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REVIEW [REVISIÓN]

REPRODUCTIVE SEASONALITY AND ITS CONTROL IN SPANISH SHEEP AND GOATS

[ESTACIONALIDAD REPRODUCTIVA Y SU CONTROL EN RAZAS ESPAÑOLAS DE OVINOS Y CAPRINOS]

A. **Gómez-Brunet, J. Santiago-Moreno, A. Toledano-Diaz**
and A. López-Sebastián

Departamento de Reproducción Animal, INIA, Madrid, Spain. Tel: +341 3474028;
Fax: +341 3474014. E-mail: gomez@inia.es
** Corresponding author*

SUMMARY

Sheep and goat breeds from subtropical, middle and high latitudes show seasonal changes in reproductive activity. In general, the breeding season starts in autumn and ends in winter, with anoestrus in spring/summer. An endogenous circannual rhythm driven and synchronised by the annual photoperiod cycle regulates the onset and offset of the breeding season. However, the timing and duration of the breeding season can be affected by interactions between the photoperiod and factors such as breed, geographical origin, nutritional and lactational status, social interactions, and the season of parturition. Seasonality in reproduction is naturally accompanied by variation in the availability and price of meat, milk and cheese over the year, affecting the economy of farmers, consumers and the food industry alike. The control of reproduction outside the normal breeding season by inducing and synchronizing oestrus and ovulation plus the use of artificial insemination and/or natural mating would help ensure the year-round availability of products. This review describes the seasonal variation in the sexual activity of ovine and caprine species with special regard to local Spanish sheep and goats breeds, examines how the photoperiod regulates their annual reproductive cycle, and discusses a number of strategies that can be used to induce and synchronise ovulation outside the natural breeding season.

Keywords: sheep; goats; reproductive seasonality; photoperiod; melatonin; male effect; progesterone; $PGF_{2\alpha}$

RESUMEN

En zonas subtropicales así como en latitudes medias y altas, las diferentes razas de ovinos y caprinos muestran cambios estacionales de su actividad reproductiva. En términos generales, la estación reproductiva comienza en otoño y finaliza en invierno, con el período de anestro en primavera/verano, estando regulado el comienzo y final de la estación reproductiva por el ritmo endógeno circanual sincronizado por el fotoperiodo. Sin embargo el inicio y duración de la estación reproductiva puede estar afectado por la interacción del fotoperiodo con otros factores tales como la raza, origen geográfico, lactación y estado nutricional, interacciones sociales y época del parto. Estas variaciones estacionales de la eficacia reproductiva, se traducen en variaciones en la oferta de leche y carne a lo largo del año, afectando a los rendimientos económicos de los productores y los precios al consumidor. El control de la reproducción fuera de la estación reproductiva mediante metodologías de inducción y sincronización de la ovulación, ya sea aplicando inseminación artificial o cubrición natural, puede asegurar el mantenimiento de la oferta de estos productos, a lo largo del año. Esta revisión describe los cambios estacionales en la actividad reproductiva de ovinos y caprinos, con especial énfasis en las razas españolas, profundizando en cómo el fotoperiodo regula el ciclo reproductivo anual, y valorando diferentes estrategias que pueden ser utilizadas para la inducción y sincronización de la ovulación fuera de la estación reproductiva

Palabras clave: ovejas; cabras; estacionalidad reproductive; melatonina; efecto macho; progesterona; Prostaglandina $F_{2\alpha}$

INTRODUCTION

Many types of production systems are used around the world to raise sheep and goats. In Spain, there are some 19.8 million sheep and 2.9 million goats. Once raised by families for their own use, these animals now lie at the centre of a meat and milk industry of great economic importance to many parts of the country (Perez *et al*., 2007; Castel *et al*., 2010). Most Spanish goat farming is orientated towards milk production.

This is a particularly important activity in the regions of Andalusia, the Canary Islands and Castilla-La Mancha, where 72% of the country's dairy goats are concentrated. Sheep farming may be orientated towards meat or milk production, though some breeds are raised to provide both commodities. Spain's sheep flocks are concentrated in five regions: Castilla y Leon (21%), Extremadura (19%), Castilla-la Mancha (16%), Aragón (11.4%) and Andalusia (12.1%) (Spanish Ministry for Agriculture, Food and Fisheries, 2009). At Spanish Mediterranean latitudes (36-42ºN), the local sheep and goats are seasonal breeders (Forcada *et al*., 1992; Gómez-Brunet *et al*., 2003, 2008; Zarazaga *et al*., 2005). The reproductive season generally extends from summer/autumn to the end of winter, with the anoestrous period in the spring months. This leads to marked seasonal variation in the availability of meat, milk and cheese, as well as fluctuations in the price of these products, a problem that affects the economies of farmers, the food industry and consumers alike. Inducing and synchronizing ovulation outside of the natural breeding season, in conjunction with natural mounting or the use of artificial insemination (AI), might allow farmers to stabilise production year round. Knowledge of the reproductive characteristics of local breeds and the identification of the environmental factors that influence the timing of their annual breeding season, would allow breeding strategies to be adapted to local environmental, economic and social needs.

