

Review

Physiological traits as affected by heat stress in sheep—A review

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Abstract

The exposure of sheep to elevated ambient temperatures induces an increase in the dissipation of excess body heat, in order to negate the excessive heat load. Dissipation of excess body heat is excluded by evaporation of water from the respiratory tract and skin surface via panting and sweating, respectively. Sweating in woolled sheep is much less effective due to the presence of the wool cover. With the elevation in environmental temperature to 36 °C, a high proportion of heat is dissipated via the ears and legs. When the physiological mechanisms of the animal fail to negate the excessive heat load, the rectal temperature increases. At the same time, such exposure of sheep to heat stress evokes a series of drastic changes in the biological functions, which include a decrease in feed intake efficiency and utilization, disturbances in water, protein, energy and mineral balances, enzymatic reactions, hormonal secretions and blood metabolites. Recent studies indicate that the suprachiasmatic nucleus (SCN) regulates the circadian and seasonal rhythms of most biological functions, particularly the reproductive functions and behaviour in mammals. The regulation includes the phasic and tonic release of hormones, oestrus and in some cases, gonadal size. This is due to the fact that there is evidence suggesting that the SCN is sensitive to changes in ambient temperature—with some cells being more responsive to cold and others more responsive to heat, although photoperiodic changes may also have a strong influence. In conclusion, it can be said that exposure of sheep to elevated ambient temperature negatively affects the biological functions which are reflected in the impairment of their production and reproduction traits.

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1. Introduction

In tropical and sub-tropical areas, indigenous sheep tend to breed throughout the year, although the sexual activity is restricted to a certain extent to the summer months (Marai et al., 2004). In such regions, a high ambient temperature is the major constraint on animal productivity (Marai et al., 1995, 1997a,b, 2000; Shelton, 2000). This effect is aggravated when heat stress is accompa-

nied by high ambient humidity (Marai et al., 1997a,b,c, 2000; Abdel-Hafez, 2002).

Exposure of sheep to elevated temperatures results in a decrease of body weight, average daily gain (ADG), growth rate and body total solids—which is reflected by impaired reproduction (Marai et al., 1995, 1997a,b,c, 2000; Shelton, 2000; Abdel-Hafez, 2002). The possible mechanisms involved in inducing the biological changes in heat-stressed sheep could have definite applications.

In the present review, the physiological background of sheep productive and reproductive traits as affected by heat stress, are highlighted. Other animals are included where applicable.

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2. Estimating the severity of heat stress

Means of estimating the severity of heat stress was proposed using both ambient temperature and relative humidity, termed as the temperature–humidity index (THI) (LPHSI, 1990; Marai et al., 2001). When temperature is measured ($^{\circ}\text{F}$), the equation to determine THI is as follows (LPHSI, 1990):

$$\text{THI} = \text{db } ^{\circ}\text{F} - \{(0.55 - 0.55 \text{ RH})(\text{db } ^{\circ}\text{F} - 58)\}$$

where $\text{db } ^{\circ}\text{F}$ is the dry bulb temperature in $^{\circ}\text{F}$ and RH is the relative humidity (RH%)/100, for sheep and goats. The obtained values indicate the following: values <82 =absence of heat stress; 82 to <84 =moderate heat stress; 84 to <86 =severe heat stress and over 86 = extreme severe heat stress (LPHSI, 1990). When the temperature is expressed in $^{\circ}\text{C}$, the equation of Marai et al. (2001) changes as follows:

$$\text{THI} = \text{db } ^{\circ}\text{C} - \{(0.31 - 0.31 \text{ RH})(\text{db } ^{\circ}\text{C} - 14.4)\}$$

where $\text{db } ^{\circ}\text{C}$ is the dry bulb temperature ($^{\circ}\text{C}$) and RH is the relative humidity (RH%)/100. The values obtained indicate the following: <22.2 =absence of heat stress; 22.2 to <23.3 =moderate heat stress; 23.3 to <25.6 =severe heat stress and 25.6 and more = extreme severe heat stress (Marai et al., 2001).

3. Effect of heat stress on body growth (ADG)

Growth, the increase in live body mass or cell multiplication, is controlled genetically and environmentally. The available nutrients, hormones and enzymes, as well as, elevated ambient temperatures are considered as some of the environmental factors that can influence ADG (Hafez, 1987; Habeeb et al., 1992).

Placental development requires the adequate and an organized interaction of vascular growth factors and their receptors—including vascular endothelial growth factor (VEGF) and placental growth factor (PlGF). Both VEGF and PlGF, acting through the tyrosine kinase receptors VEGFR-1 and VEGFR-2, have been implicated as playing a role in ovine placental vascular development. Exposure to environmental heat stress early in placental development, could impair normal placental vascular development due to lower levels VEGFR-1 (sVEGFR-1) mRNA in these tissues. Such changes in the growth factor and growth factor receptor mRNA expression, as well as, changes in VEGF, VEGFR-1 and VEGFR-2 mRNA expression, during the period of maximal placental growth, may contribute to the development of placental insufficiency, and ultimately intrauterine growth restriction (Regnault et al., 2002).

