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Review

Heat stress impacts in hair sheep production. Review

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Abstract:

In view of the problem of global warming and climate change, small ruminants may be key to maintain animal protein production since they are more heat stress tolerant than most other domestic animals. Hair breed sheep are known for their ability to grow and reproduce under conditions of high temperatures and low nutrient availability. Their adaptation to heat stress involves a complex interaction between thermoregulation mechanisms and the presence of genetic factors. These confer physiological plasticity to these breeds, allowing them to tolerate hot climates without drastically affecting their productivity. In Mexico, hair sheep are distributed in different climates throughout the country. The lack of strict reproductive seasonality in these breeds has allowed the sheep industry to maintain constant mutton production year-round. Very limited research has addressed hair breeds' ability to produce under heat stress conditions. The present review describes the effects of heat stress on reproductive performance, lamb growth and thermoregulation in hair sheep breeds.

Key words: Heat-adapted sheep, Hyperthermia, Homothermia, Sheep fertility, Hair breeds.

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Introduction

Climate change derived from greenhouse gas emissions is the principal phenomenon threatening production of animal origin food and by consequently food security[1]. The fenomenon is increasing environmental temperatures and changing circannual rainfall patterns in agroecological regions worldwide. Global warming creates climatic conditions of promote heat stress (HS) for domestic animals in regions where it has not occurred historically. In regions with naturally high temperatures HS has raised livestock mortality rates as temperatures exceed animals' capacity to maintain normothermia[2].

Small ruminant systems predominate in arid, semi-arid and desert regions because, compared to cattle, they are more able to survive in low food availability conditions and have higher HS tolerance[1,3]. High temperatures can negatively affect development and productivity in sheep since they reduce feed intake and increase energy demands due to activation of thermoregulation mechanisms. Heat stressed sheep exhibit low fertility and fetal development and growth, as well as unsuitble weight gain and feed efficiency during the fattening period[4,5,6]. High temperatures can also negatively affect sheep carcass characteristics and meat quality[3,5]. However, the degree to which HS affects productivity in sheep depends on how well a given breed is adapted to high temperatures, with hair breeds being generally less HS susceptible[7,8].

The hair sheep breeds used in Mexico were developed in hot climates, mostly in Africa, and therefore have the genetic capacity to more easily tolerate and adapt to hot climates[9]. some studies done in dry, and arid regions from northwest Mexico during the hot summer months have found that in hair sheep breeds (Pelibuey, Katahdin, Dorper and crosses) productive and reproductive variables do not decline drastically[10,11]. Activation of specific physiological, metabolic and endocrinological thermoregulatory mechanisms are partially responsible for their ability to avoid hyperthermia[11,12,13]. They also have phenotypic and genotypic characteristics that allow them to be more HS tolerant[8]. The present review addresses the effects of heat stress (HS) on reproductive behavior, lamb growth and thermoregulation in hair sheep.

Climate change and sheep production

The world's hot regions currently occupy about 50% of the surface, although projections suggest an increase due to global warming. Climate change is also generating unpredictable variations in the timing and amount of rainfall, as well as decreasing in vegetation cover and an increase in the amount of desert cover. All these effects have contributed to lowering the availability and quality of forage for livestock[1]. Compared to other domestic species, small ruminants such as sheep are well adapted to extreme climate conditions, making them an option in arid and semi-arid regions with low forage resource availability[14].

Sheep have the ability to convert fibrous and poor-quality food into products for human consumption (e.g. meat, milk and wool) under precarious production conditions in which other domestic animals (except goats) can barely survive. It should be noted that sheep from native breeds to arid and semi-arid regions are better adapted to HS and surviving in precarious extensive conditions [3,14]. Well-informed selection of appropriate breeds is therefore an effective strategy for maintaining meat production in the face of climate change[1].

In Mexico, hair sheep breeds adequately tolerate HS climatic conditions in hot agroecological regions. High temperatures in these regions are not a factor that substantially contributes to decrease reproductive capacity and growth in lambs[12,15,16]. Hair sheep breeds adapted to hot climates exhibit physiological and metabolic plasticity which allows them to tolerate this environment type without compromising their productivity[13].