This review describes the seasonal variation seen in the sexual activity of sheep and goats with special regard to local Spanish breeds, taking into account the environmental factors - especially the photoperiod - that influence this. In addition, three approaches used to control reproductive activity and to optimise fertility in local Spanish breeds are examined: 1) the use of melatonin implants combined with the male effect, 2) the use of the male effect in combination with progesterone (P4) and $PGF_{2\alpha}$ administration, and 3) the use of the male effect in combination with $PGF_{2\alpha}$ administration.

REPRODUCTIVE SEASONALITY

In 1784, the Italian Biologist Lazzaro Spallanzani wrote: *It is well known that almost all animals, except man, have a stated season for the propagation of their species*. The restriction of breeding activity to a certain time of year is a common feature in mammalian species living outside of the tropics. This is commonly viewed as having a genetic basis and to reflect the optimisation of different phenotypes to their environments (Bronson, 1989). Seasonal reproductive rhythms in wild mammalian species reflect adaptations to changes in temperature and food availability that ensures birthing occurs at the time of year optimal for the survival of newborns. Wild ruminant species have a short annual period of sexual activity (breeding season) followed by a long period of inactivity (anoestrous season) (Santiago-Moreno *et al*., 2006; Gómez-Brunet *et al*., 2010b). In domestic species, however, normal environmental pressures have become much reduced and the duration of the period of sexual activity has expanded (Hafez, 1952).

Sheep and goats were first domesticated some 10,000 years ago. Originating from a few wild goat and sheep ancestor varieties in the region of today's Iraq, Iran, Syria and eastern Turky (Zeder and Hesse, 2000), hundreds of different breeds have been developed that differ from their wild cousins in many aspects of their reproductive physiology (Shechel, 1992). Breeds originating from high latitudes and colder climates have a shorter breeding season than those from nearer the tropics. Although the photoperiod is the main environmental cue influencing this seasonality, a genetic basis for photoresponsiveness has been demonstrated (Poulton and Robinson, 1987). Thus, a wide range of periods of breeding activity may be observed between and even within breeds.

Reproductive seasonality in sheep

Ewes are seasonally polyoestrous, and their reproductive activity is characterised by the alternation between breeding and anoestrous periods. The breeding season is characterised by a succession, at regular intervals of 16-17 days, of oestrus behaviour and ovulation, while an arrest of cyclic ovulatory activity occurs during the anoestrus period (Rosa and Bryant, 2003). The change in day length is the main environmental factor regulating seasonal breeding (Karsch *et al*, 1984; Malpaux *et al*., 2001). Maximum reproductive activity is associated with short days, with the highest percentage of ewes displaying oestrus and ovulatory activity during the late summer, autumn and early winter.

Breeds of tropical and subtropical origin, those from the Mediterranean area, and those with Merino ancestry, have longer breeding seasons than those from higher temperate latitudes (Hafez, 1952). For breeds originating at latitudes of >40ºN, the breeding season starts in the early autumn when days are becoming shorter, and ends in mid-winter when day length is again increasing. Ovulation then ceases, and the animal remains anovulatory during the long days of spring-summer (Ortavant *et al*., 1985). In the UK (at 56ºN), the ewes of British sheep breeds, such as the Finnish Landrace and the Scottish Blackface, show marked seasonality, with anoestrus lasting from March/April to October, a period during which no ewe ovulates spontaneously (Wheeler and Lands, 1977). In France (at 45ºN), the breeding season of Île de France ewes starts in August and last until February, although some females show isolated ovulation events during the anoestrus season (Thimonier and Mauleon, 1969). In contrast, sheep breeds raised in subtropical (around 24ºN-34ºN; 24ºS-34ºS) or tropical areas (23ºN-23ºS) perceive no strong seasonal changes in photoperiod cues, and generally have a long breeding season: in fact they may cycle all year around and show no anovulatory period (Yenikoye, 1984; Gonzalez *et al*., 1992; Arroyo *et al*., 2007). In these breeds, seasonal reproduction may have evolved in response to seasonal rainfall patterns or nutritional conditions (Thimonier *et al*., 1986).

