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Regulation of fluid balance in goats and sheep from dry areas

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SUMMARY - Food and water intake are closely linked. Enough drinking water is a prerequisite for animals to utilize food efficiently. Goat and sheep breeds which are native to dry regions have developed strategies to cope with scarcity of food and water. However, animals from temperate regions may encounter problems in adjusting to a dry environment. This is obvious during late pregnancy and lactation, when the strain on the fluid regulatory mechanisms becomes more severe. In our studies we have found major differences in the capability to cope with shortage of food and water between the Moroccan black goat and the Swedish high-yielding domestic goat breeds; e.g., the Moroccan goat having a lower water turnover and higher thirst threshold. Likewise, the Sardi and D'man sheep breeds respond differently; the Sardi being used to harsh conditions endure both food and water deprivation better than the D'man sheep, which are kept in the oasis. Thus, it is important to consider the response of each breed to different challenges in order to select the most suitable one for production in a certain environment.

Key words: Fluid balance, regulation, dry areas, goats, sheep, review.

RESUME - *"Régulation du bilan des fluides chez des caprins et ovins de zones sèches". Les besoins des humains en protéine animale font qu'il est de plus en plus important d'utiliser toutes les terres de pâturage, qui en grande partie se trouvent dans des régions à climat défavorable. L'efficacité biologique comparative de la production de viande, fibre et lait chez les ovins et les caprins les rendent spécialement adaptés à la production à petite échelle dans des environnements difficiles. Dans ces zones, les animaux doivent bien souvent parcourir de longues distances jusqu'aux points d'eau, et subissent des périodes plus ou moins longues de manque d'eau et/ou aliment, généralement sous un fort rayonnement solaire. Ces facteurs, seuls ou combinés, constituent un défi permanent pour la productivité et pour les mécanismes homéostatiques qui régulent le bilan des fluides. L'impact de ces contraintes est censé être plus sévère lors de la gestation et de la lactation. L'objectif de cet article est de présenter un aperçu des mécanismes adaptatifs fondamentaux de régulation du bilan des fluides et de la température corporelle, mis en jeu par les ovins et caprins, qui doivent vivre et produire dans des environnements chauds semi-arides et arides.*

Mots-clés : *Bilan des fluides, régulation, zones sèches, caprins, ovins, révision.*

Introduction

The human requirements for animal protein makes it increasingly important to utilize all available pastureland, which to a large extent lies in climatically unfavourable regions. The comparative biological efficiency in meat, fibre and milk production of sheep and goats make them specially suitable for small-scale production in harsh environments. In this areas, the animals often have to walk long distances to water sources, and to experience short or long periods of water and/or feed shortage, generally under hot solar radiation. Alone, or in combination, these factors constitute a permanent challenge to productivity and to the homeostatic mechanisms regulating fluid balance. The impact of such constraint is expected to be more severe during pregnancy and lactation. The aim of this paper is to give an overview of the basic and adaptive mechanisms regulating fluid balance and body temperature that are used by sheep and goats, which have to live and produce in hot semi-arid and arid environments.

Regulation of fluid balance

The fluid and electrolyte balance of the organism is a function of the maintenance of extracellular fluid volume and osmolality and depends on the coordinated action of multiple mechanisms regulating water and sodium intake and excretion.

Water balance

It can be estimated that the obligatory water losses in sheep and goats of average weight (45 kg) living at thermoneutral conditions are about 0.5 kg of water per day by vaporization and about 1 kg per day in the urine. Renal water excretion is controlled mainly by antidiuretic hormone (arginine vasopressin) and water intake by the thirst mechanism (Fig. 1). When the body volume is reduced and/or the osmolality of the extracellular fluid increases, cells in the hypothalamus react to induce increased secretion of vasopressin and thirst (Verney, 1947; Andersson, 1953). These cells mainly respond to changes in the sodium concentration of the cerebrospinal fluid, but also other osmotically active substances, applied from the blood side of the blood-brain-barrier, can stimulate release of vasopressin and thirst (Verney, 1947; Andersson and Olsson, 1973; McKinley *et al.*, 1978). Centrally produced angiotensin II or angiotensin II from the periphery acting on the circumventricular organs in the brain (Fig. 1), act in consort with the sodium ion in the regulation of water balance (Blair-West *et al.*, 1994). Recently, a population of neurons in the hypothalamus, which are preferentially activated by intravenous infusions of hypertonic saline or angiotensin II, have been identified. They are probably the postulated sodium-osmoreceptors (Oldfield *et al.*, 1994).