During the early stage of embryonic life, total cell number and placentome size were greatly reduced and cell size only slightly decreased by exposure to warm temperatures (30–40 $^{\circ}\text{C}$, 40% humidity), compared to thermo-neutral temperatures (18–20 $^{\circ}\text{C}$, 30% humidity). This occurred when examining aspects of placental protein and energy metabolism of pregnant ewes during mid and late gestation. This was, as the ratio of RNA to DNA indicates a reduced capacity for protein synthesis in the placenta under warm environmental conditions, i.e. fetal and placental weights and total protein content are reduced. DNA concentrations were slightly higher in ewes under warm versus thermo-neutral conditions. However, placental protein and RNA concentrations (mg/g) were similar (Early et al., 1991). Regnault et al. (2000) additionally found that chronic heat exposure lowers the circulating placental hormone concentrations due to impaired trophoblast cell development—specifically trophoblast migration. The impact of heat exposure during placental growth is big enough to restrict early fetal development, even before the maximal fetal growth phase. Soto et al. (1998), however, reported the main effect of heat stress over reproductive efficiency to be during the first 17 days of pregnancy and the use of shade to be beneficial to improve the pregnancy rate in a flock.

Lamb birth weights of temperate sheep breeds show a linear decline when maintaining their dams for generations in hot, semi-arid locations. Such a decline was shown from the 6th to the 11th generation in Rambouillet lambs, while the reduction was apparent from the 2nd generation in Suffolk lambs. In Merino and Dorset Horn, lamb birth weights showed no such a decline up to the 6th and 3rd generations, respectively (Singh and Karim, 1995). Regression coefficients of birth weight on generation number were -0.082 , -0.0003 , -0.459 and 0.162 kg/generation for Rambouillet, Russian Merino, Suffolk and Dorset Horn ewes, respectively. The average birth weights were the highest in Suffolk (3.8 kg), followed by Dorset Horn (3.4 kg), Russian Merino (3.4 kg) and Rambouillet (3.20 kg) breeds, respectively (Singh and Karim, 1995). Such results give an idea regarding the level of tolerance of the mentioned temperate sheep breeds to the hot conditions.

Lamb ADG values were recorded to be lower in summer than in winter in lambs, as well as in a psychrometric chamber (30–40 $^{\circ}\text{C}$) compared to a shelter (20–30 $^{\circ}\text{C}$), for Suffolk sheep (Marai et al., 1997a; Padua et al., 1997). Similarly, body weight, growth rate, total body solids and body solids daily gain (g) were impaired following exposure to elevated temperatures (Marai et al., 1991, 1997a; Ismail et al., 1995). Regressions of body weight gain

on solar radiation exposure and in pens for 10 weeks, were -12.7 and -11.9 g/week for Comisana and -9.7 and -8.5 g for Sardinian sheep, respectively—indicating that exposure to solar radiation increased the loss in weight gain in the two breeds (Nardon et al., 1991).

The decrease in daily solids gain (g) was recorded as 51% (Habeeb, 1987) and 46%, in Friesian calves (Daader et al., 1989). In rabbit's litter at weaning, the percentage weight loss pertaining to heat stress was estimated to be 73% of the live weight at weaning. Such a value is the output of multiplying the percentage decrease in conception rate \times percentage increase in pre-weaning mortality \times percentage decline in litter weight at weaning, when exposed to a warm climate (Marai et al., 2001).

The effects of elevated ambient temperature on growth performance are the product of a decrease in anabolic activity and the increase in tissue catabolism. This decrease in anabolism is essentially caused by a decrease in voluntary feed intake of essential nutrients. The decrease, especially metabolizable energy (ME) for both body maintenance and weight gain, causes a loss in the production per unit of feed (Habeeb et al., 1992; Marai and Habeeb, 1998). The increase in tissue catabolism occurs mainly in fat depots and/or lean body mass. The latter effect is due to the catabolism of endogenous DNA and RNA purines due to the increase in catecholamines and glucocorticoids (Habeeb et al., 1992; Marai and Habeeb, 1998).

In summary, exposure of the pregnant ewe during mid and late gestation to warm ambient temperatures, greatly reduces the total embryo cell number and placentome size. In addition, lamb birth weight, live body weight gain or growth rate, as well as, total body solids and daily solids gain are impaired by exposure to elevated temperatures. In other words, it can be stated that lamb production is deleteriously affected by exposure to heat stress and this causes an economic loss. The percentage loss pertaining to heat stress has been estimated in other species (rabbits), to be more than 70% of live weight at weaning (Marai et al., 2001). Such phenomena necessitate either to protect the ewes from exposure to high ambient temperatures during the breeding season or to carry out breeding of ewes during the milder periods of the year, in the warm climate zones.

4. The physiological background on the effect of heat stress

The changes in the biological functions of sheep due to exposure to heat stress include, the depression in feed intake and utilization, disturbance in the metabolism of

water, protein, energy and mineral balances, enzymatic reactions, hormonal secretions and blood metabolites (Habeeb et al., 1992; Marai et al., 2000, 2003, 2004, 2006a).

4.1. Feed intake and utilization

Sheep have a better ability to convert fibrous, low quality feedstuffs into meat (protein) and other products than cattle (Hafez, 1987). However, moderate heat stress reduces intake and growth in young sheep consuming a high feed intake of medium quality roughage diets. This does not affect the relative responses to supplements providing principally fermentable ME or a similar amount of fermentable ME and additional metabolizable protein (Dixon et al., 1999). Supplementation of brown seaweed (Tasco) to post-harvest fescue hay was found to enhance the immune system and protect the body against prolonged heat-induced oxidative stress (Saker et al., 2004).

