

Physiological and behavioral basis for the successful adaptation of goats to severe water restriction under hot environmental conditions

M. Kaliber¹, N. Koluman¹ and N. Silanikove^{2†}

¹Department of Animal Science, Agricultural Faculty, Cukurova University, 01330 Adana, Turkey; ²The Volcani Center, Institute of Animal Science, Agricultural Research Organization (A.R.O.), PO Box 6, Bet Dagan 50250, Israel

(Received 10 December 2014; Accepted 19 July 2015)

Among domestic ruminants, goats are renowned for their ability to tolerate water deprivation, water restriction and energy restriction. However, some basic questions regarding their ability to endure water restriction under heat stress are still open. Three levels of water restriction (56%, 73% and 87% of the ad libitum) were imposed on 20 cross-bred 3-year-old female goats (75% German Fawn and 25% Hair Goat) distributed into four groups, with five animals per treatment. The experiment was conducted from the beginning of July to the end of August in a farm located in the Eastern Mediterranean region of Turkey (40 m in altitude; 36 59' N, 35 18'E), in which subtropical weather conditions prevail. The average daily temperature during the experiment was 34.2°C, whereas the highest and lowest temperatures were 42°C and 23.1°C, respectively. The average relative humidity was 68.2% and wind speed was 1.2 km/h. Weekly average thermal heat indexes during the experiment were 78.3 (week 1), 79.1 (week 2), 80.1 (weak 3), 79.8 (weak 4), 81.3 (weak 5) and on average 79.7. Feed intake, heart rate, thermoregulatory responses (rectal temperature, respiration rate), blood plasma concentrations of ions (Na, K), antidiuretic hormone (ADH), metabolites (glucose, cholesterol, creatinine and urea) and behavioral aspects (standing, walking, lying) were studied over 30 days. The responses to water restriction were proportional to the level of restriction. The reductions in feed intake (up to 13%), BW (up to 4.6%) and the increases in rectal temperature (0.5°C) and breath rate (10 respirations/min) were moderate and also were far from responses encountered under severe heat and water stresses. The increase in plasma Na (from 119 to 140 mM) and ADH concentrations (from 12.6 to 17.4 pg/ml) indicates that the physiological response to water restriction was in response to mild dehydration, which also explains the increase in blood plasma concentrations of glucose, cholesterol, creatinine and urea. Behavioral responses (reduction in walking from 226 to 209 min/day and increase in lying from 417 to 457 min/day) were associated with conservation of energy or thermoregulation (reducing the exposure to direct radiation).

Keywords: water restriction, heat stress, physiological response, adaptation, resilience

Implications

The goats used in the present study (a mix of 75% temperate breed with 25% local adapted breed) have shown remarkable capacity to endure significant water restriction for a long time. Water restriction endurance was associated with minimal disruption of plasma electrolyte and metabolite composition, thermoregulation and general well-being. The water-saving responses were activated in response to mild loss of body fluids and increase in plasma sodium concentration and ADH concentration. The results of this study help us understand the adaptation of goats to water restrictions and might be helpful for management purposes under conditions of water limitation, or as a technique to manipulate feed intake.

Introduction

The mass of body water accounts to 60% to 70% of BW and constitutes 99% of the molecules in the mammalian body (Chew, 1965). Maintaining homeostasis of body fluids is, therefore, an essential function in terrestrial mammals. For maintaining homeostasis of the body fluids, water – which is constantly lost through evaporation, urination and fecal excretion – should be replaced. In addition, at any time point, there is a need to maintain an essential minimal mass of water pool in order to preserve essential functions such as cardiovascular flow, appropriate ion balance and

[†] E-mail: nsilanik@agri.huji.ac.il

composition, as well as thermoregulation (Schmidt-Nielsen, 1983; Silanikove, 1994). Under thermoneutral conditions, food and water intake are highly related to each other in goats and other mammals (Silanikove, 1989). Feed restriction or reduced energy intake is associated with proportional reductions in water intake without loss of body fluids and changes in blood plasma composition (Silanikove, 1989 and 1994). In contrast, water deprivation induces a decrease in body fluid content and an increase in its osmolality. Heat stress increases the loss of body fluids due to sweating and panting in order to maintain thermoregulation. In order to maintain thermoregulation during periods of heat stress, animals may sweat and pant, both of which may lead to loss of body water. The main general homeostatic responses to dehydration in mammals include reductions in fecal and renal water losses, reductions in metabolism, and thus in evaporation, and protection of plasma volume (Schmidt-Nielsen, 1983; Silanikove, 1994).

