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Reproduction of small ruminants in extreme environments

Reprodução de pequenos ruminantes em ambientes extremos

Víctor Hugo Parraguez[1-2], Oscar Arango Peralta[1], Francisco Sales[3]

[1]Facultad de Ciencias Veterinarias y Pecuarias; [2]Facultad de Ciencias Agronómicas, Universidad de Chile; [3]Instituto de Investigaciones Agropecuarias, CRI Kampenaike

Resumo

Os pequenos ruminantes são espécies pouco exigentes e altamente adaptáveis a várias condições ambientais. Por isso, sua distribuição mundial é ampla, encontrando rebanhos desde o nível do mar até 5.000 metros de altitude, em climas quentes e frios, como também em regiões semidesérticas ou chuvosas. Apesar de sua capacidade adaptativa, a exposição a ambientes extremos, como altitudes elevadas e o clima frio subantártico, influenciam negativamente sua eficiência reprodutiva. Neste artigo revisamos os efeitos mais importantes dessas condições extremas sobre várias variáveis reprodutivas em pequenos ruminantes domésticos, analisando alguns mecanismos que medeiam esses efeitos, bem como uma abordagem alternativa que visa melhorar a eficiência reprodutiva nesses ambientes.

Palavras chave: pequenos ruminantes, reprodução, ambiente

Abstract

Small ruminants are undemanding species and highly adaptable to various environmental conditions. For this reason, they are widely distributed around the world, finding herds from sea level to 5000 meters of altitude, in hot and cold climates, as well as in semi-desert or rainy regions. Despite its adaptive capacity, exposure to extreme environments such as high altitudes and the sub-Antarctic cold climate, negatively influence its reproductive efficiency. In this article we review the most important effects of these extreme conditions on various reproductive variables in small domestic ruminants, analyzing some mechanisms that mediate these effects, as well as an alternative approach aimed to improving reproductive efficiency under these environments.

Key words*: small ruminants, reproduction, environment.*

Introduction

Small ruminants include sheep, goats, South American camelids (SAC), and cervids. These species are widely distributed in the world, with the exception of the SAC, which, as their name suggests, are basically found in the highlands of South America, although some years ago they have been taken as production animals to other continents. In addition to sheep and goats, two of the SAC species are domestic (lama and alpaca) and two are wild (guanaco and vicugna). Together, all domestic small ruminants have historically been an excellent alternative for the production of meat, milk, wool or fiber, hides and other by-products, at different production scales, from extensive subsistence to industrial system. Unlike other types of livestock production, small ruminants play a relevant social role, being the economic support and a source of food and shelter for the subsistence of rural populations that inhabit territories with extreme environmental conditions, where it is very difficult to develop agriculture, or raising other species for supply. Thus, we can find sheep and goats in areas with a tropical climate, with high humidity and temperature and natural grasslands of poor nutritional value, passing through areas of hot but dry climates, to areas of very cold climates, with solid rainfall, where the animals must dig through the snow to find some grass to feed on. Likewise, sheep, goats and SAC are found inhabiting different altitudinal levels, from sea level to high altitudes in mountainous areas of South America and Asia. This wide geoclimatic distribution is the expression of the adaptive capacity and low requirements of small ruminants to survive, reproduce and produce.

[1]Correspondência: vparragu@uchile.cl
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Small ruminants reproduction in arid environments

It is estimated that around 50% of the world's sheep and goat population is found in arid or semi-arid regions, usually with high temperatures and little availability of water and food (Joy et al., 2020). In the case of domestic South American camelids, although there are no formal data, it is estimated that more than 90% of the population is in the hands of small producers in the high-Andean territories of Peru, Bolivia, Chile and Argentina, territories that present wide temperature fluctuations during the day and variable supply of pastures (Ruiz-Béjar, 2019). In many cases, these species are the only ones capable of surviving and producing under these conditions, due to their high adaptability and low nutritional demands, compared to other types of productive animals (Joy et al., 2020; Ruiz-Béjar, 2019). Despite the wide thermal comfort zone of sheep (12-32ºC and up to 42ºC in native breeds of tropical climates), goats (12-24ºC and up to 44ºC in native breeds of tropical climates) and camelids (-16-20ºC, estimated for guanacos), these animals usually face heat stress, a situation that affects reproductive function and that, at present, has become more relevant due to the increase in temperature, as a result of climate change (Al-Dawood, 2017; Joy et al., 2020; Riek,et al., 2019).