Breeds of sheep from middle latitudes (35-40ºN), such as the Australian Merino and the Mediterranean breeds, have a short anoestrus period during which a variable proportion of ewes ovulate spontaneously. In Spain, most of the local sheep breeds show reduced seasonality, displaying a long breeding season (summer to winter) and a short anoestrus period of some 3-4 months, generally in the spring, during which some 15-30% of ewes remain cycling (Valls Ortiz, 1983). Measuring progesterone (P4) concentrations by radioimnmunoanalysis (RIA) in peripheral blood samples collected twice per week over a year, allowed characterizing the extension of the breeding season and the length of postpartum anoestrus in a number of local Spanish sheep breeds. For example, under natural environmental conditions at 40ºN, Spanish Manchega ewes experience a long breeding season with cyclical ovulatory activity from early July to mid-March. Thereafter, they experience an anoestrus period of about 111 days from March to June, with some ewes showing isolated ovulations during the anoestrus period (Figure 1A). (Gómez-Brunet and López Sebastián, 1991; Santiago-Moreno *et al*., 2000c; Gómez-Brunet *et al*., 2008). Reduced seasonality is also apparent in the Rasa Aragonesa (at 41ºN) and Merino (at 39ºN) breeds, with 3-4 months anoestrus from March to May/June (Forcada *et al*., 1992; Gonzalez-López, 1993; Folch and Alabart, 2000).

Although seasonal reproduction is mainly regulated by photoperiod, many other factors including breed, nutritional and lactational status, social interactions and the season of parturition, may interact with it to modulate its effect and thus influence the timing and length of the breeding season (Pope *et al*., 1989; Ungerfeld *et al*., 2004; Forcada *et al*., 2006). For example, in Manchega ewes, the onset of the natural breeding season is affected by the lambing season (Gómez-Brunet *et al*., 1992; Santiago-Moreno *et al*., 2000b). When lambing occurs in June or November, Manchega ewes experience their first postpartum ovulation within the same breeding season, about 30 days after parturition, and daily or weekly weaning does not advance the beginning of the ovulatory activity (Gómez-Brunet *et al*., 1992). In contrast, in ewes that lamb in April, postpartum anoestrus extends into the long days of spring, overlapping with seasonal anoestrus. Thus, the lambing-to-ovulation interval lasts about 112 days. All the ewes initiate cyclicity from 30 June to 17 August, coinciding with the beginning of the breeding season for this breed. Further, in a study performed under field conditions involving Manchega, Churra and Latxa ewes from commercial flocks in central and northern Spain, it was reported that the longest intervals between parturition and the onset of ovulation occurred at 150 days, when ewes lambed at the end of the breeding season (January-February) (López-Sebastián *et al*., 1991). In contrast, when lambing occurred between June and November, the first ovulations started just 24-36 days after lambing.

It has been shown that the length of seasonal anoestrus can be reduced by approximately two months in mature Rasa Aragonesa ewes when these are maintained in good body condition (body score condition [BCS] 2.8 rather than 2.3) (Forcada *et al*., 1992). In spring-born Manchega and Merino lambs, the failure to grow to appropriate body weight leads to the maintenance of the prepuberal anovulatory condition until the beginning of the next breeding season. Only lambs reaching 69.6 % and 60.1% respectively of their mean adult weight start cyclical activity in their first breeding season (López-Sebastián *et al*., 1985b: Santiago-Moreno *et al*., 2000a; Gómez-Brunet *et al*., 2010a).

In temperate regions, rams also show seasonal changes in their sexual behaviour, testosterone secretion, testicular weight, and sperm quantity and quality (Ortavant *et al* 1985), although these changes are less pronounced than those experienced by ewes. Values for the above variables are high at the end of the summer through autumn, falling greatly by the end of winter and remaining low during spring (Ortavant *et al*., 1985). The testicular volume of local Greek breeds follows a clear seasonal trend, with maximum and minimum volumes in July-August and February-April respectively (Avdi *et al*., 2004). The males of Spanish breeds (e.g.,Merino, Churra, Latxa) also show reproductive seasonality in testosterone secretion and sperm quantity and quality (Beltran de Heredia and Gabiña, 2004; Santiago-Moreno *et al*., 2005; Mazariegos *et al*., 20110; Figure 2). In the Merino (a not very seasonal breed) rams, the highest levels of testosterone and maximum testicular diameter occur during summer (from June to August). However, these rams show limited annual fluctuations in the size of their accessory glands (vesicular and bulbourethral glands) (Santiago-Moreno *et al*., 2005), in agreement with the relatively constant ejaculate volumes seen year round (Gonzalez-López, 1995). In this breed, high levels of testosterone coincide with the onset of cyclical ovulatory activity in the ewes, helping to ensure the success of sexual activity.

