Environmental cues and seasonal patterns of reproduction in goats

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Abstract
Goats usually exhibit a seasonal sexual activity and breeding at a specific season ensures the survival of offspring by coinciding parturition with the adequate period of nutrition and climate conditions. Photoperiod is the main modulator of this seasonality in goats within different latitudes. Other environmental cues like seasonal changes in ambient temperature cycles seem also to induce a synchronizing effect on this seasonality. Moreover, food availability was found to affect reproductive physiology. Indeed, an improved nutrition enhances sexual behavior in goats while under-nutrition and particularly a negative energy balance adversely impact this activity. On the other hand, the social interaction in this species also affects the expression of the physiology and the sexual behavior during the breeding season. Goats, generally display a good plasticity of adaptation to all weather including hot, cold, wet and dry ones. This peculiarity seems genotype-dependent and may be crucial for an efficient anticipation of new changes in the environmental cues related to global climatic changes. In this review we outline the effect of exogenous and endogenous factors on reproduction in goats thus providing a basis for comparing previous studies on main factors controlling the breeding seasonality in this species.

Keywords: Goats, seasonal breeding, photoperiod, ambient temperature, food availability, social cues, genotype.

INTRODUCTION

To ensure survival, animals must adapt to different abiotic seasonal changes. Such adaptation involves physiological processes, like as hibernation, molt of skin, fur and plumage, migration and reproduction in order to anticipate seasonal variations (Gwinner, 1981). Breeding activity is considered to be very seasonal, to ensure the survival of offspring by coinciding parturition with optimal seasonal nutritional and climate conditions. In temperate environments, the daylength (photoperiod) seems to be the main environmental factor driving seasonal reproduction in mammals. In non-temperate climates, other factors such as ambient temperature cycles, rainfall and food availability seem to be the most factors implicated in this process (Vázquez-Armijo et al., 2011). Goats are known to express seasonal variations in their sexual behavior. In high latitudes (> 30°, > 35° and > 40°), photoperiod and ambient temperature cycles are considered the major regulators of seasonal breeding in this species. In contrast, in low latitudes, seasonal breeding activity in goats seems to be regulated by rainfall and food availability (Vázquez-Armijo et al., 2011). However, other factors such as social and sexual interactions are also involved in the control of goat reproduction seasonality. Goat husbandry has a great economic impact in many parts of the world (Devendra and Coop, 1982) and can adapt to various climatic conditions (Delgadillo et al., 2011).

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Most experimental studies on breeding seasonality involve the effect of a single environmental factor. To our knowledge, there is no multifactorial analysis on the control of goat seasonality in temperate, desert or tropical regions. The present paper reviews the effect of abiotic and biotic factors on the seasonality of reproduction in this species by analyzing the impact of photoperiod, temperature and rainfall with subsequent food availability in a various zoogeographical areas where goats are raised (60°N to 40°S). The social and climate change effects on reproduction of goats are also discussed in this review.

MECHANISMS OF PHOTOPERIOD IN REGULATION OF SEASONAL BREEDING IN GOATS

When reproductive physiology is considered, most species can be classified as seasonal or non-seasonal breeders. In seasonal breeders, we can distinguish short days breeders and long days breeders. Goats, like sheep are considered seasonal breeders (Jainudeen et al., 2000) being short or long days breeders depending on their geographical location. In high latitudes, a great variability exists in the onset of sexual activity in goats, depending on geographic origin. For example, in France (40°N), the breeding season starts in September and finishes in March which corresponds to a short days breeder (Bodin et al., 2007). This pattern of seasonality is also observed in many other goat breeds such as the Spanish Payoya goat (Zarazaga et al., 2005), the Portuguese Serrana goat (Mascarenhas et al., 2006), the United kingdom goat (Ahmad et al., 1996), the North American goat (Mohammad et al., 1984; Amoah et al., 1996), the Italian goat (Luca et al., 2007), the Cyprus goat (Mavrogenis et al., 2006), the Greek goat (Karagiannidis et al., 2000), but also the Northern Moroccan indigenous goats (Chentouf et al., 2011), the Algerian Bedouine goat (Charallah et al., 2000), the Tunisian Maure goat (Lassoued and Rekik, 2005), the Jordan goat (Kridli et al., 2007), the Egyptian goat (Farrag et al., 2012) and the Iranian goat (Farshad et al., 2008). In subtropical regions, such as Mexico (26°N) (Delgadillo et al., 2004), in the southern latitudes regions like Argentina (30°S) (Rivera et al., 2003), Australia (Restall, 1992), southern Brazil (Balaro et al., 2016) and South Africa (Muller, 2005), the breeding season is also observed during the short days. At lower latitudes, in tropical regions, like Kenya (Ndeke et al., 2015), Indonesia (Sodiq et al., 2003), Brazil (Simplicio et al., 1986) and in subtropical regions like Tanzania (Safari et al., 2012) and Nigeria (Trevor, 1991), goats do not seem to be seasonal breeders.