From the above discussion, it appears that there are two types of drinking and water-regulatory mechanisms: the first is the food intake-dependent drinking, in which homeostasis of body fluids is achieved without perturbation of the body fluid volume and without significant changes in the osmolality of body fluids and ion composition, and the second one is drinking in response to dehydration, which is also influenced by the physiological changes induced by water deprivation.

Water restriction has been extensively studied in ruminants over the past five decades in order to evaluate and understand the physiological basis underlying their capacity to endure water shortage, as well as the effects of water restriction on feed intake and utilization (see Ahmed and El Kheir, 2004; Abioja et al., 2010; Rahardja et al., 2011 for recent studies on goats and Silanikove, 1992 for a review of older publications on ruminants). It is possible to maintain ruminants for longer periods (e.g., for entire season) on restricted water intake (Khan et al., 1978; Silanikove, 1992). Therefore, it is obvious that ruminants in general and goats in particular have the capacity to balance their water economy at a lower level than their normal water intake. Consequently, unlike in animals experiencing dehydration, the plasma tonicity and electrolyte concentrations may be in steady state throughout the water-restriction period for a longer duration (Khan et al., 1978; Silanikove, 1992). However, despite the above-mentioned extensive research, the existing information does not allow us to tell between two options that enable goats to maintain water balance under water restriction: (i) reduced feed intake is linked to reduced energy metabolism, and hence reduced water losses (Silanikove, 1989). With this option, the goats maintain homeostasis without losing body water and without changes in plasma electrolyte composition in comparison with initial conditions, and (ii) water restriction induces losses in body water content in comparison with pre-restricted levels and activates physiological responses to preserve water losses. In this case, the achievement of homeostasis of water fluids is associated with some loss of body water and increase in

plasma electrolyte composition in comparison with prerestricted conditions.

The aim of this experiment was to examine the effect of water restriction on feed intake, body fluid homeostasis, thermoregulatory responses and feeding behavior in order to understand what type of physiological responses were evoked by water deprivation.

Material and methods

The experimental procedures were approved by the ethics committee of the Faculty of Agriculture of Cukurova University. The study was carried out on 20 cross-bred 3year-old female goats (75% German Fawn and 25% Hair Goat) in the Dairy Goat Research Farm at the Faculty of Agriculture of Cukurova University from the beginning of July to the end of August (30 days). The farm is located in the Eastern Mediterranean region of Turkey (40 m in altitude; 36 59' N, 35 18'E), in which subtropical weather conditions prevail. The annual precipitation in the area is 450 mm. The actual average temperatures and relative humidity of the pens where the goats were maintained were recorded daily with a thermometer and a barometer in a nearby climatic station that belongs to the University. The average daily temperature during the experiment was 34.2°C, whereas the highest and lowest temperatures were 42°C and 23.1°C, respectively. The average relative humidity was 68.2% and wind speed was 1.2 km/h during the entire experimental period. Weekly average thermal heat indexes (THI, see Silanikove, 1992 for definition) during the experiment were 78.3 (week 1), 79.1 (week 2), 80.1 (weak 3), 79.8 (weak 4), 81.3 (weak 5) and on average 79.7. The climatic data were recorded all day long during the experiment.

The goats were housed individually in pens, which provided a space of 1.5×15 m for each goat and were located within semi-open barns (the south side of the barn was opened). The floor surface was concrete, and due to summer season there was no bedding. The goats were fed diets containing 60% concentrate and 40% alfalfa hay *ad libitum* twice daily at 0800 to 0900 h and at 1400 to 1500 h; fresh water was available at all times.

The concentrated feed composition was as follows: dry matter (DM) (88%), CP (13%), crude cellulose (14%, maximal content), crude ash (9%, maximal content), calcium (between 0.6% and 1.2%), sodium (between 0.3% and 0.6%) and phosphorus (0.4%). The alfalfa hay composition (according to conventional feed analysis in the university nutritional laboratory) was as follows: DM (88.5%), CP (13%), crude ash (6.4%), ADF (45.4%), NDF (52.9%) and crude fat (0.91%); 10 days were given for the adaptation to diets and the experimental unit.