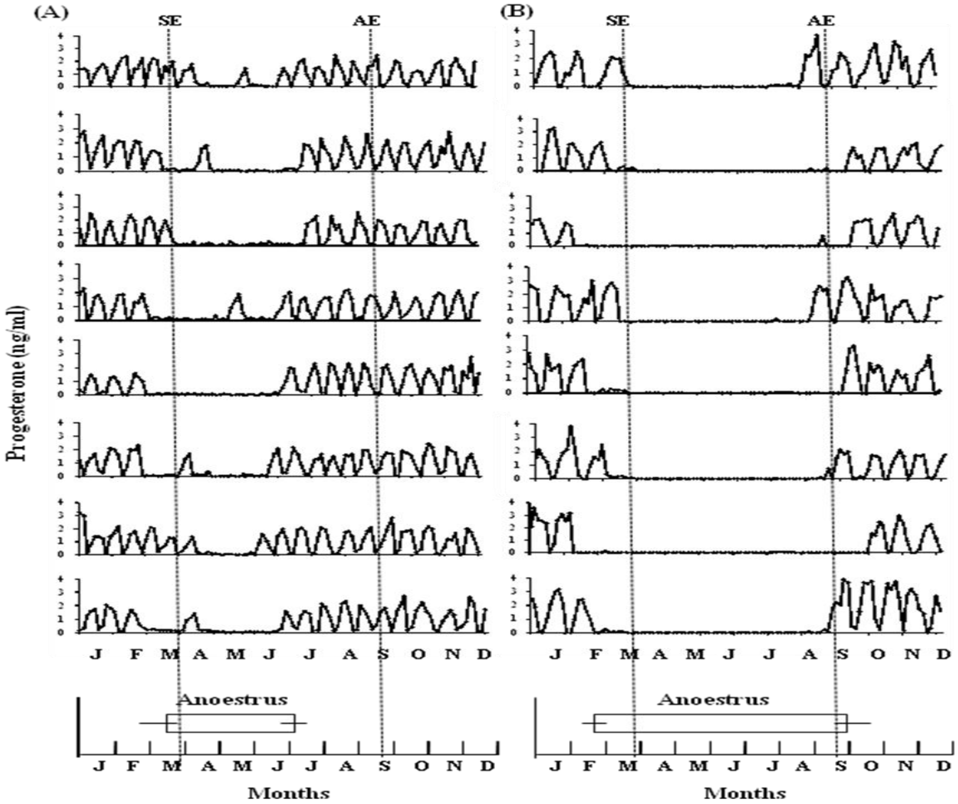


Figure 1. Annual changes in ovulatory activity in Manchega ewes (A) and Malagueña goats (B) raised at Mediterranean latitude (36-40ºN) and maintained under natural photoperiod conditions (Adapted from Gómez-Brunet et al., 2003; 2008).

Reproductive seasonality in goats

Reproductive seasonality is observed in all temperate goat breeds (Shelton, 1978; Chemineau *et al*., 1992a), and in some local breeds adapted to or originating from subtropical latitudes (Rivera *et al*., 2003; Duarte *et al*., 2008). Goats alternate annually between two distinct seasons: the sexual season characterised by a regular succession of oestrus activity and ovulation about every 21-22 days, and an anoestrus season characterised by the total absence of sexual activity. In most goat breeds, the breeding season occurs in the autumn/winter, and the anoestrus period in the spring/summer. However, great variability exists between and within breeds in terms of the timing and duration of the seasonal reproductive cycle, depending on geographic origin. For example, in France (at 46ºN), the frequency of ovulation in Alpine dairy goats varies from 0% between March and September to 100% between October and January, reflecting a long period of anoestrus (Chemineau *et al*., 1992a). In Australia (at 39ºS), Cashmere goats have a short period of ovulatory activity in autumn and winter (April to August) (Restall, 1992). In subtropical Creole goats in Argentina (at 30ºS) the breeding season extends from February/March to September, while anoestrus occurs during the months of October to January (Rivera *et al*., 2003). In goats adapted to the subtropical conditions of northern Mexico (at 26ºN), the breeding season lasts from September to February and the anoestrus season from March to August, with some goats having one or two isolated ovulations in June or July (Duarte *et al*., 2008). In other goats originating from tropical and subtropical environments, reproductive seasonality is less marked and some local breeds have just a short anoestrous period or breed all year around (Chemineau, 1986). In Chile, local goats experience only three months of anoestrus in late spring and early summer (Santa Maria *et al*., 1990), while Boer goats in South Africa experience oestrous activity all year round, with the highest percentage in oestrous in the autumn (Greyling, 2000).

In the Mediterranean regions of Spain (36-40ºN), ovulatory activity over the year has only been accurately studied in Malagueña and Payoya breeds (Gómez-Brunet *et al*., 2003, 2010c; Zarazaga *et al*., 2005). The measurement of plasma progesterone concentrations in blood samples collected twice a week showed the existence of a marked seasonality in cyclical ovulatory activity over the year. In Malagueña goats, onset and offset occur in late September/early October and February respectively (Figure. 1B). Thereafter, these animals experience a long anoestrus period (March to September) during which no ovulation occurs (Gómez-Brunet *et al.*, 2003; 2010c). In Payoya goats, the mean dates for the onset and end of ovarian activity are August 28 and January 29 respectively. In this breed, the anoestrus period occurs between February and August (Zarazaga *et al*., 2005). In Murciano-Grandina goats, Falagan *et al*. (1989) have described an anoestrus period from March to June, but provide no information regarding the onset of the breeding season. Most Spanish goats live at similar latitudes and are subjected to similar management production systems; thus it is very probable that the reproductive seasonality of other Spanish goat breeds. e.g., Florída, Verata, Blanca Celtibérica, are very similar to that of Malagueña and Payoya goats. Interestingly, while reproductive seasonality in Spanish sheep breeds differs widely from that seen in breeds from higher latitudes, the pattern of reproductive seasonality in Spanish goats is very similar to those reported in goats from other latitudes (Restall, 1992; Chemineau *et al*., 1992a; Duarte *et al*., 2008).