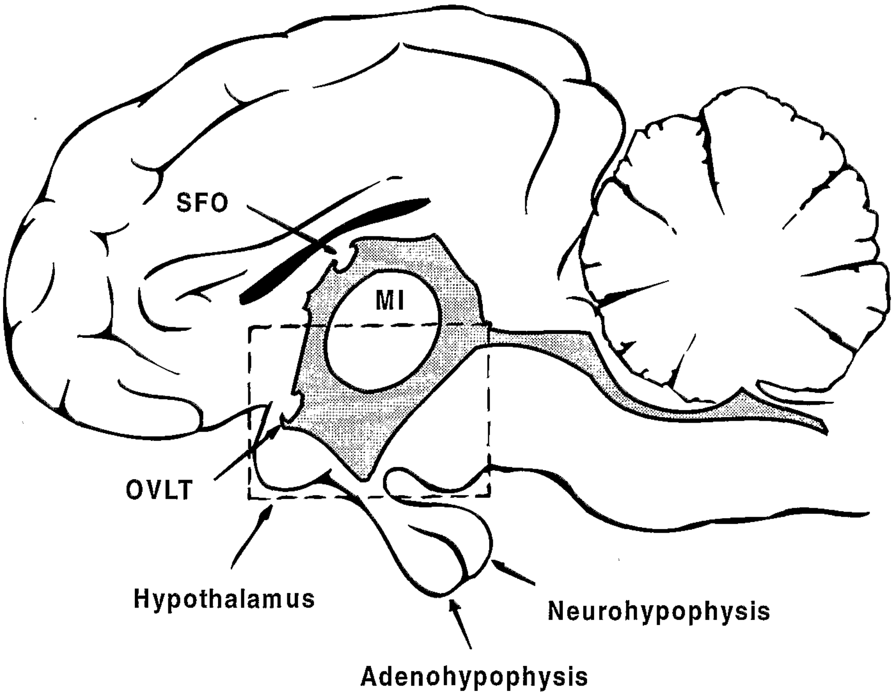

Fig. 1. Schematic drawing of the brain of a goat or a sheep. Sagittal section. SFO (subfornical organ) and OVLT (organum vasculosum of lamina terminalis) are circumventricular organs without a blood-brain barrier. MI= Massa Intermedia. Grey area: 3rd and 4th cerebral ventricles. Within hypothalamus are centres with: (i) osmo-sodium sensitive cells regulating thirst and sodium appetite, release of vasopressin and probably also natriuretic factors; (ii) thermosensitive cells regulating body temperature by cardiovascular adjustments, panting and sweating and (iii) gluco-sensitive cells regulating hunger and satiety. All these centres are interrelated.

Vasopressin acts to reabsorb water from the distal tubules and the collecting ducts of the kidneys and thereby the animal saves water. In addition, dehydrated animals reabsorb more water from the gastro-intestinal tract by osmotic forces, which results in dry faeces.

If the extracellular fluid volume becomes enlarged and its osmolality lowered, there is no thirst and no secretion of vasopressin. When vasopressin no longer acts on the kidneys, the animals respond with water diuresis, thereby eliminating the extra water.

