Environmental cues and seasonal patterns of reproduction in goats

H. FARSI[1], M. MHANI[1], M.R. ACHAÂBAN[1], R. BOUKHLIQ[2], A. TIBARY[3], K. EL ALLALI[1]

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Abstract

Goats usually exhibit a seasonal sexual activity and breeding at a specific season ensures the survival of offsprings 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 weathers 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.

Les facteurs environnementaux affectant la saisonnalité de la reproduction chez la chèvre

Résumé

La chèvre présente une reproduction saisonnière. Cette saisonnalité permet de coïncider la parturition avec la période adéquate de la nutrition et les conditions climatiques pour la survie de la progéniture. La présente revue analyse à travers les différents biotopes, les facteurs intervenant dans l'expression de cette saisonnalité de l'activité sexuelle chez cette espèce. Sous les différentes latitudes, la photopériode est le principal modulateur de cette saisonnalité chez la chèvre. D'autres facteurs environnementaux comme les changements saisonniers des cycles de la température ambiante semblent également induire un effet de synchronisation de cette saisonnalité. De plus, la disponibilité de la nourriture affecte de manière sensible la physiologie de la reproduction chez cette espèce. En effet, un état de bonne nutrition renforce le comportement sexuel chez la chèvre, alors que la sous-nutrition et en particulier un bilan énergétique négatif ont un impact négatif sur cette saisonnalité. D'autre part, l'interaction sociale chez cette espèce affecte également l'expression de la physiologie et le comportement sexuel pendant la saison de la reproduction. La chèvre présente une bonne adaptation à tous les biotopes, y compris les chauds, froids, humides et secs. Cette particularité semble dépendre du génotype et peut être cruciale pour une anticipation efficace des changements climatiques globaux.

Mots-clés: Chèvre, reproduction saisonnière, photopériode, température ambiante, disponibilité alimentaire, facteurs sociaux, génotype.

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.,*

[1] Comparative Anatomy Unit, Department of Biological and Pharmaceutical Veterinary Sciences, Hassan II Agronomy and Veterinary Institute, Rabat-Instituts, Rabat, Morocco
[2] Animal reproduction Unit, Department of Medicine, Surgery and Reproduction, Hassan II Agronomy and Veterinary Institute-Rabat, Rabat-Instituts, Rabat, Morocco
[3] Comparative Theriogenology, Department of Veterinary Clinical Science, College of Veterinary Medicine and Centre for Reproductive Biology, Washington State University
Correspondence: khalid_elallali@yahoo.fr, tibary@wsu.edu

1997). 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), and in the southern latitudes regions like Argentina (30ºS) (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 (Simplício *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 Lahlou-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 mutlisynaptic 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; Teclemariam-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 (Louw, 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 environments. The breeding season often starts when the ambient temperatures are low (Figure 1). This is important because ambient temperature affects hormonal pattern and folliculogenesis as stated above.

Most studies on the effect of ambient temperature focused on heat stress and reproduction, and like the photoperiod, ambient temperature exhibits seasonal changes that could be integrated by the nervous system. Indeed, it was suggested that the pineal indoles like 5-methoxytryptophol (5ML) were responsible for the possible effect of ambient temperature on reproduction (Vivien-Roels and Pévet, 1983). 5ML is secreted by the pineal gland and is capable of modifying sexual development and reproduction in several species, where this molecule exerts a remarkable effect on the gonads of mature and immature animals (Mullen *et al*., 1979). For example in chicks, it stimulates the development of the testes and ovaries, while in adults it shows anti-gonadal activity. 5ML has a circadian rhythm in both the pineal gland and serum which is in phase with that for melatonin, with high levels in the dark and low in the day (Mullen *et al*., 1979). The question of the effect of the seasonal variation in the light and the ambient temperature on reproduction through 5ML remains open for large animals like goats.