Heat stress induces a series of general physiological and behavioral effects, which include depression of food consumption, disturbances in the water metabolism, proteins, and energy and mineral balance, as well as alteration of enzymatic reactions, hormonal secretions and blood metabolites (Sarangi, 2018). These changes undoubtedly impact the reproductive function of males and females.

Although this topic is addressed by Dr. Alexandre Garcia Rosetto (EMBRAPA Pecuária Sudeste, Brazil) in this same symposium, I will make a brief reference to the general effects of heat stress, as part of extreme environments. In female goats and sheep, the effects are similar. Among the most relevant are: reduction of the incidence of estrus and its duration; reduction of fertility and prolificacy due to the impact of stress on fertilization and embryo survival. These negative effects are mainly explained by alterations in follicular dynamics; delay in ovulation; low frequency of pulsatility and delay in the pre-ovulatory LH peak, delay of the estradiol peak; decrease in the amount of LH receptors in the follicles; reduction in the activity of aromatase P-450 due to decreased sensitivity to FSH (Ozawa et al., 2005; van Wettere et al., 2021).

In the case of SAC, there is very little information in this regard, because these species mostly inhabit highlands, where maximum temperatures do not usually exceed 20ºC. However, llamas and alpacas have been taken to other parts of the world (mainly Australia, the USA and several European countries), where farms have been developed for commercial purposes or kept as pets, where they are temporarily exposed to environmental temperatures that can exceed by away 30ºC. Under these conditions, a temporary decrease in fertility has been observed, which then returns to normal a few weeks after the end of the exposure to heat. The data so far indicates that the main effect involved in the decrease in fertility of the species is testicular damage that affects germ cells in the seminiferous tubules, leading to transient oligospermia or azoospermia (Schwalm et al., 2007). This situation, however, has been overcome by shifting the mating season, when the temperatures are more favorable.

Reproduction of small ruminants at high altitudes

According to FAO studies (Huddleston and Ataman, 2003), there is a rural population of more than 30 million people living above 2500 masl, whose survival depends fundamentally on the raising of small ruminants. Above 3500 masl, the raising of other animals and agriculture is highly restricted by environmental conditions (low partial pressure of oxygen, low average temperature with extreme fluctuation during the day, high solar radiation, low humidity).

Exposure to high altitude has shown various effects on reproduction in mammals. A first documented recognition of the adverse effects of high altitude on the reproduction of humans and animals is found in the "Moralizing Chronicle of the Order of San Agustín", written by the priest Antonio de la Calancha (1631, Barcelona, Spain), who arrived in the Peruvian highlands accompanying the Spanish colonizers. In his chronicle, he describes that the first birth and survival of a child born to two Spaniards in Potosí (4300 masl) occurred 53 years after his arrival in Peru, which suggests serious reproductive problems in this altitude condition. In addition, he points out that the Spanish moved the Peruvian capital from Jauja (3400 masl) to Lima (150 masl), due, in part, to the reproductive difficulties experienced by the people and the livestock that accompanied them (Gonzales, 2007; Moore, 2003). The foregoing allows us to understand the scarce quantity of domestic mammals present in high altitude territories, in comparison with those found at sea level.

Sheep and goats are not native to highlands, but they have managed to survive and adapt to this condition. However, despite the large number of generations inhabiting high altitudes, the reproductive indices are lower than those observed in species kept at low altitudes. There is relatively little information on how altitude affects the reproduction of these animals. Sheep are the ones that have received the most attention and are the ones that have motivated most studies. Sheep were introduced to the heights of the Andes by the Spanish conquerors more than 500 years ago. Despite this period of adaptation of the animals to high altitude environmental conditions, reproductive efficiency at altitudes above 3,500 masl remains poor, with fertility between 40 and 48% (De Carolis, 1987; Parraguez et al., 2006). This fertility is slightly lower than that reported for local sheep breeds kept in highlands in regions near the Himalayas in Asia (~ 58%) (Acharya, 1982). However, in ewes acutely exposed to this altitude during the reproductive season, fertility is zero, at least during the first 45 days of mating with high altitude-adapted rams (Parraguez et al., 2006). These results contrast with the normal fertility (79-97%, measured as the pregnancy rate) described in sheep at sea level (Afolayan et al., 2008). A probable explanation for the reproductive failure of sheep at high altitude is an alteration in follicular growth in the ovulatory wave, with a smaller follicular size at ovulation and a reduced steroidogenic capacity (Parraguez et al., 2014). This subsequently results in luteal dysfunction during the initial pregnancy, expressed with an abnormal progestational function (Parraguez et al., 2013). In the case of sheep not adapted to high altitudes, if a female is fertile, there is a high probability that there will be no embryonic development, since luteal dysfunction persists and adequate plasma progesterone concentrations are not achieved in the mother (Parraguez et al., 2015).