In early May, the animals were divided into four groups, with five goats per group. Each group of five goats was kept together. The animals were selected based on their age, lactation number, number of kids and their live weight. Treatment 1: restricting water intake to 2 l/day; treatment 2: restricting water intake to 3 l/day; treatment 3: restricting

water intake to 4 l/day; and treatment 4: water intake ad libitum. Climate data, weight changes and feed consumptions were recorded daily. Rectal temperature (RT), respiration (RR) and pulse rates (PR) and skin temperatures of the shaved head and udder surfaces were recorded in the morning (0800 to 0900 h), midday (1200 to 1300 h) and afternoon (1800 to 1900 h) twice a week during the 4 weeks of measurements. RT was measured using a digital thermometer, and RR and PR were recorded using a stethoscope during 1 min while they were stabilized inside the pen. Skin temperatures were measured via an infrared thermometer (Testo BP-960; Shenzhen Pacom Medical Instruments, Shenzhen, China) at a distance of 10 cm from the head and udder skins. Blood samples (10 ml) were collected from the jugular vein into heparinized sterile tubes once a week in the morning before feeding and drinking water, and the separated plasma samples were stored at -20°C until analysis. The blood was centrifuged for 5 min at $3000 \times q$. The behavior of the goats was recorded using a camera system, which operated 24 h. The camera system was fixed in every barn, and the camera recordings were automatically assessed using a computer all day long during the experiment. Rumination, walking, standing and lying periods were calculated following the method of Darcan et al. (2008).

The animals were weighed individually every week in the morning (0800 to 0900 h) using automatic scales.

All analytical measurements of metabolites were carried out in duplicates and those of ADH in triplicates. Plasma cholesterol concentrations were analyzed using the Enzy-ChromTM kit (ECCH-100; Bioassay Systems, Hayward, CA, USA). Colorimetric procedures were used to measure the concentrations of glucose (Schönhusen *et al.*, 2013), urea (Meza-Herrera *et al.*, 2014) and creatinine (Silanikove, 1984). Plasma Na and K concentrations were analyzed by flame photometry (Silanikove, 1984). Plasma ADH concentrations were analyzed using a commercial kit (SKU: E06A1779; Life Sciences Advance Technologies Inc., St. Petersburg, FL, USA) according to the manufacturer's instructions.

The statistical analyses were carried out on data pooled on a weekly basis (weeks 1, 2, 3 and 4). The UNIVARIATE procedure of SAS (1999) statistical package program was used to check the normality of data. The result of this analysis showed that the data for all the measured characteristics were normally distributed. Subsequently, ANOVA procedures for repeated measures SAS (1999) were used to test the effects of water restriction on feed intake, live weight, thermoregulatory responses and concentrations of blood plasma metabolites. In the case of thermoregulatory responses, the effect of time of sampling was included. The behavioral parameters (total rumination, walking, standing and lying periods pooled on a weekly basis) were evaluated by repeated measures ANOVA. In cases of an overall difference, the Bonferroni correction for multiple comparisons was used for the behavioral parameters. When a statistical significance was detected (P < 0.05) for a particular measure, paired comparisons between means were carried out using Tukey's test to rank between the treatments.

Results

Average morning, noon and evening air temperatures, relative humidity and THI in the experimental pens throughout the experimental period are described in Table 1. The average daily temperature during the experiment was 34.2°C, whereas the highest and lowest temperatures were 42°C and 23.1°C, respectively. The average relative humidity was 68.2% and wind speed was 1.2 km/h. Weekly average THIs during the experiment were 78.3 (week 1), 79.1 (week 2), 80.1 (weak 3), 79.8 (weak 4), 81.3 (weak 5) and on average 79.7. Water intake by goats in the control group was 7.40 l/day. Water intake of 4 l/day (treatment 3), 3 l/day (treatment 2) and 2 l/day (treatment 1) imposed restrictions of 56% (treatment 3), 73% (treatment 2) and 87% (treatment 1), respectively, relative to the free water intake (FWI) in the control group (Table 2). The restrictions in FWI were associated with reduction in the average free feed intake (FFI) during the 4 weeks of measurements, which were proportional to the level of FWI restriction: 5% in treatment 1, 11% in treatment 2, 13% in treatment 3 (Table 2). Feed intake for each treatment during the experiment was quite stable, although, in treatment 1, it was lower in week 4 than in week 1 (Table 2). The FFW/FFI ratio in control goats was 4.61. Water restriction induced reductions in the ratio between water intake and feed intake, which were proportional to the level of water restriction: to 2.63 in treatment 3 (a reduction of 43%), 2.10 in treatment 2