Exposure to high ambient temperatures, augments the efforts to dissipate body heat, resulting in the increase of respiration rate, body temperature and consumption of water, and a decline in feed intake. A higher heat increment is caused by the specific dynamic action that accompanies the metabolism of feed which is highest in the case of poor quality, fibrous feedstuffs (Marai et al., 2001). Factors such as water deprivation, nutritional imbalance and nutritional deficiency may exacerbate the impact of heat stress. Sheep, however, recorded a lower sensitivity to heat stress, when compared to cattle, at a maintenance feed level. The provision of shade shelter is suggested as a practical measure applicable under extensive conditions (Silanikove-Nissim, 2000).

Studies show dry matter intake to decrease significantly following exposure to heat stress in Croix, Karakul, Rambouillet (Monty et al., 1991), Sardinian and Comisana sheep (Nardon et al., 1991). Similarly, dry matter intake per kilogram live weight was lower and the maintenance requirements were higher at high ambient temperatures. The decrease in concentrate intake by rams was estimated to be approximately 13%, without altering the roughage consumption, when kept at 35°C in a climatic chamber (Nardon et al., 1991). The daily feed intake and feed conversion also significantly decreased in Suffolk lambs under hot conditions in a climatic chamber (30.5°C), compared to a group under shelter (19.3°C), during spring (Padua et al., 1997).

Grazing time (minutes grazing/hour of the day) was significantly higher from 7:00 to 11:00 than from 11:00 to 15:00 and from 15:00 to 19:00, compared to 11:00 to 15:00 during the day and in winter (20.1 – 11.4°C), than in summer season (35.4 – 18.9°C) in sheep (Marai et al.,

1997b, 2000). Such results suggest to graze sheep during the periods of the milder weather during the day.

Digestion is the process of breaking down and dissolving feeds to be absorbed by the animal. Studies showed the digestibility of dry matter (DM), crude protein (CP), ether extract (EE) and energy (E) and metabolizable energy (ME) of diets to be depressed when the animals are exposed to high temperatures (Marai et al., 2001). The decreased effect was greatest when the proportion of roughage was 75% of the total diet (Awassi sheep). Other studies showed the ability of ruminants to digest roughage increases in warmer temperatures and decreases in colder environments (Conrad, 1985). Weniger and Stein (1992) reported the digestibility and nutrient degradation in the rumen to be significantly higher at a high ambient temperature and low relative humidity (35 °C and 50% humidity), than at a lower ambient temperature–high relative humidity (30 °C and 60% humidity) in adult Merino rams. Similarly, Shafie et al. (1994) found the digestibilities of DM, organic matter (OM), CP, crude fibre (CF) and nitrogen free extract (NFE), to be slightly more in rams maintained at 35 °C. However, Murad et al. (1994) reported an increase of ambient temperature from 18 to 35 °C to have no significant effect on nutrient digestibility in the Egyptian native sheep—except for the CF of a high roughage diet.

Ambient temperature affected feed digestibility by altering the volume of the gastro-intestinal tract and the rate of passage of the digesta through the system. The decrease in rate of passage or the increase in the retention time of the digesta apparently increased the digestibility (Conrad, 1985). Shafie et al. (1994) indicated the rumen volume and rumen temperature to be significantly higher, the rumen buffering capacity, protozoal count, total volatile fatty acid concentration and ammonia–N significantly lower and pH not affected in heat stressed rams kept at 35 °C.

In summary, exposure of sheep to heat stress is accompanied by changes in the biological functions. It include the depression in feed intake and utilization, disturbance in the metabolism of protein, energy and mineral balances, enzymatic reactions, hormonal secretions and blood metabolites. Such deleterious effects may be aggravated when the feeds include high percentage of roughages. Therefore, feeding of sheep should be carried out with low percentage of roughages during the milder periods of the day, in the warm climate areas.

4.2. Water consumption

Water is one of the most important nutrients required for the maintenance of life and is involved in many

physiological functions essential for maximum performance of farm animals. Water requirements vary and are regulated by many factors such as intake of DM, environmental temperature and loss of water from the body tissues. Sheep consume less water per unit of dry matter intake (DMI) than cattle, but the intake increases with an increase in ambient temperature. Sheep consume 2 kg water/kg DM at temperatures between 0 and 15 °C. This ratio increases to 3:1 at temperatures above 20 °C (Conrad, 1985).

Consumption of water is 9 and 11% of the total body weight during the winter and 19–25% during summer in 3-year-old sheep (Khan and Ghosh, 1989). During the first few weeks of lactation, ewes drink approximately 4 kg water/kg DM at temperatures of between 15 and 30 °C. Water intake increases markedly during pregnancy, due to the acute heat stress, with a corresponding water diuresis. Body temperature is, however, regulated during pregnancy under acute heat stress conditions by the loss of heat to ingested water and probably also via increased respiration (Conrad, 1985).