Sodium balance

Sodium is the main cation in the extracellular fluid and by its osmotic action it plays the dominant role for the regulation of body fluid homeostasis. The feed of ruminants is usually low in sodium and there is a requirement for dietary sodium since sodium is lost in the urine and faeces and occasionally by sweat and milk. Recommendations for maintenance is at present about 1 mmol/kg and day for sheep (ARC, 1980). However, this may well be abundant for sheep, and goats have been shown to perform well on a feed containing 0.3 -0.7 mmol sodium per kg and day (Michell, 1989).

The sodium content of the body is regulated by several mechanisms. The renin-angiotensin-aldosterone system acts to save sodium within the body. In addition, most mammals actively seek and voluntarily eat sodium salts (Denton, 1982). Natriuretic factors, on the other hand, endeavour to get rid of an excess of sodium.

Angiotensin II is formed locally in the brain, but also peripherally. The juxtaglomerular cells in the kidneys secrete renin, which acts on angiotensinogen circulating in the blood to form angiotensin I. Angiotensin I is converted into angiotensin II, which is synthetized in increased amounts during sodium deficiency. Angiotensin II stimulates the secretion of aldosterone from the adrenal cortex. Hyponatraemia and an elevated plasma concentration of potassium may also directly stimulate the adrenal cortex in instances where the effects of salt deficiency are more pronounced (Denton, 1982). Cortiocotrophin releasing hormone from the hypothalamus and adrenocorticotrophic hormone from the adenohypophysis seem to play a role in hypersecretion of aldosterone only if the salt deficiency is combined with severe overall stress to the organism.

Ruminants actively seek salt and consume it freely. Numerous experiments in a variety of species, including sheep, show that salt appetite increases with increasing sodium deficit. This specific salt appetite is regulated from the hypothalamic region (Fig. 1) (Denton, 1982; Weisinger *et al.*, 1982; Franci, 1994).

Excess of sodium is mainly excreted by the kidneys. According to the classical view, an increased plasma sodium concentration stimulates vasopressin secretion and thirst which leads to enlarged plasma volume. Hypernatraemic hypervolemia increases the glomerular filtration rate, the aldosterone secretion falls to nil and the reabsorption of sodium in the kidneys and gut decreases to a minimum eliminating the extra sodium.

On the other hand, several lines of evidence suggest that there are specific natriuretic factors that act on the kidneys to stimulate increased renal sodium excretion during hypernatraemic hypervolemia (de Wardener and Clarkson, 1985; Huang, 1995). Andersson *et al.* (1972) pointed at a possible central mechanism regulating renal sodium excretion during this condition, which has been confirmed in several studies (Leksell *et al.*, 1982; de Wardener and Clarkson, 1985; Franci, 1994). However, the mediator of the effect is still unsettled.

In many regions, water is not freely available. During dehydration the plasma sodium concentration continuously increases, although the plasma protein and urea concentrations may reach a steady state (Igbokwe, 1993). In the absence of drinking water, the animals cannot dilute the plasma sodium and excrete it by increasing the glomerular filtration rate. Nevertheless, dehydrated sheep develop natriuresis (Macfarlane, 1961; McKinley *et al.*, 1983a) provided they are on a comparatively high sodium intake (Michell and Moss, 1995). This points to a powerful natriuretic mechanism. Good evidence indicates that this dehydration-induced natriuresis is controlled from cells in the anterior part of the hypothalamus (Fig. 1) (McKinley *et al.*, 1983b), but, as is the case with hypernatraemic hypervolemia, the mediator of the dehydration-induced natriuresis is not known.

Vasopressin, oxytocin and atrial natriuretic peptide have been suggested as candidates both for the natriuresis seen during conditions of hypernatraemic hypervolemia and during dehydration (hypernatraemic hypovolemia).

Plasma vasopressin levels increase during dehydration. At rather high doses, vasopressin is natriuretic in sodium-repleted, well hydrated sheep and it has been suggested that it is responsible also for the dehydration-induced natriuresis. However, hypophysectomy abolished the increase in plasma vasopressin concentration during dehydration, but not the natriuresis (Park *et al.*, 1985; Franci, 1994), which speaks against this theory at least in sheep.