Table 1 Average morning, noon and evening air temperature, relative humidity and THI throughout the experimental period

Traits	Hours	Average values
Air temperature (°C)	0800 to 0900	32.25 ± 0.16
	1200 to 1300	36.15 ± 0.21
	1800 to 1900	34.23 ± 0.12
Relative humidity (%)	0800 to 0900	61.88 ± 0.56
• • •	1200 to 1300	67.43 ± 0.98
	1800 to 1900	64.89 ± 0.56
THI	0800 to 0900	84
	1200 to 1300	89
	1800 to 1900	86

THI = thermal heat index.

 Table 2 Effect of water restriction on free feed intake by the experimental goats (g/day)

		Sta	atistics			
Periods	1 (2 l/day)	2 (3 l/day)	3 (4 l/day)	Control	RMSE*	P-value**
Week 1 Week 2 Week 3	1414 1422 1367	1443 1426 1436	1515 1502 1569	1613 1617 1620	12 13 14	0.009 0.009 0.009
Week 3 Week 4	1373	1430	1488	1570	12	0.009

*RMSE = root mean square error, n = 5.

***P*-value refers to differences between treatments. Differences between weeks were significant (P < 0.045 and P < 0.038, respectively) only for treatment 1 for the differences between weeks 1 and 3 and between weeks 1 and 4.

(a reduction of 54%) and 1.44 in treatment 1 (a reduction of 69%) (Table 2).

Live weight of the control goats increased during the experimental period by 0.9 kg on average. On the other hand, live weights were reduced during the experimental period in the water-restriction treatments, and the reductions were proportional to the level of water restriction: -0.69 kg (treatment 3), -1.06 (treatment 2) and -1.55 (treatment 1) (Table 3). Weight loss between weeks 3 and 4 was the highest in treatments 2 and 1.

The effects of water restriction on RT were notable only in treatment 1: an increase of 0.51°C in comparison with controls (Table 4). Similarly, the effects of water restriction

 Table 3 Effect of water restriction on live weight of the experimental goats (kg)

		Sta	atistics			
Periods	1 (2 l/day)	2 (3 l/day)	3 (4 l/day)	Control	RMSE*	P-value**
Week 1 Week 2 Week 3	32.8 32.5 31.8	32.8 32.4 31.9	32.6 32.5 32.2	32.8 33.1 33.5	0.6 0.5 0.5	0.25 0.31 0.05
Week 4	31.3	31.7	31.9	33.7	0.5	0.05

*RMSE = root mean square error, n = 5.

***P*-value refers to differences between treatments. Differences between weeks were significant (P < 0.047 and P < 0.048, respectively) only for treatments 1 and 2 for the differences between weeks 1 and 4.

on udder skin temperature were notable only in treatment 1: an increase of 0.78°C in comparison with controls (Table 4). Head skin temperature was higher in the goats in the waterrestriction treatments in comparison with the controls and the response was proportional to the levels of water restriction: 0.40°C (treatment 1), 0.57°C (treatment 2) and 0.97°C (treatment 1) (Table 4). Water restrictions induced modest increases in the RR, which were proportional to the level of water restriction: 12.7% (treatment 3), 13.3% (treatment 2) and 19.7% (treatment 1). Water restrictions induced reductions in heart rate, which were proportional to the level of water restriction: 4.7% (treatment 3), 8.3% (treatment 2) and 9.3% (treatment 1). Time of measurement did not affect the rectal, udder skin and head temperatures as well as the RR and heart rate in all the treatment groups (Table 4).

Water restrictions were associated with increases in blood plasma concentrations of glucose, cholesterol, creatinine, sodium and antidiuretic hormone (ADH or vasopressin), which were related to the level of water restriction (Table 5). In the case of urea, the increase in blood plasma concentration upon water restriction was significant only in treatments 2 and 1. Water restriction was associated with a decrease in the concentrations in blood plasma of potassium, which was related to the level of water restriction (Table 5).

