation did not affect levels of serum glucose or those of cholesterol in Awassi ewes in their second to third month of lactation. Concurrently, no significant changes were recorded in glucose level caused by lactation beyond the first month [144]. Moreover, lactation did not affect blood total protein, albumin and globulin concentration of Awassi ewes in their mid-lactation [47]; no change in albumin was also reported in [145], however an increase in the gammaglobulin fraction was noticed. El-Sherif and Assad (2001) [94] observed a return to normal total protein levels on the fourth week of lactation most probably caused by a fall in globulin concentrations. The same authors reported that lactation significantly increased plasma albumin, albumin to globulin ratio and blood creatinine in Barki ewes under semi-arid conditions. No alteration was caused by lactation on serum urea and creatinine levels in Awassi ewes [47] and Corriedal [138]. Working with lactating Comisana subjected to 60% water deprivation, Casamassima et al. (2008) [74] reported significant elevations in serum concentration of triglycerides, albumin, total proteins and cholesterol. Intermittently watered Ethiopian Somali goats, exhibited similar physiological responses to those described in other breeds, namely increased osmolality, AVP secretion and blood protein concentration [110]. The authors also noted a significant capacity to fluctuate rectal temperature in response to heat stress reaching 5°C daily change in some animals; they also observed the activation of a water saving mechanism following the first cycle of water restriction,

resulting in lower physiological changes in subsequent cycles. A similar trend was also noted in lactating Awassi ewes subjected to intermittent watering [47].

Concerning the effect of lactation on blood pH, Hamadeh et al. (2006) [47] reported significantly higher blood pH in water restricted lactating Awassi ewes as compared to dry ones. This increase in pH is correlated to the decrease in plasma Ca^{++} and K^+ levels due to their need for milk production [47] and to the increase in plasma Na^+ and Cl^- since Na^+ is used for nutrient transport [146]. As for cortisol, lactating Awassi ewes tended to have high levels as compared to dry counterparts. However, more work is needed in order to elucidate the adaptive mechanisms of pregnant and lactating ewes to water restriction.

4.3. Milk production and composition

Water needs are reported to be the highest during lactation as compared to other physiological statuses [109]. Dehydration leads to a reduction in the blood flow to the mammary gland however, enough supply for milk production may still be achieved as supported by the sustained milk production in dehydrated goats [113] and sheep [74]. During dehydration, milk volume is generally decreased [109, 110, 147], although the Bedouin goats could maintain their milk production when watered every second day [108]. Dahlborn et al. (1997) [148] suggested that the drop in milk volume observed in some dehydrated animals was mainly the result of lack of water as such and not a reflection of the consequent decrease in feed intake; furthermore the authors suggested that this drop could be related to the alteration in casein production observed under dehydration. In fact, Silanikove (2000) [6] showed that stress leads to a chain of events including increased cortisol secretion leading the activation of the plasmin system resulting in the release of a proteose peptone with channel blocking activity (PPCB) from β -casein and interfering with lactose secretion into the lumen of the mammary gland and consequently causing a drop in production. Previous studies have indicated an increase in milk osmolality, lactose and density following water deprivation for 48 hours [109, 149, 150]. Milk osmolality is strictly controlled to keep it isotonic with plasma; the increase in lactose under water restriction, being the major osmotic component of milk, is probably a response to the increase in serum osmolality under water restriction [149]. Nonetheless, milk can be less concentrated in fat and non-fat solids and more rich in water. Alamer (2009) [150] noted a decrease in fat content of milk of 25% water restricted goats but not in those that were 50% restricted. The increase in water content [151, 152] is thought to be a form of adaptation allowing the offspring to receive the adequate quantity of water when water is not available.

5. Stress alleviation drugs

Domestic animals are routinely faced with different stressors. Most stressful conditions, including diseases [153] and farming practices such as milking [143], isolation [154], introduction to a new flock [155], road transportation [156, 157] last for only a short period ranging between hours to days. On the other hand, harsh environmental factors are probably the

stressors with the longest lasting effect since they may prevail for months. For example, heat stress and elevated ambient temperature are considered major risks affecting sheep performance [85; 158]. The negative impact of heat is translated into increased body temperature, higher respiration and heart rates followed by a drop in feed intake, redistribution in blood flow and alteration in endocrine function [158]. Low temperatures or cold leads to an equally stressful situation which affects sheep performance by increasing the metabolic rate [85,160]. Furthermore, different environmental constraints often come together such as the situation in arid and semi-arid areas during the dry season when heat stress is combined with water scarcity and low pasture quality.

Animal producers and researchers have looked for ways to alleviate the negative effects of common stressors. Stress alleviation strategies are numerous, and their availability to producers depend on the access to water and energy, the price they are able to pay and the adopted farming system [153]. These strategies vary from simple on-farm practices such as modifying the feeding pattern, feed composition [160], water management, cooling systems and environmental modifications like shading [153, 161], protection from solar radiation [153], the use of micro-sprinklers, spray jets and ventilation [162] to more scientific procedures like genetic selection [161] and others.