Another important effect of exposure of pregnant ewes to high altitude is the restriction of intrauterine growth, which leads to a decrease of 22-28% in the lamb´s birth weight, in sheep adapted and not adapted to altitude, respectively. In addition, increase in gestational length by a week in the native of highlands, has also been described (Parraguez et al., 2006). Although fetal growth is a process governed by multiple factors, it ultimately depends on the structural and functional ability of the placenta to obtain adequate supplies from the mother. At altitude, maternal-fetal hypoxemia imposes placental changes tending to improve oxygen transport to the fetus. Short-term changes include a decrease in the number of placentomes (5-30% less), but with an increase in their individual weight (~ 25% more). In addition, an increase in the cross-sectional placental area occupied by vascular lumens (~ 70% more) and the placental efficiency (~ 40% greater) is also observed. During acute exposure to altitude, these placental changes fail to prevent intrauterine growth restriction. In ewes with a long time of residence at high altitude, the placenta shows changes similar to those previously described, but of greater magnitude, which partially improves fetal growth (Parraguez et al., 2006; 2011).

In the case of rams, there are no effects of short-term exposure to altitude on ejaculate volume or total sperm motility, but there is a significant decrease (~ 30% less) in sperm concentration and viability, similar to high altitude natives. The seminal characteristic most affected by exposure to altitude is the progressive motility, with a reduction of ~ 60% in recently exposed rams and ~ 20% in high altitude natives. Regardless of the time of exposure to altitude, the seminal pH increases by approximately 10%. Plasma testosterone concentration decreases enormously (~ 70% less) in acutely exposed rams, but in highland natives there is also a decrease (~ 30% less) compared to those kept at sea level (Cofré et al., 2018). In a recent study in rams, we found that exposure to high altitude doubles sperm abnormalities, starting from three days after exposure to this environment, which normalizes around after 6 months of permanence. In addition, the diameter and height of the seminiferous tubules are reduced by ~ 17% and 14%, respectively, which is associated with the reduction of all cell types that compose them. These morphological changes tend to normalize after 3 to 6 months of permanence in the altitude (Fuentes and Parraguez, data not yet published). This indicates not only a detrimental effect of altitude on fertility in newly exposed sheep and rams, but also confirms that animals native to altitude have only a partial adaptation of their reproductive function.

In goats, information on the effects of altitude on reproduction is extremely scarce, incomplete and often confusing, since the works usually refer to some specific breed descriptions, rather than to the environmental conditions in which the animals are kept. One study suggests that altitude has negative reproduction effects, prolonging the age of females at first conception and parturition, increasing the interpartum period and decreasing prolificacy. Likewise, as has been described in high altitude sheep, the gestational period in goats is also prolonged (Joshi et al., 2018). In goat breeds adapted to high altitude, puberty occurs around one and a half years of age (Aggarwal et al., 2005; Yue et al., 2017), which is considered very late compared to goat breeds developed at low altitude, where puberty occurs before six months old (Shelton, 1978). Goats that show rapid acclimatization to altitude conditions also achieve good reproductive indices within two generations kept at high altitude (Bharti et al., 2018). Prolificacy in all breeds is also low, with the majority of pregnancies being monotocas (Bharti et al., 2018; Hussain et al., 2010). The weight at birth of the kids is highly variable and highly dependent on the breed. However, it is considered that it should be at least 6.6% of the mother's weight (Morand-Fehr, 1981), a value that, in general, is lower at high altitudes (Aggarwal et al., 2005; Hussain et al., 2010). In males, the information is even scarcer, but it is known that puberty at high altitudes is delayed (Alilo et al., 2012), with males being able to reproduce at 18 months of age (Aggarwal et al., 2005) explained in part by a dysregulation in the testicular synthesis pathway of testosterone (Awad et al., 2015), which could be consistent with that reported in rams (Cofré et al., 2018).