Water restrictions affected all the behavioral aspects described in Table 6. The behavioral changes were most notable and always significant in goats of treatment 1. In most cases, the responses were also significant in goats

Table 4 Effect of water restriction on thermoregulatory responses of the experimental goats

			Trea	Statistics			
Parameters	Time	1	2	3	Control	RMSE*	P-value**
Rectal temperature (°C)	0800	39.3	39.0	38.9	38.9	0.02	0.05
	1200	39.4	39.0	38.9	38.8	0.02	0.05
	1800	39.4	39.1	38.9	38.9	0.02	0.05
Average		39.3	39.0	38.9	38.9	0.02	0.05
Head skin temperature (°C)	0800	34.1	33.2	33.5	33.1	0.01	0.05
	1200	34.0	33.5	33.5	32.7	0.01	0.05
	1800	33.5	33.6	33.6	32.4	0.01	0.05
Average		33.9	33.5	33.5	32.9	0.01	0.05
Udder skin temperature (°C)	0800	34.3	33.2	33.3	33.3	0.01	0.05
	1200	33.4	33.6	33.4	33.1	0.01	0.15
	1800	34.3	33.7	33.5	33.3	0.01	0.05
Average		33.9	33.5	32.9	32.9	0.01	0.05
Respiration rate (respiration/min)	0800	45	47	51	55	1	0.01
	1200	43	48	47	51	1	0.01
	1800	45	49	47	55	1	0.01
Average		44	48	48	53	1	0.01
Heart rate (beat/min)	0800	56	57	61	63	1	0.01
	1200	57	58	59	62	1	0.01
	1800	57	58	59	62	1	0.01
Average		57	58	60	63	1	0.01

Week effect was not significant, and therefore the results were pooled. Time of measurement effect was not significant. For rectal, head and udder skin temperatures, the results were significant only between treatment 1 and control. For respiration rate and heart rate, the results of the three water-restricted groups were significantly different from the control.

*RMSE = root mean square error, n = 5.

** *P*-value refers to differences between treatments.

Table 5 Effect of water restriction on the concentrations of blood
 plasma metabolites of experimental goats

		Treatments			Statistics		
Parameters	1	2	3	Control	RMSE*	P-value**	
Glucose (mg/100 ml)	70	67	62	57	1	0.01	
Cholesterol (mg/100 ml)	62	54	51	47	0.5	0.05	
Urea (mg/100 ml)	55	51	50	48	0.4	0.05	
Creatinine (mg/100 ml)	0.43	0.39	0.35	0.31	0.01	0.01	
Sodium (mEq/l)	140	135	129	119	1.2	0.01	
Potassium (mEq/l)	3.61	3.75	4.02	4.54	0.03	0.01	
ADH (pg/ml)	17.4	16.1	14.6	12.9	0.1	0.01	

ADH = antidiuretic hormone.

Week effect was not significant, and therefore the results were pooled. For all the parameters, the differences between water restriction treatment and control were significant.

*RMSE = root mean square error, n = 5.

** P-value refers to differences between treatments.

Table 6 Effect of water intake restriction on the behavioral aspects of experimental goats

		Treatments			Statistics		
Parameters	1	2	3	Control	RMSE [*]	<i>P</i> -value ^{**}	
Rumination time (min/day)	429	438	462	468	2	0.05	
Duration of walking (min/day)	209	215	217	226	2	0.05	
Duration Of standing (min/day)	348	342	324	329	3	0.05	
Duration of lying (min/day)	454	445	427	417	3	0.01	

Week effect was not significant, and therefore the results were pooled. For rumination time and duration and walking, the differences were only significant between treatment 1 and control. For duration of standing and duration of lying, all the water-restriction treatments differed significantly from the controls. *RMSE = root mean square error, n = 5.

** P-value refers to differences between treatments

of treatment 2. Water restrictions affected the feeding behavior as follows: decrease in rumination time, decrease in the duration of walking, increase in the duration of standing and increase in the duration of lying.