Heat stress in hair sheep

Decreased feed intake and activation of the hypothalamic-pituitary-adrenal axis in response to HS results in low productive and reproductive behavior in sheep, which affects herd productivity[4,17]. However, these alterations are not as marked in hair sheep as they can be in wool breeds[5,12].

Effects on reproduction

Fertility in hair sheep seems to be more affected by photoperiod and nutritional signals than by high environmental temperatures. Estrus and ovulation are reported to be unaffected by summer HS[12,15,16], although corpus luteum functionality (based on blood progesterone levels) decreases in response to acute[18] and chronic HS[12,15]. This decrease in progesterone may be due to premature regression of the corpus luteum, as reported in Pelibuey sheep after being subjected to 37 ± 2.5 °C in a environmental chamber, although early embryonic development was unaltered[18].

The mechanism by which hair sheep maintain reproductive activity and fertility in hyperthermia conditions remains unknown. Heat stress is known to reduce reproductive function due to activation of the hypothalamic-pituitary-adrenal axis (stress axis), which suppresses function of the hypothalamic-pituitary-gonadal axis (reproductive axis)[1]. The stress axis promotes synthesis and release of cortisol in the adrenal glands, and this hormone inhibits production of gonadotropin-releasing hormone (GnRH) at the hypothalamus level[17]. It is necessary to stimulate synthesis and release of follicle-stimulating hormone (FSH) and luteinizing hormone (LH) in the pituitary gland, and both pituitary hormones are needed to produce and release fertile ovules[19]. Given that cortisol levels increase in hair sheep in response to HS[7], so two hypotheses could explain the lack of HS effect on their fertility: 1) lower reproductive axis sensitivity to increased cortisol levels, and 2) the increase in cortisol levels.

Moreover, HS apparently alters pre- and post-natal offspring development in sheep. gestational hyperthermia can reduce placental development and growth, promoting a decrease in the transfer of fetal-maternal nutrient[11]. Fetal growth can consequently be delayed, leading to weak, low-birth weight lambs with a high possibility of perinatal death[20].

Compared to winter thermoneutral conditions, summer HS during the last third of pregnancy did not affect lamb birth weight, but can reduce prolificacy and litter birth weight in hair sheep(6). Since progestogens and equine chorionic gonadotropin were used to synchronize and thus increase the percentage of twin lambing in this study, the lower prolificacy in summer may be due to fetal reabsorption in response to high temperatures. Clearly, when possible, it is best not to schedule births during the hottest months in warm regions.

Effects on lamb growth

Under Mexico conditions, there is few information available about the HS impact on growth and development of hair breed lambs. The enviromental temperature is a factor that partially controls the feed intake in animals; so, HS in lambs has been associated with lower dry matter intake, higher water intake and a increase in metabolizable energy requeriments to activate thermoregulation mechanisms(1,4). In other words, HS increases maintenance energy requirements in a body scenario in which energy intake via feed is reduced(1,14); under these circumstances growth in lambs slows or stops and nutritional efficiency is reduced. In extreme cases, mainly observed in non-adapted breeds, the energy balance becomes negative, making use of these breeds untenable in hot climates(2).

In a study using Dorper x Pelibuey lambs, HS was found to reduce growth rate by 28% and feed efficiency by 20%(5). Under Mexico conditions, there is few information available about the HS impact on growth and development of hair breed lambs. The environmental temperature is a factor that partially controls the feed intake in animals; so, HS in lambs has been associated with lower dry matter intake, higher water intake and an increase in metabolizable energy requirements to activate thermoregulation mechanisms(21,22). This negative effect on productive performance in fattening lambs was associated with increased energy expenditure in the thermoregulation process; indeed, hyperthermia in sheep can increase nutritional maintenance requirements by 10 to 20%(23).