Exposure of sheep to hot environmental conditions induces a marked increase in water turnover, as well as water intake (Monty et al., 1991; Ismail et al., 1995; Padua et al., 1997). The increase in water turnover was recorded to be 6% in the winter and 7% in summer (Khan and Ghosh, 1989). It has also been reported that mountain (Timhadit) and desert sheep breeds (D'man) surpass the arid breeds (Sardi and Beni Guil), in terms of the water turnover. During pregnancy, the water turnover is lower than during lactation, under heat stress conditions (Benlmlih, 1988). Water intake (frequency/h) was significantly higher at 11:00 to 15:00 and 15:00 to 19:00 than at 7:00 to 11:00 and in the summer than during the winter (Marai et al., 1997b, 2000). Water intake increase was determined to be 50%, while water loss decreased by approximately 25% in the faeces and 40% in urine, during heat stress. Insensible water loss (by diffusion of water from the skin) was two times higher at 35 °C, than at below 18 °C (Shafie et al., 1994). In summary, exposure of sheep to hot environmental conditions induces a marked increase in water turnover, as well as, water intake.

4.3. Thermo-regulatory function

Evaporation becomes the most important avenue for heat dissipation, since sweating in sheep is much less important than respiratory evaporation—due to the presence of a wool coat. Under long periods of exposure to heat, animals develop certain mechanisms to produce less body heat. Of these mechanisms are the decrease in

feed intake and in heat production—as well as stretching out the body to loose as much heat as possible (Marai et al., 1997a). When the environmental temperature rises to 36 °C, the ears and legs of sheep dissipate a high proportion of the heat, as these areas contribute about 23% of the body surface area (Johnson, 1987).

Thermo-regulatory function traits include respiration rate and rectal temperature. In Table 1, the effects of environmental temperature on respiration, pulse rate and rectal and skin temperatures, are set out.

4.3.1. Respiration rate

Respiration rate can be an indicator of heat stress (Habeeb et al., 1992). In mammals, respiration is directed at the elimination of CO₂ from the tissues of the body and the provision of O₂ under thermo-neutral conditions, and evaporation of moisture from the respiratory tract and prevention of hypothermia under high ambient temperatures. Sheep loose approximately 20% of total body heat via respiratory moisture in a neutral environmental temperature (12 °C). The moisture loss increases and accounts for approximately 60% of the total heat loss at high ambient temperature (35 °C) (Thompson, 1985).

During summer, the respiration rate is higher than in winter for sheep (Fahmy, 1994; Marai et al., 1997c) and when walking (Khan and Ghosh, 1989; Abi-Saab and Saleim, 1995). In other words, the heat stress during summer is characterized by an increase in respiration rate (Table 1).

During the summer, respiration rate is significantly lower during the mild time (8:00) than the hot time of the day (15:00) in sheep (Table 1). In Egyptian Rahmani, Ossimi and Ossimi × Suffolk crossbred ewes, the same trend was observed and respiration rate was markedly lower at 8:00 than at 12:00 and 16:00, of which the latter rate was similar in Rahmani, Ossimi and Ossimi × Suffolk crossbred ewes during winter and summer (Shalaby, 1985; Yousef, 1985; Marai et al., 1997c).

With regard to the effect of humidity, when a load of high relative humidity was superimposed upon an already high ambient temperature, there was a further increase in respiratory frequency in sheep. This was related to an increase in the perception of warmth (Marai et al., 2002b).

Type of nutrition consumed seemed to affect the respiration rate under heat stress conditions. Bluett et al. (2001) observed that in a summer lamb finishing trial, respiration rate was higher in lambs grazing Yatsyn 1 than those grazing Aries HD perennial ryegrass cultivars (77 breaths/min versus 74 breaths/min).

The respiration rate of the lamb was recorded as 400 respirations/min under high ambient temper-

atures. However, when the temperature was raised enough to suppress respiratory evaporation, respiration rate decreased markedly and tended to stabilize at 155–200 respirations/min—and appeared much deeper than during normal shallow panting.

4.3.2. Rectal temperature

The rectal temperature is often used as a representative measurement of animal core temperature, for practical purposes (Nieslon, 1995). Sheep are strict homeotherms, i.e. animals strive to maintain their body temperature within a fairly narrow range, even under adverse climatic conditions. Rectal temperatures vary between 38.3 and 39.9 °C under thermo-neutral conditions. An increase in the ambient air temperature from 18 to 35 °C is accompanied by significant increases in rectal temperature in sheep (Abdel-Samee, 1991; Fahmy, 1994; Shafie et al., 1994; Marai et al., 1997c, 2000). Rectal temperatures of 42 °C and above are considered as dangerous (Thwaites, 1985).

Exposure to heat stress is registered by the temperature–humidity index that includes both ambient temperature and relative humidity (LPHSI, 1990; Marai et al., 2001). During the year, significant variation in rectal temperature was observed. These values were markedly lower during winter than during summer in rams (Marai et al., 1997c; El-Darawany, 1999b; Abdel-Hafez, 2002). A similar trend was observed in the same trait in the different breed types as shown in Table 1. During the day, the rectal temperature was markedly lower at 8:00 than at 12:00 and 16:00, of which the latter two were very similar (Table 1) (Shalaby, 1985; Marai et al., 1997c, 2000).

Generally, sheep as homeotherms maintain their body heat balance by dissipation of the excess heat from their bodies, when exposed to elevated temperatures. This is accompanied by many biological functions, of which the increase in respiration rate or panting is the most obvious reaction. Under such conditions, the animal's body temperature expressed in rectal temperature increases, when the body fails to maintain its heat balance.