Oxytocin has convincingly been shown to cause natriuresis in rats (Huang, 1995). However, dehydration could not raise plasma oxytocin concentrations neither in goats (Thornton *et al.*, 1986) nor sheep (Thornton *et al.*, 1987), which makes it unlikely that this hormone is involved in dehydration-induced natriuresis in ruminants.

Atrial natriuretic peptide has been shown to have natriuretic, diuretic, hypotensive and haemoconcentring effects (de Bold *et al.*, 1981). It is secreted in response to large extracellular loads of saline. However, its physiological role in regulating the sodium balance in goats (Olsson *et al.*, 1994) and sheep (Parkes *et al.*, 1987) appears to be small. Instead, atrial natriuretic peptide may regulate the distribution of fluid between the blood plasma compartment and the interstitial space, since a small increase of the plasma ANP concentration decreases plasma volume in the goat (Olsson *et al.*, 1994).

Interaction between food and water intake

Water intake is related to dry matter intake. During eating, especially in a hungry animal that eats rapidly, the saliva and other gastric juices start to flow. This leads to hypovolemia and hyperosmolality (Blair-West and Brooks, 1969), which explains why ruminants drink mostly in connection with feeding.

During pregnancy, the dry matter intake increases, which is accompanied by a greater water intake. The mean water intake increases with litter size (Forbes, 1968; Benlamlih *et al.*, 1985), but the individual variations are great (Olsson *et al.*, 1982). The demands of the enlarged extracellular fluid volume and organs beside the feto-placental unit (e.g., liver, gut) contribute the accelerated water turnover. The increased water turnover may be due either to a primary polydipsia or to an enhanced urinary water loss leading to secondary polydipsia. In favour of a primary thirst stimulus is the observation that the dipsogenic response to an intravenous load of hypertonic sodium chloride increased during pregnancy (Benlamlih and Karlberg, 1983). In favour of secondary polydipsia is the observation that the concentrating capability of the kidneys are less during pregnancy and to some extent also during lactation (Olsson *et al.*, 1982; Benlamlih *et al.*, 1985). During lactation water intake is related both to dry matter intake and milk production.

Food deprivation decreases water intake in many species, e.g., man (Wolf, 1958), and goats (Chaiyabutr *et al.*, 1980; Dahlborn and Karlberg, 1986; Dahlborn, 1987a). The explanations have been several. One is that prandial drinking is abolished (Cannon, 1919). Another that, in small ruminants, lack of food, and especially its content of potassium, impedes the sodium uptake from the reticulum-rumen causing hyponatraemia and hypo-osmolality (Dahlborn and Karlberg, 1986; Holtenius and Dahlborn, 1990). This theory is strengthened by experiments in which it was shown that giving goats saline to drink did not improve the sodium uptake from the reticulo-rumen during food deprivation (Dahlborn, 1987b). Hyponatraemia forces water to be transported into cells, including the osmo-sodium sensitive cells in the hypothalamus (Fig. 1), thereby attenuating the urge to drink (Andersson, 1978).

However, additional mechanisms must also be operative. Goats, which have access only to cold drinking water during food deprivation, gradually diminish their water intake as mentioned above. However, if pregnant (Olsson *et al.*, 1995) or lactating goats (Fig. 2) were offered warm water they drank almost, or even as much, as before food was removed. Therefore, the temperature of the drinking water has to be added to factors such as lack of dry matter intake and hyponatraemia in order to explain the inhibition of thirst during food deprivation.