Thermoregulation in hair sheep

Activation of compensatory and adaptive mechanisms allow hair sheep to efficiently tolerate temperatures above the upper limit of their thermoneutral zone without drastically compromising their productivity. The thermoneutral zone for sheep is generally between 12 and 27 ºC[1,4], although in hair breeds the upper limit is considered to be 30 ºC[24], highlighting their natural tolerance for higher temperatures.

The type of HS to which sheep are exposed is generally evaluated based on the temperature-humidity index (THI). Sheep in general can begin to experience HS at THI>72 [25], although one report for specific heat-tolerant breeds indicates it to begin at 82 units, with three HS levels: moderate (82 to <84), severe (≥84 to <86) and very severe (≥86)[4]. This information needs to be taken with caution since other sources indicate that hair sheep begin to show signs of HS at THI values between 78 and 79 units[24]. Since hair sheep tolerate higher temperatures than wool sheep, it is much more probable that HS in any sheep breed begins below 79 units and not at 82 units. More research is needed on the precise inflection point when sheep begin to manifest HS symptoms, as has been established in other domestic livestock species.

Hair sheep's greater tolerance to HS conditions is the result of genetic and phenotypic adaptations, as well as the activation of physiological, metabolic and endocrinological mechanisms. These aid in maintaining an adequate body water balance and normothermic conditions (38.3 to 39.9 ºC) at a low energy cost[5,13]. Several of the mechanisms activated by hair sheep in response to HS conditions are also activated by wool sheep but the latter still exhibit greater increases in body temperature as ambient temperature rises[26].

Genetic adaptations

Hair sheep breeds are genetically predisposed to be more tolerant of high ambient temperatures than most wool breeds[8]. For example, Blackbelly sheep were found to have lower rectal temperature (RT) and respiratory rate (RR) than Dorset wool sheep under HS conditions[20]. Pelibuey sheep were also reported to have greater thermoregulatory capacity than Suffolk sheep under acute HS (37 ± 2.5 °C for 6 h/d)[18]. This genetic variability is associated with the portability of thermo-tolerance genes, which have received little attention in hair sheep. One study found that hair sheep are more tolerant to HS because they activate thermo-tolerance genes associated with expression of heat shock proteins (HSP)[26]. Under HS conditions, HSP confer protection to cells to prevent apoptosis, and are therefore partially responsible for the adaptation of hair sheep to HS[27].

In addition to having lower RT and RR than Suffolk sheep, Pelibuey sheep also had a higher concentration of HSP70 (2.86 *vs* 0.53 ng / mL) when exposed to HS in a climatic chamber[26]. The reduced HSP70 expression in Suffolk sheep was associated with a decrease in the viability of *in vitro*-cultured blood mononuclear cells and consequently a lower adaptation to hot climates. The HSP70 genetic marker is the most widely expressed in sheep and goat breeds adapted to HS environmental conditions[26,27,28]. In hair sheep, only genes linked to synthesis of HSP70 have been detected, but several genes have been identified that are associated with thermo-tolerance in HS-adapted small ruminants. Hair sheep may also be carriers of some of these genes, although further research is needed to confirm this possibility.

In native desert sheep, thermo-tolerance genes have been identified that are associated with skin color and pigmentation (FGF2, GNA13, PLCB1), energy and digestive metabolism (MYH, TRHDE, ALDH1A3 and GPR50), and immune response[9,28,29]. Some mutations in the G1270A and C888T polymorphisms linked to the GPR50 gene, associated with better thermal tolerance, were recently found in HS-adapted sheep breeds in India[29]. In another study, expression of genes linked to prolactin were found to affect maintenance of extracellular fluid volume, water intake, sweat gland regulation and seasonal growth of hair in sheep[30]. This could explain why HS-adapted sheep breeds, including hair sheep, are able to efficiently use metabolizable energy and water, and maintain homeothermal conditions at a minimum energy cost in high temperature scenarios.

Based on the presence of thermo-tolerance genes in HS-adapted sheep, assisted genetic selection based on genetic markers could be an effective tool for identifying sheep with an outstanding capacity for heat tolerance and HS adaptation. Studies are already under way in some Mediterranean countries for selection of small ruminants by genetic markers linked to thermo-tolerance[31]. Selection of thermo-tolerant hair sheep individuals can also be done effectively using biological markers such as physiological, endocrinological and biochemical thermoregulation mechanisms as well as phenotypic adaptations. Much more data is currently available on these aspects than on genetic markers associated with thermo-tolerance.