4.4. Pulse rate

The pulse rate reflects primarily the homeostasis of circulation along with the general metabolic status. The rate increases on exposure to high environmental temperature (Table 1) (Aboul-Naga, 1987). This increases blood flow from the core to the surface to give a chance for more heat to be lost by sensible (loss by conduction, convection and radiation) and insensible (loss by diffusion water from the skin) means. Alexiev et al. (2004),

Table 1
Effects of environmental temperature on respiration and pulse rates and rectal and skin temperatures in sheep

Breeds	Ambient temperature (°C)	Respiration rate (+resp./min)	Pulse rate (pulses/min)	Skin temperature (°C)	Rectal temperature (°C)	References
Temperate breeds						
Corriedale	8.0 h	45.0 ± 3.39	70.2 ± 5.85		39.0 ± 0.20	Mittal and Gosh (1979)
	15.0 h	110.2 ± 16.92	102.0 ± 13.91		40.7 ± 0.26	
Finnish	0.0	72.0 ± 18.1	82.5 ± 6.7		40.6 ± 0.2	El-Sheikh et al. (1981)
	+2 h	159.0 ± 9.2	79.5 ± 3.9		41.0 ± 0.2	
	+4 h	122.0 ± 10.0	73.8 ± 1.4		40.7 ± 0.1	
IL-de-France	0.0	83.0 ± 7.9	77.3 ± 1.4		39.7 ± 0.2	
	+2 h	149.0 ± 5.3	80.6 ± 2.9		40.2 ± 0.2	
	+4 h	129.0 ± 7.2	86.2 ± 2.7		39.9 ± 0.1	
Rambouillet	24 °C	98.0 ± 1.9		35.1 ± 0.1	39.8 ± 0.1	Singh et al. (1980)
	40 °C	271.0 ± 22.6		38.8 ± 0.1	41.2 ± 0.1	
Suffolk	0.0	76.3 ± 6.3	88.0 ± 11.0		39.9 ± 0.1	El-Sheikh et al. (1981)
	+2 h	137.0 ± 13.6	82.5 ± 3.8		40.6 ± 0.2	
	+4 h	104.0 ± 7.2	73.6 ± 9.8		40.2 ± 0.1	
Indian breeds						
Marwari	28.8 °C (8.0 h)	42.3 ± 4.59	66.1 ± 2.22		38.7 ± 0.27	Mittal and Gosh (1979)
Magra	28.8 °C (8.0 h)	40.1 ± 5.05	65.4 ± 4.19		38.8 ± 0.19	Singh et al. (1980)
Malpura	24.0 °C	50.0 ± 6.3		34.6 ± 0.2	39.6 ± 0.1	
	40.0 °C	129.0 ± 4.2		38.0 ± 0.2	40.2 ± 0.1	
Chokla	24.0 °C	48.0 ± 8.3		34.5 ± 0.30	39.7 ± 0.1	
	40.0 °C	126.0 ± 4.6		38.4 ± 0.2	40.3 ± 0.2	
Egyptian breeds						
Barki	0.0	45.7 ± 15.5	73.3 ± 4.2		39.2 ± 0.1	El-Sheikh et al. (1981)
	+2.0 h	96.3 ± 4.1	65.3 ± 4.1		39.8 ± 0.2	
	+4.0 h	75.7 ± 6.4	71.0 ± 9.6		39.4 ± 0.1	
Rahmani	0.0	33.8 ± 1.7	64.9 ± 1.6		39.1 ± 0.1	El-Sheikh et al. (1981)
	+2.0 h	89.6 ± 9.2	77.7 ± 2.6		39.2 ± 0.2	
	+4.0 h	47.3 ± 5.0	66.8 ± 3.9		39.3 ± 0.1	
	Winter					
	8:00	25.0 ± 1.2		33.9 ± 0.15	38.3 ± 0.06	
	14:00	26.8 ± 1.2		34.5 ± 0.15	38.8 ± 0.06	
	Summer					
	8:00	31.2 ± 1.2		36.1 ± 0.15	38.2 ± 0.06	
	14:00	45.4 ± 1.2		37.4 ± 0.15	38.3 ± 0.06	
Ossimi	0:00	33.7 ± 2.6	66.7 ± 2.5		39.2 ± 0.1	El-Sheikh et al. (1981)
	+2.0 h	99.5 ± 2.3	81.9 ± 4.6		39.5 ± 0.03	
	+4.0 h	48.0 ± 6.6	77.8 ± 3.2		39.3 ± 0.1	
Crossbreds						
Rambouillet × Chokla	24 °C	58.0 ± 5.		34.5 ± 0.3	39.5 ± 0.1	Singh et al. (1980)
	40 °C	160.0 ± 8.7		37.8 ± 0.2	39.9 ± 0.3	
Rambouillet × Malpura	24 °C	70.0 ± 4.6		34.8 ± 0.3	39.6 ± 0.0	
	40 °C	160.0 ± 13.0		38.0 ± 0.02	40.1 ± 0.3	
Suffolk × Ossimi	Winter					Marai et al. (1997c)
	8.0 h	62.9 ± 2.31		34.8 ± 0.04	38.5 ± 0.05	
	12.0 h	87.5 ± 2.4		38.2 ± 0.07	39.03 ± 0.05	
	16.0 h	89.8 ± 2.4		38.3 ± 0.07	39.2 ± 0.05	
	Summer					
	8.0 h	71.1 ± 1.4		36.8 ± 0.07	38.8 ± 0.02	
	12.0 h	98.8 ± 1.4		38.2 ± 0.07	39.5 ± 0.02	
	16.0 h	95.5 ± 1.4		38.3 ± 0.07	39.5 ± 0.02	

0.0: Before exposure; +2.0 h: after 2.0 h exposure; +4.0 h: after 4.0 h exposure; +resp.: respiration; exposure: exposed to high ambient temperature.

however, reported the heart rate to accelerate during the peak hour of the heat load (15:00) in ewes that had ad libitum access to water due to the increased cutaneous blood flow. The same authors reported breed differences to exist in the rate of cutaneous cooling. At very high temperatures, the pulse rate may decrease due to a decrease in the metabolic rate.