Discussion

The experimental conditions that prevailed during the experiment indicate that the goats were subjected to moderate heat stress (Silanikove and Koluman, 2015). This study shows that cross-bred goats are able to cope with a substantial reduction in FWI (up to 90%) for a long period (>1 month) under heat stress, without significant adverse effects on energy balance and thermoregulation capacity, and it also identifies some of the mechanisms involved.

When water supply is unlimited, there is a close interrelationship between the amount of food consumed and the amount of water consumed in ruminants as well as in other mammals (Chew, 1965; Silanikove, 1989). This relationship derives from the close inter-relationship between energy and water fluxes in mammals (Silanikove, 1989). Imposing reduction of feed intake of roughage diets to about 45% of the *ad libitum* intake was reflected by a similar reduction in water intake in desert and non-desert goats (Silanikove, 1989). In contrast, in the present experiment, the reduction in FFI upon restricting FWI was proportionally much lower than the level of water restriction imposed. Similar moderate reduction in feed intake in proportion to considerable imposition of water restriction (33% and 67%) was found in breeds of tropical (Abioja et al., 2010) and desert goats (Alamer, 2009). In cows, with 50% drinking water restriction, the reduction in feed intake was 20% lower than that during when water was available ad libitum (Burgos et al., 2001). Thus, although in cows the reduction in feed intake upon water restriction was also lower than the level imposed by feed restriction, the relative reduction in feed intake was greater than that found in goats. It can be concluded that the present results are consistent with the notion that (i) goats are better adapted to desert conditions than cows by being less sensitive to water deprivation and water restriction (Silanikove, 1992, 2000a and 2000b) and that (ii) the physiological basis for the inter-relationships between food and water intake in response to food restriction are different from those controlling the response to water restriction, particularly under heat stress.

Collectively, the present results suggest that the imposed levels of water restriction induced dehydration of body fluids in comparison with control goats and that the physiological responses were targeted on conservation of body fluids. There should be no problem for goats to maintain BW and energy balance on 30% to 40% reduction in feed intake, and desert goats can maintain BW even with 50% to 60% reduction in feed intake (Silanikove, 1986 and 1987). Thus, the loss of BW found in the present experiment cannot be explained by the modest reduction in feed intake, particularly if taking into consideration that the digestibility of the diet was most likely increased under the present conditions (Silanikove, 1985 and 1992). The concentration of ADH increased under deficit in body fluids in order to preserve body water: reduction in plasma volume was associated with an increase in sodium concentrations, the major ion in extracellular fluids, and with a parallel increase in ADH concentrations (Andersson, 1977; Maltz et al., 1984). Thus, lack of evidence for appreciable energy deficit and the evidence for reduced plasma volume in proportion to the level of imposed water restriction are the most probable explanations for the proportional increase in glucose, cholesterol, creatinine and urea concentrations under water restriction. Similar increase in blood plasma metabolites upon water restriction of 20% and 40% was found by Casamassima et al. (2008) in lactating sheep.

Exposure of goats and sheep to heat stress was found to be associated with a regulatory increase in body fluid volume and plasma volume (Silanikove, 1988 and 1992; Rahardja *et al.*, 2011). Thus, a putative regulatory increase in body water and plasma volume before initiation of water restriction when water was freely available may explain why the dehydration imposed by water restriction did not bring it to a level that affected substantially feed intake and thermoregulatory responses. The imposed dehydration did not bring the goats to the dehydration level, which would put at risk their cardiovascular and thermoregulatory functions.

Although all the animals were subjected to similar heat stress, the thermoregulatory symptoms in those subjected to water restriction were more pronounced as reflected by the increase in the temperature of the most exposed area – the head skin. Nevertheless, the increase in deep (rectal) temperature and udder skin temperature were quite modest in comparison with the responses of animals that were exposed to severe heat stress (Silanikove, 2000a), indicating that the heat stress under the present conditions did not induce significant challenge on the thermoregulation capacity of the goats. For comparison, under dehydration, the mean daily maxima of deep temperature was 0.5°C to 0.9°C higher in dehydrated goats than in hydrated ones, which was a result of a reduction in evaporative heat loss (Baker, 1989; Jessen et al., 1998). Thus, only in treatment 1, in which the restriction level was 90% of control, the prevailing heat stress induced an increase in deep body temperature that resembled a modest response under combined effects of heat stress and dehydration. Consistently, the increase in RR, which is the main avenue to dissipate heat in goats (Silanikove, 2000a), was modest.