In this quest for stress alleviation in domestic animals, researchers have tested special drugs and/or nutritional supplements. Trials showed that a pre-transportation administration of ascorbic acid to goats facilitates the transition from depression to excitation; it exhibited potential depression amelioration after road trips [163] and significantly decreased weight loss caused by transportation under unfavorable thermal conditions [164]. Ali et al. (2005) [156] reported that a single dose of the anti-stressor xylazine administered to sheep and goats before road transportation considerably ameliorated the effects induced by the stressful stimulus; whereas a pretreatment with sodium betaine (a test compound) had no significant effects. Electrolyte therapy was also found effective in reducing stress of transportation in market cattle allowing a better meat quality and a reduction in live weight loss [157].

In this review we will focus on two compounds that appear to have a good potential for stress remediation in domestic animals: Vitamin C which is tolerated at high doses without apparent side effects [165] and aspirin which showed some potential advantages warranting further investigation [166-168].

5.1. Vitamin C

Although ruminants biosynthesize ascorbic acid under normal conditions and do not need any additional supplementation [45], and even though vitamin C administration is not a common practice in adult livestock nutrition [169] scientists however, decided to study the effect of Vitamin C administration to sheep under water-stress conditions [60, 61, 64, 92] and goats facing the stress of transportation [163, 164]. These trials were encouraged by promising results obtained on weaned pigs [170], Japanese quails [171], rabbits [172] and broilers [173] under stress.

Ascorbic acid is known for its function as an antioxidant mainly due to its redox properties; it acts as a free radical scavenger in numerous cellular oxidation processes [174] and has been demonstrated to be helpful for young ruminants in acclimatizing to cold stress [175]. Ascorbic acid plays an important role in modulating the immune response by enhancing neutrophil function and minimizing free radical damage [176] and by improving antibody response to antigen [177]. Concurrently, Minka and Ayo (2007) [164] reported that administering Vitamin C to Red Sokoto goats before transportation reduced the post-journey effect to a minimum or eliminated it completely; however the impaired animals' homeostasis was rapidly recovered after the trip.

A daily dose of Vitamin C was reported to decrease weight loss in adult female Awassi subjected to a water-restricted regime [61, 63] while this effect was not significant in other trials [63, 64, 92]. The alleviation of body weight loss can be explained by improved feed intake [92] and better feed conversion, also observed in other animals in stressful conditions and supplemented with vitamin C [164, 171, 178]. The ameliorated effect of ascorbic acid on weight loss during short-term transportation of goats in hot weather [164, 179] proves the advantage of Vitamin C supplementation in order to maintain an adequate live body weight for slaughter.

Vitamin C supplementation to sheep alleviated the effect of dehydration on PCV [61] but not on hemoglobin [61, 63]; while in goats submitted to transportation under unfavorable climate conditions, Vitamin C significantly decreased levels of both PCV and Hb [164]. It was also found that supplementing Vitamin C to deficient pigs increased hemoglobin levels probably due to increased iron absorption [180].

Lower serum protein concentrations were reported in Vitamin C administered water-restricted Awassi as compared to non-supplemented counterparts [61], while others found no significant differences in total protein and globulin levels due to Vit C [92]. The effect of vitamin C on albumin levels is inconclusive as well: although some [61] noted lower concentrations in treated ewes, others [47] reported higher values of albumin in treated animals. The daily Vitamin C dose also plays a considerable role on blood parameters: a daily dose of 5g significantly increased serum creatinine and urea concentrations as compared to 3g and to control [92]. This might be considered as an enhancement to the adaptive mechanisms of Awassi sheep to water restriction. However, in other experiments no effect of Vitamin C was observed on creatinine levels [63] warranting further investigations on the role of Vitamin C in urea and creatinine dynamics during dehydration.

In an experiment conducted in order to study the effect of Vitamin C on fat mobilization under water stress, Jaber et al. (2011) [64] reported no significant effect of this drug administration on adipocyte diameter, fat mobility and weight loss in water deprived sheep. Authors speculated that a daily dose of Vitamin C (3g or more) may be more helpful in increasing fat mobilization under water stress than single high dosages; they agreed that more work would be essential to confirm the observed trends.

A tendency for higher cholesterol levels was observed under Vitamin C administration [60, 61, 63]. Vitamin C interferes in norepinephrine formation, an important hormone that in-

creases fat mobilization [172], it is also essential in carnitine formation, which upon reacting with acetyl CoA forms acetylcarnitine that transports fatty acids into the mitochondria to be oxidized [60].

Reports on the effect of Vitamin C on osmolality are scarce. However, Karnib (2009) [63] and Hanna (2006) [106] observed increased osmolality in water-stressed vitamin C supplemented Awassi ewes, but the mechanism of such phenomenon is still not well understood. Results obtained on the effect of Vitamin C on blood electrolytes are not very clear and need more elaborated work. Ghanem et al. (2008) [60] reported that Vitamin C administration alleviated the effect of water restriction as reflected in lower Na^+ and Cl^- (Figure 2). The authors attributed this observation to the role of vitamin C in norepinephrine formation, which affects the kidney function and therefore water and electrolytes dynamics. On the other hands, [72] reported an opposite result in one experiment while in a second experiment Na^+ and Cl^- were the same between supplemented and un-supplemented water restricted ewes.