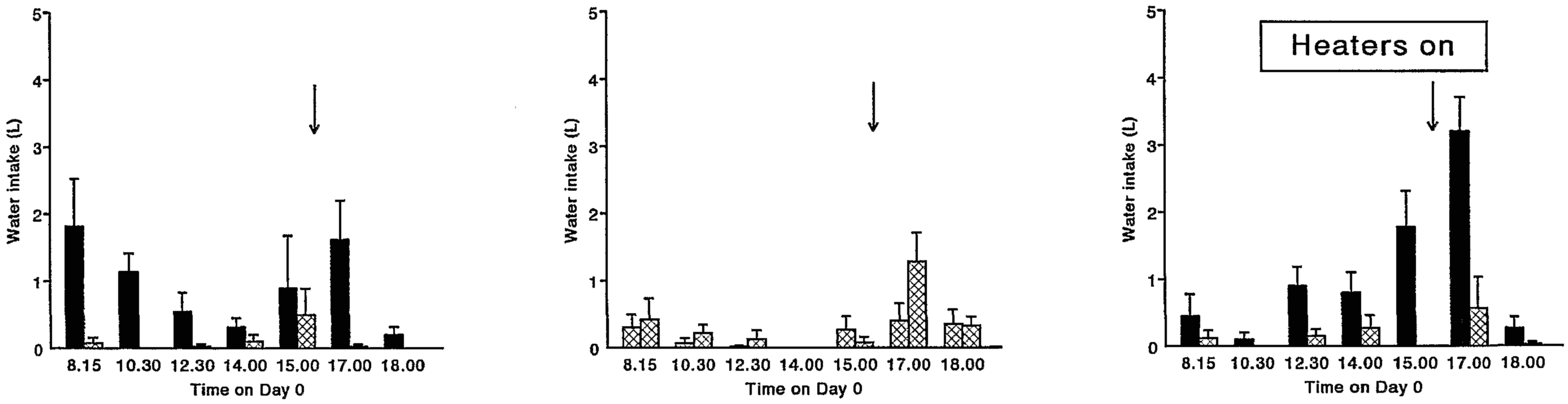

Fig. 2. Water intake in six lactating goats, which had been food deprived for 24 h. The goats were kept individually in pens, each with two water buckets. *Left:* One of the buckets contained warm water (35ºC; *black bars*) and the other cold water (15ºC; *crossed bars*). *Middle:* Cold water was given in both buckets. *Right:* Warm water and cold water was offered as in the experiment to the left. In addition, heaters were turned on at 10.45 h and room temperature elevated from 19 to 38-41ºC and kept there until 17.00 h. Arrow denotes re-feeding. (Means and SE). Note that the goats preferred to drink warm water and that they drank large amounts especially during heat stress (Olsson, *et al.*, 1996b; with permission).

The glomerular filtration rate becomes lowered and urinary water excretion depressed in food deprived lactating goats having moderately cold water available (around 20ºC) (Dahlborn and Karlberg, 1986). However, pregnant goats that had access to warm drinking water often developed a water diuresis (Olsson *et al.*, 1995). Therefore, diminished water intake during food deprivation is probably physiological in the sense that it reflects an adjustment to other reactions of the body.

Interaction between fluid balance and thermoregulation

Temperature perception is mediated by peripheral thermoreceptors and thermosensitive units in the central nervous system. Warming of the pre-optic region of the hypothalamus activates all available physiological and behavioural heat-loss mechanisms. Several adaptive reactions to heat stress have been described. First, the animals try to avoid heat stress by seeking shade and avoid grazing during the warmest time of the day. Second, a long, thick, greasy fleece may help to insulate sheep from the solar radiation (Macfarlane *et al.,* 1958). Third, circulatory adjustments consisting of inhibition of sympathetic nervous vasoconstrictor fibres come into action to achieve maximal skin vasodilatation. Fourth, the rectal temperature rises simultaneously with activation of the panting and sweating mechanisms. Lastly, the animals decrease their food intake and metabolic rate.

Sheep use panting, not sweating, as the main route for evaporative cooling (Brook and Short, 1960; Degen, 1977), whereas goats use both panting and sweating (Baker, 1989). In shorn sheep a sweating rate amounting to about 30 g m^{-2} h^{-1} has been reported. Among goats, the desert adapted Nubians and black Bedouin goats are examples of comparatively good sweaters (about 150 g m^{-2} h^{-1}), whereas the Swedish domestic goat and the Saanen goat sweat less (Jenkinson and Robertshaw, 1971; Dmi'el *et al.*, 1979; Dmi'el and Robertshaw, 1983; Olsson *et al.*, 1996a).