Taniguchi et al. (2004) in particular, reported hepatic blood flow to tend to be greater at 35 than 20 °C. The absorption of acetate and propionate, as well as the O₂ uptake by the portal-drained viscera were significantly higher at 35 than 20 °C. The increased O₂ uptake may be a cause for heat load under hot temperatures, in sheep. Sakurada and Hales (1998) also indicated endotoxins to play a role in determining the heat tolerance and it (the heat tolerance) is improved by physical fitness. During hyperthermia (rectal temperature of up to 42 °C in a 42/39 °C environment), fit compared with sedentary sheep exhibited a greater increase in cardiac output—an increase in blood flow through the arteriovenous anastomoses to higher levels with less reduction in blood flow to the ileum, and a greater increase in blood flow to the myocardium, turbinates, nasal mucosa, and respiratory muscles. Under normo-thermic conditions, blood flow in the brain, ileum and diaphragm was higher in fit than in sedentary animals. Endotoxins were likely to come from the lumen of the gut, as reduction of gut blood flow formed part of the normal response to heat stress. It is suggested that the improvement of heat tolerance by physical fitness is caused by a greater cardiovascular capacity which not only permits greater perfusion of heat-loss from tissues, but also the maintenance of a better gastrointestinal tract blood supply—thereby better maintaining the normal barrier to movement of endotoxins from the gut lumen to the plasma. Sedentary animals, with their lower cardiovascular capacity, redistribute more blood away from the gut during environmentally induced hyperthermia—thus allowing endotoxin-induced fever to aggravate hyperthermia (Sakurada and Hales, 1998).

During summer, the pulse rate was significantly higher than during winter, in Barki sheep (Ismail et al., 1995). The same trend was observed in grazing sheep (Khan and Ghosh, 1989; Abi-Saab and Saleim, 1995). During the day, the pulse rate was significantly lower in the morning (8:00) than during the afternoon (15:00) in Corriedale, Marwari and Magra sheep in summer (Table 1).

Generally, in the wide range of environmental temperatures that comprise the thermo-neutral zone, sheep maintain their heat balance via vasomotor control by regulating the amount of blood flowing through the cuta-

neous vessel, by either vasodilation or vasoconstriction. Vasodilation stimulates the pilomotor centre to flatten the hair cover to allow better heat dissipation through conduction, convection and radiation (sensible means). In addition some heat is lost by evaporation (through the lungs and by sweating) and also from the surface of the body as a result of diffusion of water through the skin as insensible perspiration. As the ambient temperature increases, the pulse rate, as well as, the circulation of blood increase to transfer heat from the core to the periphery.

4.5. Skin temperature

The mammalian skin is an important pathway for heat exchange between the body surface and the environment. Skin temperature is the result of the adjustment of the skin blood flow that ends with regulation of the heat between the body core and skin (Habeeb et al., 1992). Skin temperature was recorded to be highest during summer and lowest during winter in sheep (Fahmy, 1994; Marai et al., 1997c). During the day, the skin temperature was lower at 8:00 than at 12:00 and 16:00—of which the latter two were similar, during summer conditions (Shalaby, 1985; Yousef, 1985; Marai et al., 1997c, 2000). Table 1 illustrates similar trends in skin temperature measurements of sheep, either during the year or during the day.

Generally, it can be stated that skin temperature of sheep differ according season of the year and time of the day and it becomes higher with an elevation in ambient temperature.

In short, exposure of sheep to elevated ambient temperatures, coincides with an increase in the dissipation of excess body heat—in order to balance the excessive heat load. Dissipation of excess body heat is performed by evaporation of water from the respiratory tract and skin surface via panting and sweating, respectively. However, evaporation by panting in sheep becomes the most important avenue for heat dissipation, as sweating in woolled sheep is much less effective—due to the presence of the wool coat. When the environmental temperature increases to 36 °C, the ears and legs of sheep dissipate a high proportion of the heat.

4.6. Scrotal skin temperature

The difference between abdominal and testicular temperature is approximately 4 °C in rams and bulls. A high ambient temperature significantly increases the scrotal skin temperature in males (Taylor and Bogart, 1988) and consequently, the scrotal skin temperature was recorded

to be significantly higher in summer than in winter, in rams (El-Darawany, 1999b). Semen damage is directly related to elevated subcutaneous scrotal temperature, as reflected by the testes temperature. Pinto et al. (2001) reported heat stress to cause temporary interruption of sperm production and sperm motility and secondary defects seemed to be the most sensitive criteria in Santa Ines hair—rams.