Like rams, bucks from temperate regions show marked seasonal variation in their reproductive activity (Ortavant *et al*., 1985). For example, in Alpine and Saanen bucks maintained at 46ºN, the reduction in day length in autumn is accompanied by an increase in testosterone secretion, an increase in the libido, and an increase in quantitative and qualitative sperm production (Delgadillo *et al*., 1991; Delgadillo and Chemineau, 1992). In males from subtropical Mexico (at 26ºN), testicular weight, testosterone secretion and semen quality and quantity vary seasonally, with higher values during the breeding season (May/June - December/January) (Delgadillo *et al*., 1999). In local Greek bucks (at 40-42ºN), testosterone secretion is low from January to May, and high from June to November (Todini *et al*., 2007). The males of Spanish breeds (e.g., Murciano-Granadina, Verata, Malagueña, Florída) from southern Spain (36-38º N) also show reproductive seasonality (Figure 3), but in contrast to those from higher latitudes, maximum testicular activity (testicular diameter and testosterone secretion), sexual behaviour (measured as reaction time) and semen production occur in spring/early summer (April-July), with minima in autumn/winter (Roca *et al*., 1991, 1992; Perez and Mateos, 1994, 1996; Arrebola *et al*., 2010). The ancestral practice of reproductive activity management in these Mediterranean areas is based on the use of the male effect in April-May-June. At this time, males have sufficient libido and produce enough sperm to mate successfully with the females. This contrast to the goat management at higher latitudes (for example, in France at 46º) and at subtropical latitudes of Mexico (26ºN) where the males need light treatment to encourage sexual activity to induce in the females synchronous ovulations outside of the breeding season oestrus (Delgadillo *et al*., 2001; Chemineau *et al*., 2008).

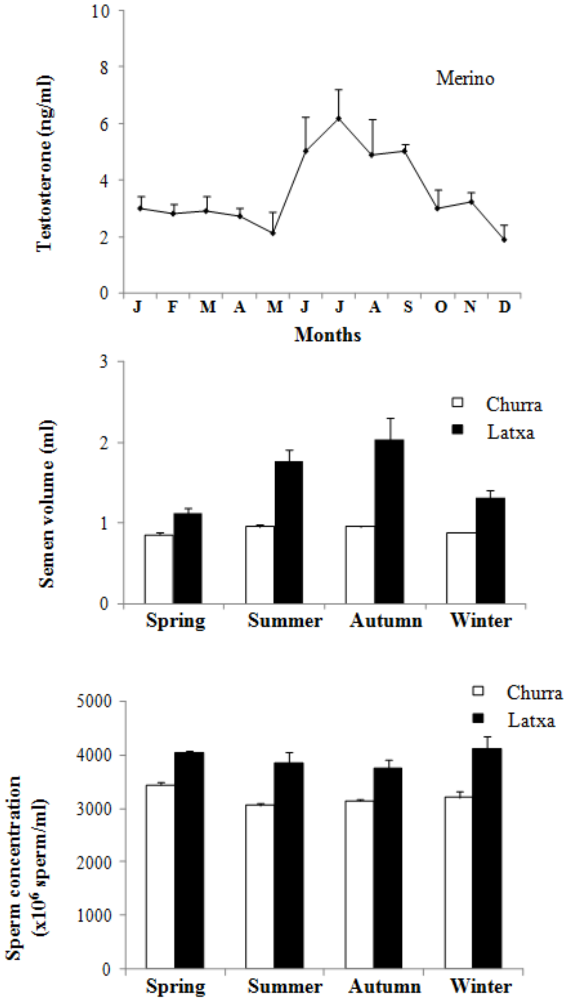


Figure 2. Seasonal changes (mean ± SEM) in testosterone secretion, semen volume and sperm concentration in different Spanish sheep breeds (Adapted from Beltran de Heredia and Gabiña, 2004; Santiago-Moreno et al., 2005; Mazariegos et al., 2010).