Cerebral thermal sensors and sensors regulating thirst and release of vasopressin are interrelated at the hypothalamic level (Fig. 1) and heat defense mechanisms are adjusted according to the water balance of the animal (Taylor, 1970; Baker, 1989).

Heat defense mechanisms in goats are related to their water balance and the mode of heat stress. Solar radiation stimulates sweating in the fully hydrated animal. As the animal becomes dehydrated sweating from the trunk subsides, but it still sweats on the head which makes it possible to keep the head region cooler (Dmi'el, 1986). As dehydration continues, sweating is suppressed and the animals rely more and more on panting (Baker, 1989). To switch from sweating to panting serves two purposes. First, panting involves no losses of salt and thereby blood plasma volume is better preserved. Second, panting involves cooling of the blood passing the nasal area, which makes it possible to keep brain temperature lower than deep body temperature (Baker, 1982; Robertshaw and Dmi'el, 1983). This is important since the dehydrated goat can not prevent its deep body temperature to rise.

Upon rehydration the animals starts to sweat within minutes. This happens before the water intake has caused any change in plasma osmolality (Baker, 1989). The act of drinking causes a rapid, transient rise in arterial blood pressure and the plasma adrenaline and noradrenaline concentrations and an immediate fall in the elevated plasma vasopressin concentration in goats (Olsson and Baker, 1989). It has been proposed that these reactions are due to nervous reflexes initiated by receptors in the mouth stimulated by the drinking of fluid (Thrasher *et al.*, 1981) and that they are involved also in the onset of sweating (Baker, 1989).

In several species of East African ungulates, increased passive fluctuations of body temperature during conditions of heat and dehydration contribute to water conservation by reducing evaporative water losses (Taylor, 1970). Similar mechanisms are employed both by sheep (Degen, 1977) and by goats. In the latter species, the regulatory importance of this mechanism becomes most evident during pregnancy and lactation. Dehydrated heat stressed pregnant and lactating goats allow their rectal temperature to rise significantly above nonpregnant, nonlactating levels as does their panting frequency (Fig. 3).

The fact that sheep and goats have to rely on panting to keep body temperature at a tolerable level endangers another homeostatic system, namely the acid/base balance. Goats seem more prone than sheep to let thermoregulation predominate over the homeostatic control of acid/base balance.

Panting is meant not to affect ventilation, but in response even to moderate heat stress, it leads to respiratory alkalosis in goats. The kidneys respond by exchanging hydrogen for sodium ions with resultant natriuresis (Augustinsson *et al.*, 1986). This reaction has to be kept in mind especially in lactating goats, with a large drain of sodium from the body by the milk, if they are kept in a hot climate where feed is low in sodium content.

Pregnant and lactating goats and sheep markedly increase their water intake during heat stress. We have clearly shown that this behaviour is not an expression of the need to cool the body, because the animals prefer to drink warm water (Olsson *et al.*, 1995; Olsson and Hydbring, 1996). In these experiments the animals voluntarily overhydrated themselves; a behaviour also shown in heat stressed lactating sheep (Thompson *et al.*, 1981; Abdalla *et al.*, 1993). The water may be warm in hot surroundings and since water is not always available, anticipatory drinking may be one reason for the excessive water intake (Fitzsimons, 1979).