When examining the breeding seasons together with the environmental cues (including photoperiod) (Figure 1) and by month of the year worldwide (Figure 2), we see a relationship between environmental cues and zoogeographical distribution of goats. Results show that under high and moderate latitudes (Figure 1), the breeding season is closely related to the changes of photoperiod. Indeed, in northern hemisphere countries, the patterns are always a mirror image of those seen in the southern hemisphere (Figure 2). Reproductive activity is always observed during short days.

In tropical regions (Figures 1 and 2), goats tend to show sexual activity throughout the whole year. This is mainly due to the absence of annual changes in photoperiod (and probably ambient temperature). Under these latitudes, goats are not able to detect seasonal changes in the environment and therefore are not able to limit their reproductive activity to a specific season. In equatorial regions and nearby tropical zones there are seasonal cycles in the annual rainfall and subsequently in food availability (Vivien-Roels and Pévet, 1983). Analysis of data of figure 1 shows no breeding season in the equatorial geographical zone in Kenya and Brazil despite seasonal cycles of rainfall. This indicates that the absence of seasonality in equatorial regions is likely to be related to photoperiod length and probably ambient temperature too.

It is also interesting to note that although goats are known as seasonal breeders; there are some specific breeds that do not express seasonal breeding. These include different breeds over the world such the Drâa goats in Morocco (Boukhliq and Lahlo-Kassi, 1989), goats in China (Lui et al., 2015), in India (Harikrishna et al., 2013), in Pakistan (Ahmad et al., 2014) and in Soudan (Ismail et al., 2011) (Figures 1 and 2). The extended breeding season in such breeds does not seem to be related to the environment because other goat breeds seem to show reproductive cyclicity in the same latitudes (Figures 1 and 2). We think that such peculiarities could be explained by the goat genotypes and feeding level (Zarazaga et al., 2009).

Photoperiod was long considered as the main environmental cue driving the breeding seasonality in small ruminants. Several experiments have demonstrated the effect of adaptation to environmental lighting (Reiter, 1978, 1974; Hoffman, 1965; Lincoln, 1979 and 1992; Lincoln and Short, 1980; Lincoln and Richardson, 1998; Lincoln et al., 2001). Over the last few decades, photoperiodic treatments were used to control seasonal breeding in sheep, horses and goats (Chemineau et al., 2008). In goats, artificial light treatments (e.g., a regimen of one month of long days and one month of short days), were found to induce ovulation, estrous behavior and to achieve high fertility rates during the out-of-season period. This treatment can be potentiated by the so-called “male effect” (Chemineau et al., 2008). The control of the seasonal breeding in goats by artificial lighting indicates that under natural conditions, photoperiod may be the main modulator of breeding seasonality.

Photoperiod was also shown to act on reproduction through the pineal hormone, melatonin. The use of melatonin implants can modify the breeding season in goats. Melatonin treatment induces higher fecundity and maintains estrous and ovulatory activities beyond the normal breeding season and is able to induce reproductive activity during the non-breeding season (Chemineau et al., 1992; Zarazaga et al., 2009). Melatonin is secreted at night and acts on the hypothalamo-pituitary-gonadal axis by providing a time signal to the brain (Vivian-Roels and Pévet, 1983). Mammals perceive information about photoperiod through changes in the duration of the melatonin nocturnal peak (Bartness et al., 1993; Goldman, 2001). The secretion of melatonin includes reception of light by the retina. The photic signal
is conveyed to the pineal gland through multisinaptic pathways including the retino-hypothalamic tract, the suprachiasmatic nuclei, the hypothalamic paraventricular nuclei, the intermediolateral cell column of the spinal cord and the superior cervical ganglia (Tournier et al., 2003; Larsen et al., 1998; Tecleriam-Mesbah et al., 1999). Norepinephrine released during night time from sympathetic innervation of the pineal gland induces synthesis of melatonin by pinealocytes (King and Steinlechner, 1985; Stehle et al., 2001). The duration of the nocturnal melatonin peak is proportional to the duration of the night (Illnerova et al., 1984; Pévet et al., 1991; Tast et al., 2001; El Allali et al., 2005).