Phenotype adaptations

Hair sheep's phenotypic characteristics also provide them adaptability to HS[9]. The fact that they have hair instead of wool is an advantage in terms of heat loss, both by non-evaporative and evaporative means[7,13]. Being relatively thin and short, the hair facilitates air flow across the skin allowing transfer of heat accumulated on the body surface to the environment by radiation or convection[7], or, more efficiently, by evaporation of sweat[8]. Wool, in contrast, is a very effective insulator that prevents air flow over the skin and maintains heat in the body. Consequently, non-evaporative body heat dissipation mechanisms and sweating are ineffective in regulating body temperature in wool breeds[32,33]. In addition, the number of sweat glands and the area they occupy are greater in hair breeds than in wool breeds, meaning sweating is a more effective body heat dissipation mechanism in hair breeds[8]. Skin thickness is another phenotypic factor that causes inter-breed differences in thermoregulatory capacity; hair sheep have thinner skin than wool sheep, which favors dissipation (radiation and sweating) of core body heat through the skin[33].

Skin color is known to affect the ability of shorn sheep to transfer excess body heat to the environment or vice versa[8,33]. Light colored hair and skin in hair sheep is beneficial for animal comfort because it allows them to have a lower heart rate, RT and RR compared to dark-colored hair sheep[34]. This occurs because light colors reflect solar radiation while dark colors absorb it; therefore, the darker the hair and skin color the greater the body heat accumulation in dark-haired animals[8,32,34]. In terms of thermoregulation, hair sheep breeds benefit from having hair rather the wool, but even hair and skin color can improve their adaptation to hot climates.

Physiological mechanisms

Sheep require very little energy to maintain normothermia within the thermoneutral zone[35]. However, temperatures above the upper limit of the thermoneutral zone can compromise this homeostatic balance[3]. Under these conditions, the first response of sheep includes physiological adjustments to dissipate excess body heat load[35]. If this is insufficient, endocrinological and metabolic thermoregulation mechanisms can also be activated.

Therefore, higher RR and water intake, but lower feed intake, is commonly observed in heat-stressed hair sheep.

Increased RR is the main mechanism implemented to avoid hyperthermia in sheep under HS[32,33]; indeed, regardless of breed, sheep under HS dissipate at least 60% of body heat load via the respiratory tract[4]. Under high temperatures RT in sheep increases in parallel with RR[3,13]. These physiological responses to HS (i.e. increased RT, RR and other physiological constants) occur naturally in all sheep breeds[12,13,20,26], but increases in the average values of these physiological variables are lower in hair sheep than in wool sheep[20,26,33]. This suggests that hair sheep breeds may implement other physiological adjustments, or adjustments of another nature (e.g. reduction of motor activity or metabolic activity), in conjunction with increased RR[20,32,35].

The lower RR observed in hair sheep may be related to continuous loss of body heat through the skin in HS environments[32,33]. So, under HS, the need for heat dissipation produces vasodilation and redistribution of blood flow towards the peripheral tissues to increase skin sensitivity and promote heat loss via radiation, convection and sweating[4,36]. Water evaporation through cutaneous sweating is low (~10%) in hair sheep, meaning that heat loss through the respiratory tract (60 to 90%) is the most important under hot conditions[36,37]. Therefore in hair sheep increased RR and heat losses through the skin work synergistically to make thermoregulation more efficient[13].