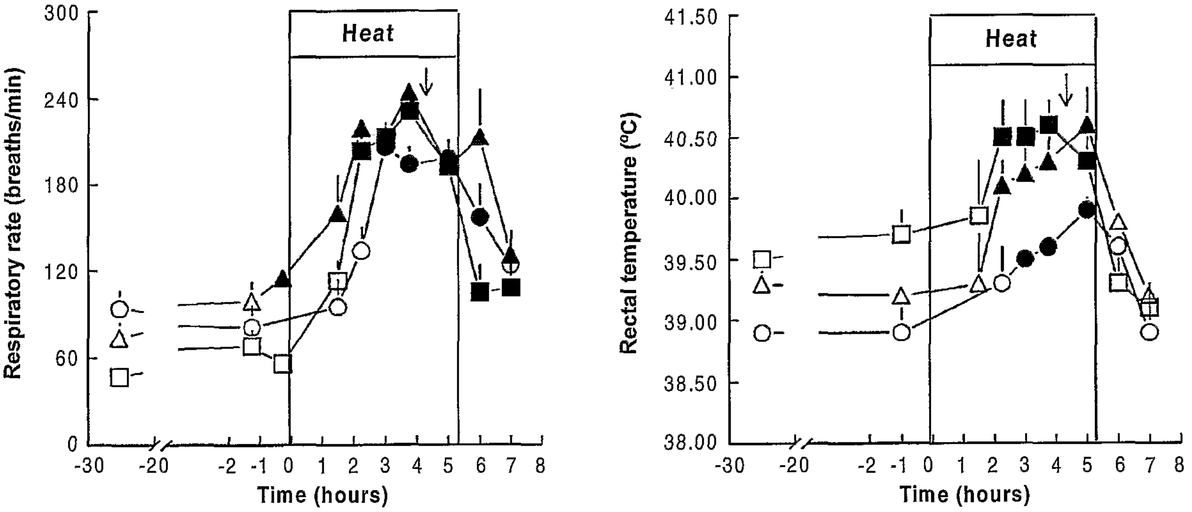

Fig. 3. Respiratory rate and rectal temperature in pregnant (Δ———Δ), lactating (□———□), and nonpregnant, nonlactating (O———O) goats during dehydration and rehydration. At time = 0, the goats had been water deprived for 26 h. "Heat" denotes the time when ambient room temperature was elevated from 20 to 38-39.5ºC (Means ± SE). When symbols are filled the values are significantly different from pre-dehydration values ($P<0.05$ or less). Pregnant goats had a significantly higher respiratory rate than nonpregnant, nonlactating goats from time 0 to time = 2 h, and lactating goats at time = 2 h ($P<0.05$) (From Olsson *et al.*, 1996a, with permission).

Adaptation to environmental constraints

Goat and sheep breeds which are native to dry regions possess basically the same physiological mechanisms for maintaining their fluid thermoregulatory homeostasis as other breeds. However, they have developed strategies to use the utmost of the regulatory systems in order to cope with heat stress and scarcity of food and water (Silanikove, 1992).

Water saving mechanisms

The kidneys of sheep and goats have comparatively long loops of Henle, which makes it possible to create a high osmotic gradient in the medullary papilla resulting in a concentrated urine. Increased blood plasma osmolality elevates medullary osmolality and by the action of vasopressin a maximally concentrated urine (up to 5000 mosm/kg) is obtained in a dehydrated animal. In this manner, only the water which is absolutely necessary for excretion of waste products is lost from the body.

Water storing capacity

The ruminant has the great advantage that it can store around 15% of its body weight as water in the rumen. The fully hydrated Bedouin goat has an enlarged extracellular and ruminal fluid volume (Shkolnik *et al.*, 1980). This may be an important reason why these animals can endure long dry seasons when they are watered only every 3rd or 4th day. Their water deficit may amount to 25% of their body weight after 4 days without water. When given access to water, they replenish all their needs within a few minutes. If they have no food and are heat stressed, the water is reabsorbed extremely slowly. If food is available, water and sodium is reabsorbed but still at a slow rate. The comparatively slow absorption of water from the gastro-intestinal tract protects them from haemolysis (Shkolnik *et al.,* 1980) and water diuresis is seldom noticed (Wittenberg *et al.,* 1986). Thereby water losses are kept at a minimum.