Correlation coefficients between the scrotal-skin temperature and serum testosterone, libido, motility, sperm concentration and conception rate were significantly negative and significantly positive with dead and total abnormal sperm (El-Darawany, 1999a). Abdel-Hafez (2002) recorded a non-significant positive correlation between scrotal-skin temperature and reaction time, percentage sperm abnormalities, dead sperm and acrosomal damage. Non-significant negative correlations were recorded between scrotal skin temperature and semen pH, semen ejaculate volume, sperm motility percentage and sperm cell concentration ($\times 10^9$ ml).

The scrotal skin temperature of rams increases with an increase in ambient temperature either for the season of the year or during the day. Such changes deleteriously affect the reproductive capacity of the animals. This suggests a mechanism to protect the rams from exposure to the high ambient temperature during the breeding season or to carry out breeding during the milder periods of the year, in the warm climate areas.

In general, exposure of sheep to elevated ambient temperatures evokes a series of drastic changes in biological functions, which include a decrease in feed intake efficiency and utilization and disturbance in metabolism of water balance. At the same time, it augments the efforts to dissipate excess body heat.

5. Heat syndrome

Exposure of the animal to a high environmental temperature, stimulates the peripheral thermal receptors to transmit suppressive nerve impulses to the appetite centre in the hypothalamus—causing a decrease in feed intake. Thus, less substrates become available for enzymatic activities, hormone synthesis and heat production, which minimizes the thermal load (Habeeb et al., 1992). Exposure to more heat, suppresses the production of hormone releasing factors from the hypothalamic centre, causing a decrease in pituitary hormone secretion, e.g. insulin and possibly thyroxine (Habeeb, 1987). The metabolic pathways slow down, causing a drastic impairment of protein utilization. This is due to the dramatic decrease in DMI, apparent digestibility, volatile fatty acids production, rumen pH and electrolyte concentra-

tion in rumen fluid and a shortage in energy substrates, hormones and enzymes (Habeeb et al., 1992). Under these conditions, protein synthesis becomes unable to counteract the protein catabolism which leads to a negative nitrogen balance. Such destruction of protein tissue is due to the increase in glucocorticoid hormones (proteolytic hormones), responsible for protein catabolism. The increase in glucocorticoid hormones may occur through an increase in gluconeogenesis which delivers the amino acids to the corresponding α -keto acids, the hepatic capture of amino acids or via inhibiting oxidation of glucose that are essential for providing energy required for peptide synthesis. The increase in catecholamines (lipolytic hormones) or the decrease in insulin responsible for protein anabolism may also contribute to tissue destruction (Habeeb, 1987; Habeeb et al., 1992).

In summary, the exposure to high ambient temperatures, is a major constraint on animal productivity—as it evokes a series of drastic changes in the animals' biological functions, which include the depression in feed intake efficiency and utilization, disturbances in the metabolism of water, protein, energy, and mineral balances, enzymatic reactions, hormonal secretions and the blood metabolites. Such changes result in the impairment of production and reproduction performance. The effect of heat stress is aggravated when heat stress is accompanied by high humidity.

6. Adaptation to hot climates

The adaptation of new sheep breeds to unfamiliar environments may often be either a matter of chance or as a result of trial and error—owing to the great complexity of the environment and the unexplained idiosyncrasies of breed in respect to factors like terrain (Hafez, 1987). The possibility of a breed to adapt in a certain region can be predicted by constructing climographs, i.e. plotting means of monthly maximum and minimum THI values in the original and new locations. Similarities in position, shape and area of the two patterns so formed after joining for 12 months, indicate such a possibility. The monthly means of temperature and relative humidity were separately used in plotting the climographs. However, disease and parasite criteria, feed availability, prices of inputs and products and the market situation, have to be considered.

Sheep adapted to hot climatic conditions should maintain the expression of their hereditary functional potential, during life. In other words, animals should show least variation from the normal in traits, when raised under such conditions. To realize this, the animals should

be morphologically and physiologically equipped to withstand an increase in heat and drought, i.e. such traits have to assist excess body heat dissipation, as much as possible (Habeeb et al., 1997; Marai and Habeeb, 1998).

The morphological characteristics preferred to the hot climate breeds should include a large skin area to live weight ratio, shielded eyes, pigmented skin and eye lids (to lessen susceptibility to eye cancer) and a light coloured or white body cover. In addition, the ability of animals to walk long distances, to adjust to low water intake, to high intake of salts either in drinking water or in forages, to poor quality food, to harsh treatment and to resist ticks and other pests, should be involved (Habeeb et al., 1997).

6.1. Measurement of adaptability

The evaluation of the level of adaptation to heat stress, based on the lowest rectal temperature, respiratory frequency and physiological variables as the main parameters under high temperatures, was found to be insufficient (Cardoso et al. (2002). Finocchiaro et al. (2005) reported the genetic correlation between the general additive effect and the additive effect of heat tolerance to be negative ($r = -0.8$) for both daily milk and fat-plus-protein yields during all periods considered. In other words milk yield is antagonistic to heat tolerance. Selection for increased milk production will reduce heat tolerance.