As in sheep, the photoperiod is the main factor controlling reproductive seasonality in goats (Malpaux *et al*., 2001; Chemineau *et al*., 2008). However, nutritional status and sociosexual factors can interact with the photoperiod and modulate reproductive activity in both sexes (Walkden-Brown *et al*., 1999; Scaramuzzi and Martin, 2008). For example, in Spanish Payoya goats, the anoestrus period is reduced by one month in animals fed at maintenance level compared to those fed over twice the maintenance level. The shorter anoestrus of does on the better diet is due to both delayed entry into anoestrus and an earlier resumption of ovarian cyclicity (Zarazaga *et al*., 2005). In this breed, the response of luteinizing hormone (LH) secretion to photoperiod variation is modified by the feeding level such that nutritional deprivation reduces secretion of pituitary LH, which in turn leads to anovulation and anoestrus (Zarazaga *et al*., 2011a,b). In bucks, a higher feeding level does not modify the onset or the end of reproductive activity (as measured by changes in testosterone secretion), but sexual behaviour in late spring is improved (Zarazaga *et al*., 2009b). In subtropical does a high nutrition level increases reproductive activity during anoestrus (Urrutia-Morales *et al*., 2009).

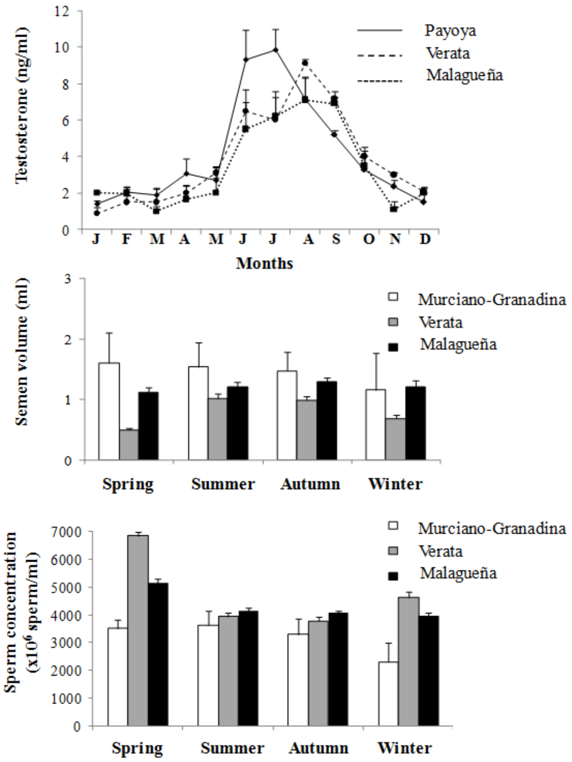


Figure 3. Seasonal changes (mean ± E.S.M) in testosterone secretion, semen volume and sperm concentration in different Spanish goats breeds (Adapted from Perez and Mateos, 1994; 1996; Arrebola et al., 2010; Gómez-Brunet et al., unpublished data).

PHOTOPERIODIC CONTROL OF THE CIRCANNUAL REPRODUCTIVE RHYTHM OF SHEEP AND GOATS: REFRACTORY STATES AND ENDOGENOUS RHYTHMS

Sheep and goats are considered short-day breeders since, under natural environmental conditions, reproductive activity begins during the shortening days of late summer and early autumn, and ends during the lengthening days of late winter and early spring (Hafez, 1952), Further, under artificial conditions, short days (SD) stimulate reproductive activity while long days (LD) inhibit it (Chemineau *et al*., 1992b.). The photoperiod has been shown the main factor driving the annual reproductive cycle in these species. This was achieved by subjecting them to numerous and varied light–controlled experiments using inversion of the annual photoperiod cycle, the use of 2-3 month alternating SD/LD treatments, the acceleration of annual photoperiod changes, medium-term maintenance under a constant LD or SD photoperiod (which induce refractoriness), and long-term maintenance under constant LD or SD photoperiods (to verify the existence of an endogenous circannual rhythm of reproduction) (Malpaux *et al*., 2006).

Regardless of the light regimen followed, the pineal gland regulates the change in the reproductive function via its endocrine activity, which is synchronised by the dark-light cycle. Photoperiod information perceived by the eyes is transmitted via a multi-synaptic pathway to the pineal gland, where the light is translated into a daily cycle of melatonin secretion characterised by high levels of secretion at night and low levels during the day (Arendt, 1998). The duration of the nocturnal secretion of melatonin, reflecting the length of the night, regulates the pulsatile secretion of gonadotropin releasing hormone (Gn-RH) from the hypothalamus. In sheep, long-duration melatonin presence (SD) stimulates the Gn-RH system and LH. Thus, changes in Gn-RH secretion induce corresponding changes in LH secretion, in turn determining the presence or absence of ovulation in the female and sexual activity in the male (Karsch *et al*., 1984; Malpaux *et al*., 2001; Chemineau *et al*., 2010).

In general, mammals regulate their reproductive responses to seasonal change via two mechanisms: through a direct response to changes in the photoperiod, or through an endogenous circannual rhythm synchronised by photoperiod cues. Studies in sheep (Karsch *et al.*, 1989) have shown that each reproductive transition is generated endogenously – the reflection of a circannual reproductive rhythm synchronised by photoperiod. In addition, in many seasonal species it has been shown that the specific effects of SDs and LDs are not permanent, and that photorefractoriness occurs when animals are subjected to a constant photoperiod, with spontaneous reversion of the reproductive physiological condition to the previous photoperiodic state (Lincoln *et al*., 2005).