Benefits of Vitamin C in decreasing stress hormones was reported by several authors: some [181] observed that ascorbic acid intake resulted in a drop in adrenal and plasma corticosterone levels, others showed that vitamin C eliminated the secretion of cortisol in animals subjected to stress [182]. Still others did not observe any effect of Vitamin C administration on cortisol concentrations in stressed animals [61, 122, 124]. Serum cortisol is a better marker for acute stress than for chronic stress [125]. While Vitamin C and cortisol interact, the anti-cortisol role of Vitamin C is still unclear and needs more research.

Concluding with Vitamin C, it has been shown that the most important parameter in highlighting the role of Vitamin C in counteracting the effect of water deprivation on sheep is the observed decrease in weight loss. Consequently, further work is warranted in order to elucidate the mechanisms of action of Vitamin C, and to determine the best dose recommendations that would increase the adaptive capacities of shepherds and flock keepers to the changing weather and increasing global warming.

5.2. Aspirin

Acetyl-salicylic acid ASA or aspirin has been used for ages as an antipyretic and analgesic agent [183]. New studies have emphasized the role of aspirin in the treatment of some types of cancer [168] and cardio-vascular diseases [184] although data on the effect of aspirin in animal production is contradictory. On one hand, supplementation of 20ppm of ASA to layer chicken under hot climates improved the number of eggs as well as their weight; it increased feed intake, improved fertility and hatchability [185]. On the other hand, chronic feeding of ASA had detrimental results to layer breeders with concerns for early hen livability and egg quality [186]. In mammals, aspirin reduced scouring and improved growth rate when supplemented to weanling pigs at a level of 125 or 250 ppm [166]. It also reduced plasma cholesterol levels in rats [167], and protected rats from colon cancer [168]. Recently, the role of aspirin in the protection from oxidative stress has been highlighted.

The role of aspirin in alleviating stress has been investigated in adult Awassi ewes subjected to water and feed restriction has been studied [62]. Treated animals with a daily dose of

100mg of ASA lost more weight than the untreated animals. However, the difference was not statistically considerable. Similar results had been reported in broilers [187] and weanling pigs [166].

Aspirin did not have any effect on rectal temperature; perhaps these results highlight the capacity of Awassi to remain thermostable even under dehydration [10, 35]. No changes were detected in PCV and hemoglobin levels [62] confirming that salicylates do not usually alter these two parameters [188]. Moreover, results of the experiment revealed that aspirin has no effect on plasma concentrations of proteins, globulin and albumin. Similarly, no significant differences in the levels of urea, creatinine and osmolality were observed between treated and untreated animals. Furthermore, no significant effect of aspirin was observed on any fat mobilization indicator i.e. cholesterol, insulin, free fatty acids and leptin.

Other studies investigating the role of aspirin in water and feed stressed ruminants are not found. The available literature covers stress resulting from transportation and exposition to new environment [189] and physical pain caused by tail docking [190].

Further studies using different doses of aspirin could be done. Additional experiments might also help clarify the antioxidant property of aspirin and its effect on the ruminant immune system which might be compromised under stress.

6. Conclusion

This review helped in highlighting the adaptability of indigenous small ruminant breeds to water stress and the changes it induces under different physiological statuses. Most small ruminants respond to water stress by decreasing their feed intake, resulting in weight reduction due to water and body mass loss. The rumen plays an important role as water reservoir both in times of dehydration, to maintain blood volume, and upon rehydration to prevent hemolysis. Similarly, modulating saliva production and osmolality is an important mechanism for facing dehydration and rehydration cycles.

A ten-year research track on the Awassi demonstrated the key mechanisms that this breed activates in facing water stress. Strong water conservation is achieved at the level of the kidney, as reflected by a drop in urine output and increased blood Na^+ , albumin and urea along with hyperosmolality. Furthermore, the Awassi seems to adapt to an intermittent watering regime after a couple of cycles by re-adjusting its blood volume and constituents to a new status tending toward control levels. Finally, the Awassi mobilizes its fat stores, including the fat-tail, to overcome the shortfall in dietary energy intake. This breed could be maintained, during the hot months and in times of severe water shortage, on short intermittent watering regimes. However, severe dehydration will ultimately result in detrimental effects on milk production, reproductive success, lambs' weight gain and disease resistance, particularly during gestation and peak lactation.

Stress alleviating supplements such as vitamin C show some promise in decreasing the effects of dehydration. Many tracks still need to be explored in future research such as feeding

and nutritional manipulations to alleviate water stress, with special attention to the long-term effects of such approaches on overall productivity and welfare. The identification of breeds that show high adaptability to arid and semi-arid regions with an acceptable level of productivity is also important.

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