The relatively high water-to-food intake ratio in the control goats reflected most likely the high rate of water used for maintaining thermoregulation by evaporation (Silanikove, 1988). Imposition of water restriction enforced the animals to use different strategies, which applied much more economic use of water for maintaining the water balance and thermoregulation, and this switch was reflected by marked reduction in the water-to-feed intake ratio. A Similar sharp reduction in the ratio between water and feed intake in response to water restriction was also found by Ahmed and El Kheir (2004) in the Sudanese desert goats and Abioja *et al.* (2010) in the West African tropical goats.

As noted above, the most notable physiological and behavioral responses in the water-restricted animals were those associated with preventing water loss. The increase in body temperature allows goats to save on water losses, and under harsher conditions the level of thermolability may be much higher than during euhydration (Baker, 1989). Water flux is the product of pool size and the exchange rate of the pool. Thus, the reduction in body water pool content contributes to reduce water losses. The main component of water losses from the body is evaporation (cutaneous and respiratory), which is directly linked to the metabolic rate of the organism (Silanikove, 1989). Heart rate in mammals is proportional to heat production (Brosh, 2007). Thus, the reduction in heart rate in the water-restricted goats suggests that they reduced their metabolism in order to conserve water and to compensate for the reduction in feed intake. The RR, even in treatment 1, was much lower than those induced under combination of dehydration and heat stress

(Baker, 1989; Jessen *et al.*, 1998), indicating that the goats in the present experiment were still far from situations that necessitate induction of heavy panting to maintain thermoregulation (Silanikove, 2000a).

The reduction in walking and the increase in lying activity are two factors that explain the more economical energy metabolism. The increase in standing activity may reflect a thermoregulatory behavioral response: in the standing position, the goats may direct themselves to position with respect to the sun, so that lower proportion of their body surface will be exposed to direct radiation (Silanikove, 2000a). The reduction in meal size under water restriction explains the reduction in feed intake and is consistent with the results of Burgos *et al.* (2001) in cows. The reduction in meal size may also explain the lower rumination in the water-restricted goats.

Conclusion

The goats used in the present experiment (a mix of 75% temperate breed with 25% local adapted breed) have shown remarkable capacity to endure significant water restriction for long time (>30 days), with minimal disruption of plasma electrolyte and metabolite composition, thermoregulation and general well-being. An ability to maintain good homeostasis of body fluids, energy and thermoregulation was achieved, presumably by being pre-adapted to potential water shortage under heat stress (higher level of body fluids) and by activating a range of physiological and behavioral water-saving mechanisms. However, this study has shown that the water-saving responses were activated in response to mild loss of body fluids and an increase in plasma sodium and ADH concentrations.

Acknowledgment

This study was supported by Scientific Research Fund of Cukurova University.

References

Abioja MO, Osinowo OA, Adebambo OA, Bello NJ and Abiona JA 2010. Water restriction in goats during hot-dry season in the humid tropic: feed intake and weight gain. Annales de Zootechnie 59, 195–203.

Ahmed MMM and El Kheir IM 2004. Themoregulation and water balance as affected by water and food restrictions in Sudanese desert goats fed good-quality and poor-quality diets. Tropical Animal Health and Production 36, 191–204.

Alamer M 2009. Effect of water restriction on lactation performance of Aardi goats under heat stress conditions. Small Ruminant Research 84, 76–81.

Andersson B 1977. Regulation of body fluids. Annual Review of Physiology 39, 185–200.

Baker MA 1989. Effects of dehydration and rehydration on thermoregulatory sweating in goats. Journal of Physiology (London) 417, 421–435.

Brosh A 2007. Heart rate measurements as an index of energy expenditure and energy balance in ruminants: a review. Journal of Animal Science 85, 1213–1227.

Burgos MS, Senn M, Sutter F, Kreuzer M and Langhans W 2001. Effect of water restriction on feeding and metabolism in dairy cows. American Journal of Physiology: Regulatory Integrative Comparative Physiology 280, R418–R427.

Casamassima D, Pizzo R, Palazzo M, D'Alessandro AG and Martemucci G 2008. Effect of water restriction on productive performance and blood parameters in comisana sheep reared under intensive condition. Small Ruminant Research 78, 169–175. Chew RM 1965. Water physiology of mammals. In Physiological mammalogy. vol. II, (ed. W Mayer and RG Van Gelder), Academic Press, New York.