The average relative deviations (ARD) from normal (regardless either positive or negative), due to exposure to hot climates, in thermal, water and/or nitrogen balances of the animals (or in all traits measured), could be used in the estimation of parameters for detection of adaptability to a hot climate (Habeeb et al., 1997; Marai and Habeeb, 1998) as follows:

$$\text{Adaptability (\%)} = [100 - \text{ARD}] \times 100.$$

In rams, El-Darawany (1999a) and Marai et al. (2006b) used tunica dartos indices (TDI—but with different equations) to measure the ability of the male to tolerate increased ambient temperatures. The scrotum actively controls its own temperature through the function of the tunica dartos muscle—which is interpreted as the distance between the testes and the abdominal wall. This muscle, thus defines the magnitude of vascular heat exchange and is performed by the contraction of the tunica dartos muscle of the scrotum—pulling the testes toward the body to increase its warmth, when the environmental temperature is low. During high ambient temperatures, the reverse occurs to dissipate as much as

possible of the excess heat from the testes (Taylor and Bogart, 1988).

The tunica dartos muscle can be used as an index (TDI) to measure the ability of the male to tolerate increased ambient temperatures, as it reflects the magnitude of vascular heat exchange. During high ambient temperatures, the tunica dartos muscle extends to dissipate as much of the excess heat as possible from the testes.

7. Role of the suprachiasmatic nucleus (SCN) in the regulation of body temperature

Ambient temperature seems to play an important role in controlling the seasonal reproduction in sheep. It is clear that in the hot climatic regions, the onset of the breeding season begins at different times of the year—either with decreasing and/or increasing daylight length (Marai, 1987; Marai et al., 2006c).

The severe hot conditions in summer disturb the physiological functions and affect the sexual activity in ewes deleteriously (Habeeb et al., 1992). In other words, the elevation of ambient temperature during summer, is closely related and may be due to the increase in daylight which plays a major role in affecting sheep reproductive activities via disturbance of physiological activities—similar to that reported by Abdel-Samee and Marai (1997) and Marai et al. (2002a,b) regarding induced ovulators (e.g. the camel and rabbit, respectively). This means that sheep show a regularity in breeding during the year in warm regions—in the absence of heat stress, as shown in the other poly-oestrous animals (Marai et al., 2006b).

However, in the temperate zones, it is well known that photoperiod, through its effects on pineal and melatonin secretion, is the main cue controlling gonadotrophin activity of the hypothalamo-hypophyseal system—which controls gonadal activity. Poly-oestrous females such as the ewe and the hind have a distinct breeding season, during which they undergo a series of oestrous cycles (17 days in ewe and 18 days in the deer). The ewe or hind continues to show ovulatory cycles until spring, by which time photoperiod is increasing. Outside the breeding season, these animals remain sexually quiescent (Pelletier, 1996). The length of the breeding season depends on the breed of the ewe, but in the hind it occurs during October to January. In the ram, the breeding season is not as rigidly limited, as in the ewe. Sperm production, sexual behaviour, testis size and plasma testosterone and FSH levels are all maximal during the autumn under natural conditions—which suggest decreasing daylight to be the stimulus for seasonality

(Merkt et al., 1990; Musa et al., 1990). Meanwhile, factors such as nutrition, management and rainfall (Bono et al., 1989; Arthur, 1992) may override the effects of photoperiod and allow breeding to occur throughout the year, near the equator—i.e. the breeding season can adapt to climatic and nutritional changes (Arthur et al., 1985). So for example, Marai et al. (2006c) reported camels to be truly poly-oestrus, with a continuous supply of required nutrients. Certain studies have indicated a variation in the timing and length of the breeding season to be due to environment, which includes geographic, climatic and/or nutritional factors (Sighiri and Driencourt, 1999). In other words, managerial and nutritional effects, environmental factors such as temperature, humidity and light, as well as, visual or olfactory cues, are likely to affect the system centres controlling productive activity. These may be considered as factors that trigger the onset or increase the sexual activity.

7.1. The suprachiasmatic nucleus

There is a vast source of information suggesting that the hypothalamus, in particular the suprachiasmatic nucleus, is an important structure regulating the circadian and seasonal rhythms of most biological functions – particularly reproductive function and behaviour in mammals (Pando and Sassone-Corsi, 2001) – including the phasic and tonic release of hormones, oestrus and in some cases gonadal size (Buijs et al., 2003). This is due to the fact that there is evidence suggesting that the SCN is sensitive to changes in ambient temperature, with some cells being more responsive to cold and others more responsive to heat—although photoperiodic variation may also have a strong influence (Burgoon and Boulant, 2001). Furthermore, the molecular mechanisms that regulate rhythmicity, such as the cyclic changes in the expression of biological functions, can be altered by exposure to temperature changes (Majercak et al., 1999).

The SCN is sensitive to changes in ambient temperature and may be an important structure regulating the circadian and seasonal rhythms of most biological functions—particularly reproductive function and behaviour in sheep.

8. Conclusions

Exposure to high ambient temperature causes impairment of reproductive functions in sheep. The effect of heat is aggravated when heat stress is accompanied with high ambient humidity. Exposure to elevated ambient temperature evokes a series of drastic changes in animal biological functions, which include a decrease in

feed intake efficiency and utilization, disturbances in the metabolism of water, protein, energy and mineral balances, enzymatic reactions, hormonal secretions and blood metabolites. Studies showed the suprachiasmatic nucleus to regulate the circadian and seasonal rhythms of most biological functions, particularly reproductive function and behaviour in mammals, including the phasic and tonic release of hormones, oestrus and in some cases gonadal size.

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