The seasonal message of the nocturnal peak of melatonin, which is able to inform the body about the season, is initially built from its daily and circadian rhythm. It's been demonstrated for the first time in the camel, that the daily variations in ambient temperature are able to induce a plasmatic rhythm of melatonin secretion (El Allali *et al*., 2013). This is evidence that the ambient temperature is a real Zeitegeber (Timer). This means that daily and seasonal biological rhythms such as reproduction could be synchronized by daily and seasonal cycles of ambient temperature. In a recent study, it was established as in the camel, melatonin in Moroccan goats is also driven by ambient temperature cycles (Farsi and El Allali; unpublished data). Ambient temperature and photoperiod have a synchronized pattern during the seasons of the year (Figure 1). Our recent work revealed that melatonin is higher when ambient temperature is low (El Allali *et al*., 2013). Thus, it seems that photoperiod and ambient temperature are agonists in their action; with reproduction being activated when photoperiod is short and ambient temperature is low.

EFFECT OF FOOD AVAILABILITY AND RAINFALL

In goats, besides photoperiod and probably ambient temperature, other environmental cues, such as rainfall and food availability, are likely to be involved in the control of the breeding season (Mani *et al*., 1996). Food availability, which is important for the offspring survival, is considered as an ultimate factor controlling the breeding season (Lofts, 1975; Gwinner, 1981). Other environmental cues, such photoperiod and temperature, are just proximate factors allowing the prediction of the best period of food availability and better climate 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