The SAC have been living in the highlands of South America for about 10,000 years, so they are perfectly adapted to these conditions. Currently, there are large herds of domestic SAC living from sea level, up to approximately 5000 masl. At any altitude level, the potential fertility of females is high, with 90% of the females getting pregnant after 3 mounts. It should be noted that SAC are induced-ovulators, so the moment of presentation of the male for copulation is highly important. Despite, the proportion of pregnant females that reach term delivery is highly variable (50-90%). According to Peruvian researchers (Bravo and Sumar, 1985), the alterations of uterine migration and implantation with early losses, before 60 days after mating, are the main cause of this variability. In our experience, however, the main losses occur later, when pregnant females face food shortages during the cold and dry season in the highlands (Ellmen, 2004).

Reproduction of small ruminants in cold environments

The territories located above parallels 50 north and south are characterized by low annual average temperatures (≤ 10ºC), with very cold winters, where snow usually covers the natural grasslands for long periods. The production of small ruminants is an important economic activity in these territories, particularly of sheep, given their wide thermal comfort zone and great resistance to cold (Joy et al., 2020).

The southern Patagonia of Chile is an example that represents extensive sheep rearing systems in cold climates, where, in general, the only source of food is the natural prairie. Due to the reproductive seasonality of the species, the mating season usually occurs during the fall, after having spent a season with an adequate abundance of grasses. This favors the reproductive activity expression with all its potential, normally achieving a high fertility rate with natural mounting (over 85%) and a little lower with artificial insemination (Latorre and Sales, 1999; Parraguez et al., 2000). However, pregnant ewes must go through a large part of their gestation during the winter, where the low quality and quantity of pastures offered by the natural prairies do not cover the requirements of gestation. Given the practical and economic difficulties of supplementing forage and/or concentrates in extensive rearing, the nutrient demands of placental and fetal growth are covered using maternal body reserves, with an evident decrease in the ewe body condition (Sales and Strauch, 2006). Under these conditions, it is common to observe pregnancies with fetal growth restriction, which results into low birth weight of the lambs, higher neonatal mortality and lower weight gain until weaning, being these effects accentuated in multiple pregnancies (Sales et al., 2018; Parraguez et al., 2020), which is why producers tend to avoid this type of pregnancy, discarding a good alternative to improve the efficiency of the herds.

All roads lead to Rome…

The investigation of the origins of the main negative effects on reproductive activity, both from exposure to high altitude, and from undernourishment in cold environments, has led us to a common pathway, hypoxemia and oxidative stress.

At high altitude, hypobaria imposes a decrease in the partial pressure of oxygen (PO_2) in the inspired air. At altitudes above 2800 masl, the reduction of PO_2 by at least 30% compared to sea level, results in unwanted reproductive effects in animals, as previously described. Studies in sheep kept between 3600 and 4000 masl show significant reductions in arterial oxygen pressure (<63 mm Hg) and in hemoglobin saturation (<85%), compromising the supply of oxygen to the tissues (Parraguez et al, 2006; 2011). This hypoxemia induces oxidative stress, this state being partially responsible for the deficit in reproductive function, including intrauterine growth restriction and low birth weight[16-20]. Similarly, ewes that develop their gestation with undernourishment in cold environments and fail to maintain adequate body condition, show a reduction in PO_2 in umbilical venous blood and consequently, hypoxemia and placental-fetal oxidative stress, especially in twin pregnancies (Sales et al, 2018). The final result, as in ewes exposed to high altitudes, is low birth weight (Sales et al, 2018), with the consequent higher risk of mortality and lower postnatal growth (Gootwine et al., 2007).

Interestingly, in both extreme environmental situations, strategic supplementation with antioxidants makes it possible to avoid oxidative stress and its adverse effects on affected reproductive traits. In the case of ovine exposed to hypobaric-hypoxic high-altitude environments, antioxidant therapy has shown to improve seminal quality in rams (Cofré et al., 2018), the expression of sexual receptivity in ewes and it fertility (Parraguez et al, 2006), and the birth weight of lambs (Parraguez et al. 2011). On the other hand, in undernourished sheep pregnancies developed in cold environments, the supplementation of antioxidants has allowed to increase the weight of the lambs at birth and the pre-weaning growth (Parraguez et al., 2020).

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