In dry and arid climates, the circadian patterns for RT, RR and hair coat temperature from different body regions of hair sheep change in response to environmental temperature during spring (thermoneutral), but under summer HS, hair coat temperatures fluctuate with environmental temperature while RR changes as heat losses through the skin are insufficient[13]. This circadian rhythm of RR under natural conditions of high temperature is probably a physiological adaptive mechanism developed by hair sheep to maintain homothermia without compromising organism hydration. A recent study done during the summer in the arid northwest of Mexico reported that hair sheep developed adaptive heterothermia during the hottest month (August)[38]; a mechanism used by desert-adapted homeotherm animals [39]. The adaptive heterothermia mechanism allows animals to tolerate a greater body heat load during daylight hours and then dissipate heat when solar radiation is minimal or non-existent, mainly through a drastic increase in RR[35,39]. This adaptation prevents dehydration in desert homeothermic animals during the hottest seasons of the year[39].

In response to higher RR and sweating, increased water intake also functions as a cooling mechanism and a way of compensating for the water deficit created by increases in water vapor loss through the respiratory tract[4,6,40] and sweating[8,36]. A marked reduction in feed intake and digestion also occurs as a thermoregulation mechanism[4,6,7,40]. This reduction in feed intake may be regulated at the endocrine level and be intended to reduce endogenous production of metabolic heat[4].

Endocrinological mechanisms

The physiological and behavioral responses triggered in heat-stressed animals are regulated at the neuro-endocrine level[17,41]. Under HS conditions it is common to observe a reduction in blood levels of the thyroid hormones T_3 (triiodothyronine) and T_4 (thyroxine), both responsible for mediating animal metabolism, as a mechanism to decrease production of metabolic heat[39]. Hair sheep are no exception: a study in which a climatic chamber was used to induce HS in pregnant Blackbelly and Dorset ewes, found that T_3 and T_4 concentrations decreased in both breeds at 33.8 °C, although these changes were minor[20]. This suggests that hair sheep are able to effectively maintain their metabolism in balance when under thermal insult.

The effect of HS on thyroid hormone levels in hair sheep may be due to increased hypothalamic synthesis of the tyrosine inhibitor factor (TIF)[1]. The HS stimulates peripheral thermal receptors which in turn suppress the hypothalamus's appetite center, causing greater TIF synthesis and release. This in turn reduces release of thyroid stimulating hormone (TSH), negatively affecting hormonal production in the thyroid gland[3,41]. Release of T_4 is more sensitive to HS than release of T_3[42], suggesting that T_4 is more closely associated with reductions in feed intake and, thus, with endogenous reductions in metabolic heat.

Cortisol is another hormone vital to the process of adaptation to stressors[17,41]. This glucocorticoid is a mediator of hepatic gluconeogenesis; an important function since availability of glucose in the organism is essential during a state of alarm or stress because it functions as an energy source with rapid cellular availability[41,42,43]. Elevated serum cortisol has been found in response to HS in hair sheep breeds, as well as in other breeds not found in Mexico but adapted to HS (e.g. Malpura in India)[40,42]. This is a response to the body's need for energy to cope with the extra expenditure involved in activating evaporative type thermoregulation mechanisms. Higher cortisol levels are therefore linked to higher blood glucose levels from activation of hepatic cell metabolism[3], as well as to increased release of cholesterol, a blood metabolite that is converted to cortisol by enzymatic action in the adrenal gland[17,41].

Insulin is a metabolic hormone important in energy metabolism regulation under HS conditions in sheep[44]. Levels of insulin increase in response to HS, producing hyperinsulinemia, which may be a strategy to protect correct pancreatic functioning and promote higher heat-shock protein (HSP) production[45]. Thus, while HS reduces feed intake, hyperinsulinemia prevents lipolysis and increased concentrations of non-esterified fatty acids, excesses of which can cause apoptosis of pancreatic β cells[46]. Heat stress-induced hyperinsulinemia also helps to maintain live weight, body condition and at least minimal weight gain, since even when feed intake is reduced, insulin prevents the use of body reserves[47]. A study done using the heat-adapted Afshari sheep breed found reductions in body maintenance requirements under severe HS conditions since the sheep continued to gain weight even after a 17.5% reduction in feed intake[44]. This positive effect of HS in adapted breeds may be related to alterations in post-absorptive metabolism generated by elevation of blood insulin concentrations[44,45]. Notably, HS effects on insulin secretion in hair sheep has not been studied, but some studies suggest a similar metabolic adjustment may occur[5,12,15,38]. This would partially explain why sheep breeds continue to grow under HS.