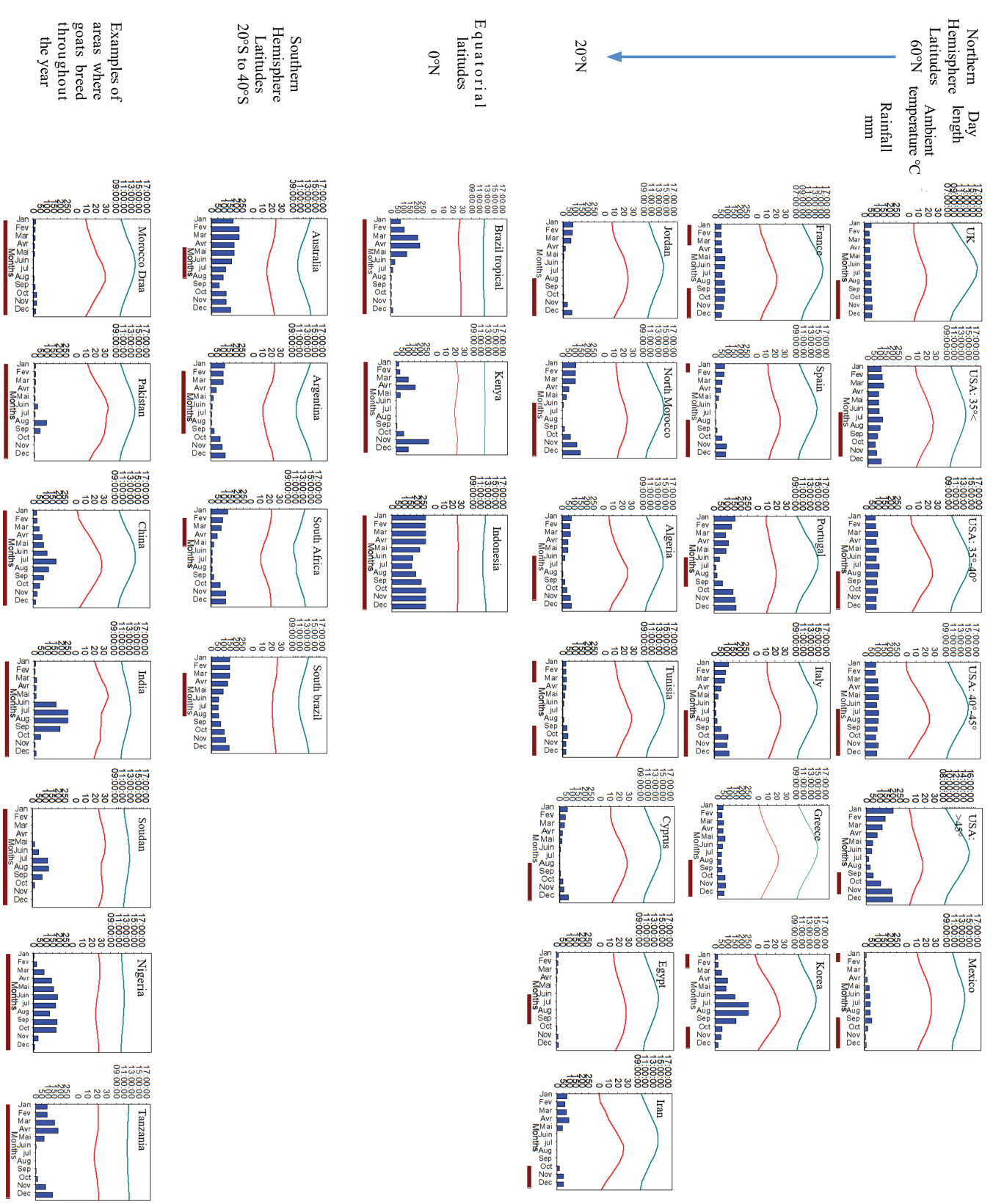

Figure 1: Distribution of the breeding season in goats (indicated by the red bar below each panel) as well as photoperiod (Green curve), ambient temperature (Brown curve) and rainfall (histograms). Examples of some non-seasonal goat breeds are also given. Data on the breeding season were obtained from 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).