During the long days, the peak of melatonin in goats is short, which inhibits sexual activity whilst during short days the melatonin peak is large, which stimulates reproductive function via the control of the pulsatile secretion of GnRH/LH (Chemineau et al., 2010). Recent data brought evidence that melatonin acts on GnRH/LH neurons through a new discovered population of neurons called the Kisspeptins and RFRP neurons (Revel et al., 2006; Clarke et al., 2009; Desroziers et al., 2010; Dardente et al., 2016). In goats, kisspeptin signaling plays an important role in the pulsatile secretion of GnRH and LH to control the breeding season in this species (Wakabayashi et al., 2010).

**EFFECT OF AMBIENT TEMPERATURE**

When ambient temperatures are high, reproductive activity in animals seems to be limited to a specific period of the year, to ensure the survival of the offspring (Nakao et al., 2008). Excessive high ambient temperatures may prevent reproductive activity (Ungerfeld and Bielli, 2000). In fact, heat stress was found to induce a decline in follicular responsiveness to LH in goats (Kanai et al., 1995), a decrease in plasma concentrations of estradiol and LH receptors, while the ovulation is delayed (Ozawa et al., 2005). However, even if high temperature affects negatively reproduction activity, goats, like camels in arid and semi-arid areas, are more adapted to reduce the effect of heat stress on their physiological processes (Louv, 1984). Unlike European breeds, goats raised in arid and semi-arid regions are relatively smaller in size and have a conformation that minimizes water expenditure (Silanikove, 2000) and their breeding season is longer than in temperate or subtropical regions. The long breeding season increases the chance of conception under these conditions. In order to understand how environment drives the breeding season in mammals, food availability should not be considered on the same grounds as photoperiod and ambient temperature. Feeding is able to drive circadian rhythms (Feillet et al., 2008) but there is no evidence that food availability can provide a direct signal to the brain to modulate the predictive homeostasis. Moreover, food seems to be directly involved in the reparative adaptation of reproductive physiology. It is well known that nutrition and body condition score are major factors affecting breeding season. Indeed, a body scoring below 40-60% of normal weight was found to cause a delay in follicular growth (Blanc et al., 2004), and to affect the onset of ovarian cyclicity (Walkden-Brown et al., 1994). Sustained undernutrition induces a delay in estrous behavior for a shorter period, compared to normally fed goats. Similarly, fasting causes large changes in concentrations of reproductive hormones.
Examples of areas where goats breed throughout the year:

- **Southern Hemisphere Latitudes**: 20°S to 40°S
- **Equatorial latitudes**: 0°N
- **Northern Hemisphere Latitudes**: 60°N to 20°N

Figure 1: Distribution of the breeding season in goats (indicated by the red bar below each panel) as well as photoperiod (Green curve), ambient temperature (Brown curve) and rainfall (histograms). Examples of some non-seasonal goat breeds are also given. Data on the breeding season were obtained from the literature on seasonal breeding in each country. For each location, photoperiod data were gathered from the website (http://otaff.ca/soleil/?lang=en_CA) and ambient temperature and rainfall from the website (http://fr.climate-data.org).
Figure 2: Monthly distribution of the seasonality of reproduction in the goats in some countries around the world (green color). The red dots indicate some areas where goats are not seasonal. (Countries shown on the maps correspond to the results of our literature search on the relevant goat breeding season around the world)
and ovulation rate in goats (Al-Azraqi et al., 2007). In Payoya bucks, higher nutritional plane induces better sexual behavior (Zarazaga et al., 2009), indicating that feeding is an important factor for normal breeding season in goats.

In the ewe, the follicular growth passes through two major stages. Basal folliculogenesis, which affects follicles less than 2 mm for 6 months, is closely dependent on insulinemia and not to pituitary hormones (Monget, 1998). The energy status and dietary supplementation at the end of the luteal phase (just before estrus) significantly increases the ovulation rate. This practice, called “flushing”, leads to an increase in the ovulation rate by increasing the insulinemia and without changing the plasma concentration of pituitary hormones (Monget 1998; Martin et al., 1994). At the end of pregnancy: an energetic deficiency accompanied by high energy requirements, especially at the end of gestation, can lead to an increased mobilization of fatty acids to produce energy. This mobilization leads to an accumulation of ketone bodies which creates a state of toxemia in the ewe and directly affects the viability of the female and her fetus. In arid and semi-arid regions (i.e. high solar radiation, high ambient temperatures, limited water availability and unpredictable food resources), the breeding season is usually longer than in temperate regions (Hamadeh et al., 1996, Amoah et al., 1996) and, therefore, kidding occurs when food and climate become more favorable for the offspring.