The small black Moroccan goats use a low water turnover as a mechanism to economize on water (Hossaini-Hilali, 1993). This appears mainly due to a low voluntary water intake. Thus, the water intake: dry matter ratio was 1.7 in the lactating black Moroccan goat, while in European breeds it ranges between 3-4 (Chaiyabutr *et al.*, 1980; Dahlborn and Karlberg, 1986; Giger-Reverdin and Gihad, 1991). When angiotensin II was infused intravenously to the black Moroccan goat, no drinking response was evoked (Hossaini-Hilali and Olsson, 1996), while similar infusions induced drinking in the Swedish goats (Olsson *et al.*, 1992). The urine volume is small in the Moroccan goat, but the urine osmolality and plasma vasopressin concentrations are not exceptionally high, not even after water deprivation for 48 h.

When dehydrated black Moroccan goats were allowed free access to water, they drank slightly in excess of their body weight loss. This resulted in hyponatremia and hypo-osmolality, but no water diuresis was observed. Thus, also this breed can store water in its extracellular fluid (Hossaini-Hilali *et al.*, 1994). However, black Moroccan goats that were loaded with water amounting to 10% of their body weight eliminated half of the load within 6 hours (Hossaini-Hilali *et al.*, 1994), which is close to the retention time reported in Swedish goats (Olsson *et al.*, 1992). In contrast, the camel shows consistent delay (25 h) in eliminating the water load (Benlamlih *et al.*, 1992). If Moroccan goats were deprived of food, their water intake remained unchanged for at least 24 h in contrast to European breeds (Hossaini-Hilali, 1993). This reaction may be an adaptive response to the harsh environment in which the animals are kept.

Desert sheep do not seem to be quite as tolerant as the Bedouin goat to dehydration, but the desert adapted breeds have larger capacity to withstand dehydration than breeds native to temperate climates. The extracellular water space of the tropical Merino sheep was estimated to be greater than that found in Merinos from temperate zones or in non-Merino breeds (Macfarlane *et al.*, 1961). In the four main sheep breeds from Morocco (Benlamlih, 1987), the water turnover was 20 to 50% lower than that reported in German mutton Merino and Awassi sheep (Degen, 1977). Water deprivation for 48 h induced a more pronounced dehydration in D'man than in Sardi sheep ewes; the Sardi being used to the arid regions of Morocco whereas the D'man sheep are used to an unlimited water supply since they are kept in the oasis (Benlamlih and Derqaoui, 1993). It appears that desert sheep can well stand to be watered only every second day, but with longer intervals there is body weight losses, higher risks for abortion and decreased milk production (Aganga *et al.*, 1990; Ahmed and Abdelatif, 1994).

In lactating animals, considerable amounts of water may be lost via the milk. Despite continued eating, the milk secretion dropped quite rapidly in the water deprived black Moroccan goat (Hossaini-Hilali *et al.*, 1994). In contrast, the Bedouin goat was able to maintain an almost undisturbed milk production during 48 h of water deprivation (Maltz and Skholnik, 1980). For comparison, European goat breeds maintain milk production during 24 h of water deprivation, but thereafter milk secretion declines rapidly partly due to the lack of water and partly due to decreased food intake (Dahlborn, 1987a).

Conclusions

The hypothalamus serves as the main integrative control centre for the homeostasis of body temperature, extracellular fluid balance and food intake. The brain receives information both from the periphery and from the central nervous system itself. All this information is integrated in the hypothalamus and appropriate effector systems are activated to maintain the internal mileau of the animals.

Long term heat acclimation is characterized by increased efficiency of the thermoregulatory organs (respiratory tract, sweat glands, cardiovascular system). Breeds of sheep and goats have developed adaptive mechanisms to sustain heat stress with or without concomitant scarcity of water and food, but detailed information on changes at the organ level is presently limited. Research in that direction will improve our understanding of management requirements for production and wellfare of animals kept at harsh conditions.

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