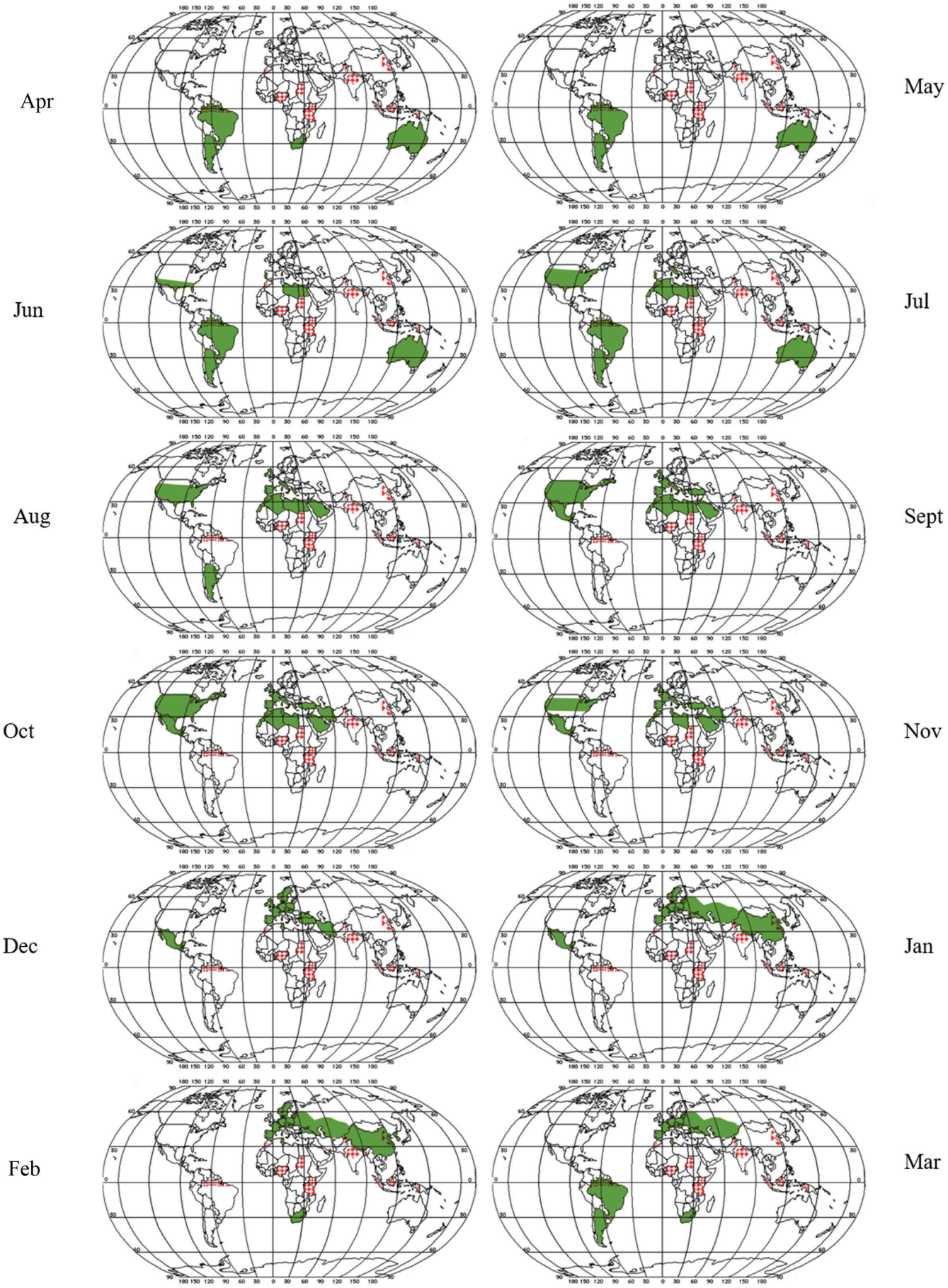

Figure 2: Monthly distribution of the seasonality of reproduction in the goats in some countries around the world (green color).The red dots indicate some areas where goats are not seasonal. (Countries shown on the maps correspond to the results of our literature search on the relevant goat breeding 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 insulinaemia 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

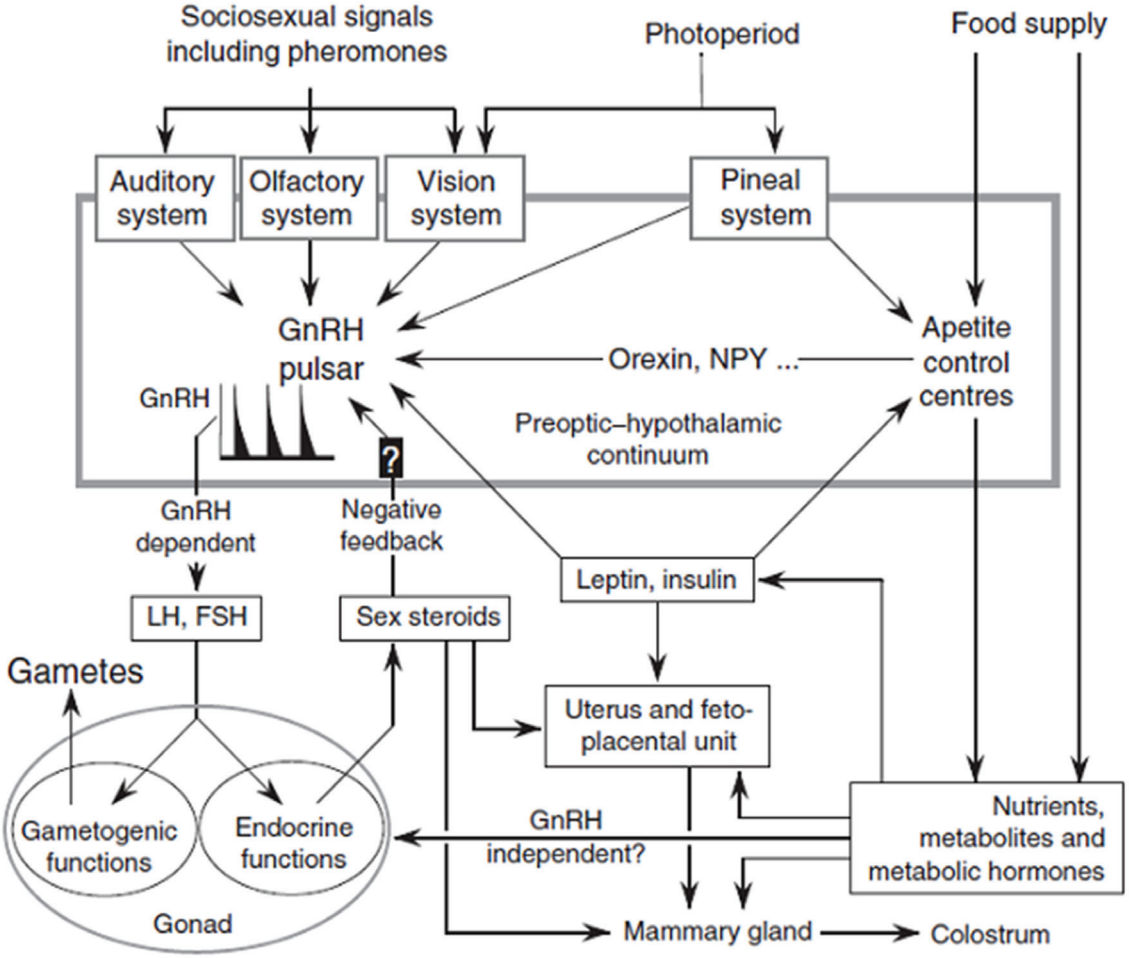

Figure 3: Environmental inputs into reproduction in small ruminants (Martin et al., 2004)

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 BIOTOPE 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.