Endogenous reproductive rhythm in sheep

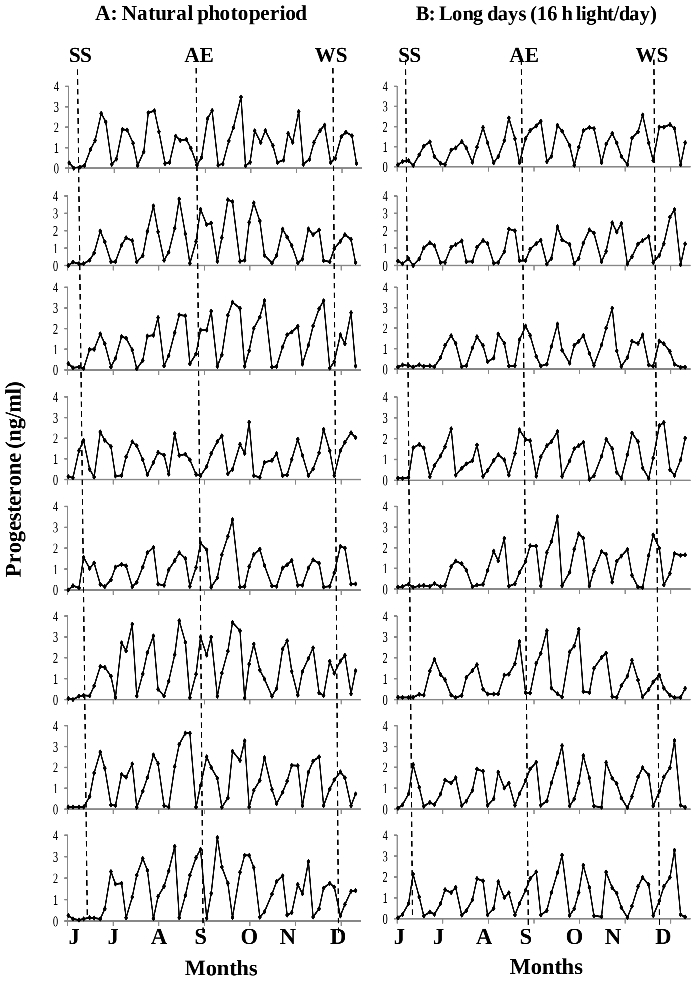
In sheep from higher temperate latitudes, refractoriness to inhibitory LD and stimulatory SD photoperiods plays a central role in regulating seasonal reproductive transitions (Karsch *et al*., 1986). In fact, artificially constant SDs from the winter solstice onwards do not prevent the breeding season from ending (Robinson and Karsch, 1984; Malpaux et al., 1987), nor do artificial constant LDs from the summer solstice onwards prevent the onset of the breeding season (Robinson *et al*., 1985). In highly seasonal sheep breeds, the existence of an endogenous reproductive rhythm is supported by studies in which ewes were exposed to constant short (8h light/day) or long days (16h light/day) or an equinoctial (12h light/day) photoperiod over a long period; the animals alternated between periods of sexual rest and sexual activity (Karsch et al., 1989). Indeed, the annual reproductive cycle is the product of an endogenous circannual rhythm that is not directly driven by the photoperiod. However, it is synchronised by it through its control of the circadian rhythm of melatonin secretion (Woodfill *et al*., 1994). The duration of elevated melatonin levels over the long days of spring-summer provides the signal for day length to synchronise the rhythm of reproductive neuroendocrine activity, allowing reproductive activity to commence in the autumn (Malpaux *et al*., 1989; Barrell *et al*., 2000). The ever shorter days between the summer solstice and the autumn equinox are the critical signal involved in timing the end of reproductive activity in mid-winter (Malpaux *et al*., 1988) which contributes to ensuring the proper duration of the breeding season (Malpaux and Karsch, 1990; O'Callaghan *et al*., 1991a).