Darcan N, Cedden F and Çankaya S 2008. Spraying effects on some physiological and behavioral traits of goats in subtropical climate. Italian Journal of Animal Science 7, 77–85.

Jessen C, Dmi'el R, Choshniak I, Ezra D and Kuhnen G 1998. Effects of dehydration and rehydration on body temperatures in the black Bedouin goat. Pflügers Archives – European Journal of Physiology 436, 659–666.

Khan MS, Ghosh PK and Sasidharan TU 1978. Effect of water restriction on plasma proteins and on blood and urinary electrolytes in Barmer goats of the Rajasthan desert. Journal of Agricultural Science 91, 395–398.

Maltz E, Olson K, Glick SM, Fyhroquist F, Silanikove N, Choshniak I and Shkolnik A 1984. Homeostatic responses to water deprivation or hemorrhage in lactating and non-lactating Bedouin goats. Comparative Biochemistry and Physiology 77A, 79–84.

Meza-Herrera CA, Calderón-Leyva G, Soto-Sanchez MJ, Serradilla JM, García-Martinez A, Mellado M and Veliz-Deras FG 2014. Glutamate supply positively affects serum cholesterol concentrations without increases in total protein and urea around the onset of puberty in goats. Animal Reproduction Science 147, 106–111.

Rahardja DP, Toleng AL and Lestari VS 2011. Thermoregulation and water balance in fat-tailed sheep and Kacang goat under sunlight exposure and water restriction in a hot and dry area. Animal 5, 1587–1593.

SAS 1999. SAS Institute Inc., SAS Online $\mathsf{Doc}^{\circledast}$, Version 8, Cary, NC: SAS Institute Inc., 1999.

Schmidt-Nielsen K 1983. Animal physiology: adaptation and environment. Cambridge University Press, Cambridge.

Schönhusen U, Junghans P, Flöter A, Steinhoff-Wagner J, Görs S, Schneider F, Cmetges C and Hammon HM 2013. First-pass uptake and oxidation of glucose by the splanchnic tissue in young goats fed soy protein-based milk diets with or without amino acid supplementation. Journal of Dairy Science 96, 2400–2412.

Silanikove N 1984. Renal excretion of urea in response to changes in nitrogen intake in desert (black Bedouin) and non-desert (Swiss Saanen) goats. Comparative Biochemistry and Physiology 79A, 651–654.

Silanikove N 1985. Effect of dehydration on feed intake and dry matter digestibility in desert (black Bedouin) and non-desert (Swiss Saanen) goats fed on Lucerne hay. Comparative Biochemistry and Physiology 80A, 449–452.

Silanikove N 1986. Interrelationships between feed quality, digestibility, feed consumption, and energy requirements in desert (Bedouin) and temperate (Saanen) goats. Journal of Dairy Science 69, 2157–2162.

Silanikove N 1987. Effect of imposed reduction of energy-intake on resting and fasting heat-production in the black Bedouin desert goats. Nutrition Reports International 35, 725–731.

Silanikove N 1988. Impact of shelter in hot Mediterranean climate on feed intake, feed utilization and body fluid distribution in sheep. Appetite 9, 207–215.

Silanikove N 1989. Interrelationships between water, food and digestible energy intake in desert and temperate goats. Appetite 12, 163–170.

Silanikove N 1992. Effects of water scarcity and hot environment on appetite and digestion in ruminants: a review. Livestock Production Science 30, 175–193.

Silanikove N 1994. The struggle to maintain hydration and osmoregulation in animals experiencing severe dehydration and rapid rehydration: the story of ruminants. Experimental Physiology 79, 281–300.

Silanikove N 2000a. Effects of heat stress on the welfare of extensively managed domestic ruminants. Livestock Production Science 67, 1–18.

Silanikove N 2000b. The physiological basis of adaptation in goats to harsh environments. Small Ruminant Research 35, 181–193.

Silanikove N and Koluman N 2015. Impact of climate change on the dairy industry in temperate zones: predications on the overall negative impact and on the positive role of dairy goats in adaptation to earth warming. Small Ruminant Research 123, 27–34.