**SOCIAL CUES**

Besides above cited factors, other environmental stimuli including social interactions are also considered regulators of the breeding season in goats (Walkden-Brown et al., 1993). These social cues are mainly related to the presence of males. Interaction with males during the breeding season stimulates the secretion of GnRH pulses in females and can also stimulate ovulation (Scaramuzzi and Martin, 2008) (Figure 3). A similar effect of females on males was reported (Martin et al., 1994). In fact, exposure to estrus females can induce an increase of testosterone levels in males. Female-female interaction effect also exists as estrous females can induce ovulation in anestrous ones (Walkden-Brown et al., 1993; Restall et al., 1995). One of the characteristics of this social interaction in goats is that when the dominant does get in contact with new introduced males, they ovulate earlier than non-dominant does (Alvarez et al., 2003). Indeed, in addition to the behavioral changes, the interaction between male and female seems capable to induce some physiological changes in the goat, like in the sudoriferous glands in the skin, the site of production of the putative pheromones that stimulate the reproductive system (Martin et al., 1994), through olfactory bulbectomy that can trigger the onset of the breeding season (Martin et al., 1994). In natural conditions, goats are simultaneously exposed to several environmental

![Figure 3: Environmental inputs into reproduction in small ruminants (Martin et al., 2004)](image-url)
factors including photoperiod, ambient temperature, food availability and social cues. The interaction between these factors allows the synchronization of the reproductive rhythm (Figure 3). Social cues, like other factors, induce pulsatile secretion of GnRH. However, this hormonal response is largely dependent on the genotype of the goat (Martin et al., 2004).

EFFECT OF GENOTYPE AND BIOTYPE CHANGES ON SEASONAL REPRODUCTION IN GOATS

For a better understanding of the seasonality of reproduction in goats, it is necessary to consider the interactions between all environmental cues but also the genotype of the animal. In small ruminants, the dominant response of the hypothalamic-pituitary system to an environmental factor is dependent on the genotype of the animal. For example, in Suffolk rams, seasonal breeding is linked to photoperiod; while in Merino rams it seems to follow changes in food availability. This variation may also concern goats in the different latitudes (Martin et al., 2004). When the photoperiod is a dominant inducer of the breeding season, the effect of other factors such as nutrition and social cues depend on the degree to which the genotype considers the response to photoperiod (Martin et al., 2004). This interaction between intrinsic factors (such as genotype) and extrinsic factors makes it possible to explain the responsiveness of goats to a dominant cue in their environment. On the other hand, Chemineau et al., (1992) have shown that seasonal activity in temperate Alpine goats was unchanged when females were experimentally exposed to a simulated tropical photoperiod (Figure 4), showing insensitivity to different stimuli compared to the usual biotope of native goats. In contrast, María et al. (2011) have shown that, under natural conditions, does of different origin and genotypes (Alpine goat, Nubian and Criollo × Nubian), present a seasonal reproductive pattern similar to that of subtropical does in Mexico (22° N, Figure 4). Another example illustrating such adaptation is seen in sheep. It is known that the reproductive cycle begins in the northern hemisphere when daylength decreases and starts in the southern hemisphere when daylength increases. However, the transfer of ewes from southern to northern hemisphere induces a resynchronization of reproduction to the new northern location, starting breeding in autumn (Lofts, 1975). It can be concluded that, under natural environmental conditions, several factors are involved in the synchronization of breeding seasonality in goats.

CONCLUSION

It appears that the photoperiod is the main modulator of the seasonality of reproduction in goats in the different latitudes. Other cues such as seasonal changes in ambient temperature cycles, food availability, social interactions and genotype are also thought to modulate seasonality of reproduction in this species. As compared to other domestic animals, goats show a good adaptive plasticity, depending upon to the genotype, which allows it to anticipate climate changes to adapt its physiology, specifically that of reproduction.

Figure 4: Individual ovulatory activity in Alpine, Nubian and Criollo × Nubian female goats maintained under tropical latitude (22°N). Rectangles represent progesterone measurements and each line represents one doe (María et al., 2011)
REFERENCES


Muller C.J.C. (2005). Genetic parameter estimation and breeding plans for the South African dairy goat herd, PhD: Dissertation submitted to the Department of Animal Sciences, Faculty of Agricultural and Forestry Sciences, University of Stellenbosch, in partial fulfillment of the requirements for the degree.