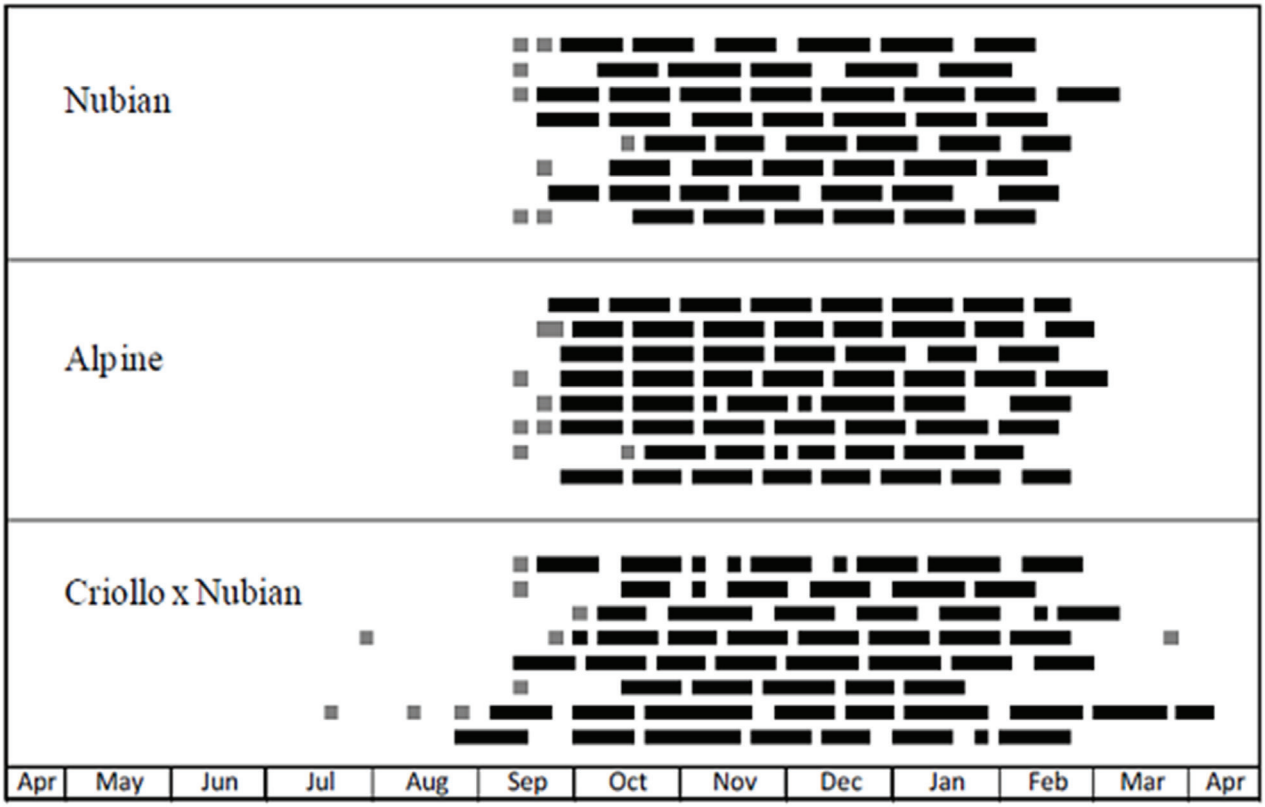

Figure 4: Individual ovulatory activity in Alpine, Nubian and Criollo × Nubian female goats maintained under tropical latitude (22°N). Rectangles represent progesterone measurements and each line represents one doe (María et al., 2011)

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