Epinephrine and norepinephrine act as hormones or neurotransmitters in thermoregulation in sheep, but no research has been done on their activity in heat-stressed hair sheep. In animals undergoing HS it is known that epinephrine and norepinephrine activate cardiovascular function to ensure sufficient blood supply to vital organs [43,48]. Epinephrine is also related to hepatic gluconeogenesis and lipolysis, metabolic processes necessary for supplying energy to thermoregulation systems[49].

Biochemical mechanisms

In hair sheep, activation of physiological adjustments intended to maintain normothermia in hot climates is closely linked to changes in blood analyte levels, or perhaps, changes in some blood analytes may be directly caused by HS either as a reflection of the ability to adapt or the lack thereof[50]. One study reported that serum concentrations of glucose, cholesterol and triglycerides in Dorper x Pelibuey lambs declined due to chronic HS during the summer in a desert region of northwestern Mexico[13]. In this study RR increased by more than 100%

compared to values observed in spring (thermoneutral period), suggesting that the decrease in metabolites responded to the high energy expenditure of the respiratory tract muscles during the increased RR. In addition, serum urea levels increased and potassium levels decreased without affecting sodium concentrations, indicating no net loss of body water content via urine, feces and sweat. This suggests that hair sheep have adaptive metabolic mechanisms that reduce the probability of becoming dehydrated. In another study done in the same desert region of Mexico(38), hair sheep were found to activate a post-absorptive energy metabolism under chronic and intense HS conditions, whereas under acute HS, glucose was the main source supplying the energy expenditure implied with increased RR. High blood glucose levels in response to acute HS can be explained by increased cortisol levels, a hormone that stimulates gluconeogenesis to provide glucose as energy for cells(44).

The HS effects on blood analyte concentrations vary widely across different studies, making it difficult to explain the metabolic adjustments made by hair sheep to survive and adapt to hot climates. Factors such as breed, age, HS type, nutrition, physiological status and others must therefore be considered when interpreting results. For example, in a recent study using heat-stressed Dorper x Pelibuey lambs, lack of shade in pens was found to promote an increase in metabolite concentrations related to energy and lipid metabolism, but not in protein metabolism(50). In the same study, increases in blood sodium and chlorine electrolytes were observed and were attributed to higher water intake. Another study using Dorper x Pelibuey ewes under natural HS conditions found that animal age and lactation status altered blood glucose, cholesterol and urea concentrations, but not blood concentrations of triglycerides, total protein and electrolytes(51). Additionally, weaned lambs and lactating ewes had lower glucose and cholesterol concentrations compared to nulliparous and non-lactating multiparous ewes. In the lambs this response was attributed to higher RR in lambs, whereas in the lactating ewes it was attributed to the effect of nutrient redistribution for synthesis of milk lactose and fat. Using sheep of a genotype similar to those used in these studies, it was reported that the uterine environment during the last third of gestation had no effects on variations in blood metabolite and electrolyte concentrations in heat-stressed lambs during the fattening period(52). Nutritional restriction has also been shown to have little effect on blood metabolite concentrations linked to energy metabolism in late pregnancy sheep in a hot climate(11).

Conclusions and implications

Hair sheep breeds are characterized for being rustic and easily adaptable to different production conditions, including those in which the climate is most frequently extreme heat and forage quality is poor. Apparently, hair breeds have the ability to grow and reproduce under heat stress conditions because they have thermo-tolerance genes, and phenotypical advantages in terms of their skin and hair which allows them to dissipate body heat through evaporative or non-evaporative routes more efficiently than wool breeds. Circadian respiratory rate patterns, as well as skin characteristics and metabolic adjustments, allow hair sheep to effectively reduce body heat load, perhaps at a lower energy cost than in wool breeds. Given the pressing challenges of global warming and climate change, selection of heat-tolerant and nutrient-efficient breeds will become increasingly necessary to guarantee animal protein production.

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