As mentioned earlier, Spanish Mediterranean sheep breeds have a long breeding season. However, the extent to which these breeds use the photoperiod to regulate their annual reproductive cycle remains unclear. To address this, our group examined whether refractoriness to long and short days in Spanish Manchega sheep, which show reduced seasonality, determines the onset and the end of the breeding season respectively, as occur in highly seasonal breeds. Ovulatory activity was monitored via the measurement of plasma P4 (collected twice per week) in intact Manchega ewes exposed to artificial LDs (16 h light/day) from the summer to the winter solstice (June to December), to simulated SDs (Melatonin implants) from the winter to the summer solstice (December to June), or maintained under natural photoperiod (NP) conditions for 40ºN (from 10 h 17' to 16 h 3' light per day from the winter to summer solstice). The LD Manchega ewes responded similarly to sheep breeds from higher latitudes studied by Robinson *et al*. (1985). The onset of seasonal ovulatory activity occurred at the same time in ewes maintained under constant LDs as in those under NP conditions (16 and 5 July respectively; Figure 4) (Gómez-Brunet *et al*., 2008). Interestingly, in the SD ewes, two animals, showed continuous cyclical ovulatory activity over the course of the experiment, while the six remaining ewes entered anoestrus two months later than their natural photoperiod counterparts (16 May and 15 March, respectively; Figure 5). (Gómez-Brunet *et al*., 2001). Indeed, the SD Manchega ewes responded differently to highly seasonal SD ewes raised at high latitudes (>52ºN) (Robinson and Karsch, 1984; Malpaux *et al*., 1987), but in a fashion similar to less seasonal ewes kept at 39-40ºN (Minton, 1990). Altogether, these results show that in Spanish Manchega sheep, refractoriness to LDs regulates the onset of the breeding season, as it does in highly seasonal sheep breeds from higher latitudes. However, also indicate that in less seasonal breeds, refractoriness to SDs might not be the most important physiological mechanism regulating the onset of anoestrus (unlike in highly seasonal breeds). Differences in seasonality among sheep breeds might therefore be related, at least in part, to the degree to which refractoriness to short days governs the transition into anoestrus.

Refractoriness is conceptually considered to be the first step in the expression of an endogenous circannual reproductive rhythm (Malpaux *et al*., 2006). Thus, in a second study, we determined the ovulatory activity (via the measurement of plasma P4 concentrations collected twice per week) in two groups of intact Manchega ewes subjected to either a constant photoperiod of LDs (16 h light/day) or NP conditions for 40ºN for 16 months, between June (Year 1) and October (Year 2). As expected, under the NP conditions the ewes showed well–defined seasonality in their cyclical ovulatory activity (Figure 6A). During the first year all females showed ovarian cycles from July to March; thereafter, they experienced an anoestrus period of 112 days, before starting cyclicity again by July in Year 2. The LD ewes also showed seasonal variation in their ovulatory activity but the timing of these changes was profoundly modified by the photoperiod treatment (Figure 6B). In these animals, the onset of ovulatory activity in the first year of study was no different to that seen in their NP counterparts (July 2 and 3 respectively). However, the end of ovarian cyclical activity, and the subsequent behaviour of these animals in the following cycle, differed. Five ewes ended cyclical ovulatory activity between December 21 and February 18 in Year 1; then, after an anoestrous period of about 196 days, four of these animals started ovarian cycles by May 23 before stopping again by August 31 (Year 2), and then remaining anoestrous until the end of the experiment. The other three ewes showed continuous cyclical ovulatory activity during the first year of the study but stopped cyclicity by July of the second Year. Thereafter, one of the ewes experienced progesterone cycles at irregular intervals until September before becoming definitively anoestrous, while the other two remained anoestrous for 153 days from July until the end of the experiment (Figure 6B). These results show that Spanish Mediterranean breeds of sheep, with their reduced seasonality, appear to use an endogenous circannual rhythm to generate their reproductive transitions (Gómez-Brunet *et al*., 2008), as do highly seasonal breeds from higher temperate latitudes. However, in the Spanish breeds, the circannual ovarian reproductive cycle is differently expressed, and they are much more sensitive to changes in the photoperiod than breeds of higher latitudes. The long days of spring may be critical for resetting the endogenous reproductive rhythm of Spanish Mediterranean sheep breeds, as they are in breeds from higher temperate regions (Malpaux *et al*., 1989; Barrell *et al*., 2000), but with a shorter lag time (about 3-4 months shorter) between the perception of the photoperiod signal and the onset of the breeding season.

Endogenous reproductive rhythm in goats

In goats from temperate, subtropical and Mediterranean latitudes, it is well established that artificial LDs inhibit and artificial SDs stimulate reproductive activity (Bisonnette 1941; Chemineau *et al*., 1992b; Delgadillo *et al*., 2004; Duarte *et al*., 2010; Zarazaga *et al*., 2011a). In Spanish Payoya goats, the mean intervals between the shift from long to short days, and from short to long days, to either stimulate or inhibit ovulatory activity (measured by determining plasma LH concentrations in ovariectomised does subcutaneously treated with a constantly-releasing oestradiol 17β implant [OVX+E]) are approximately 66 and 22 days respectively (Zarazaga *et al*., 2011a). These intervals are shorter than those described for Saanen dairy goats from higher temperate latitudes (Chemineau *et al*., 1986), probably due to breed differences.


A: Natural photoperiod

B: Long days (16 h light/day)

Figure 4. Ovulatory activity of Manchega ewes raised at latitude 40º 25'N maintained either under the natural photoperiod (A) or long days (16 h light/day) (B) between June 22 and December 31. WS = winter solstice; SS = summer solstice; AE: autumn equinox (Adapted from Gómez-Brunet et al., 2008).

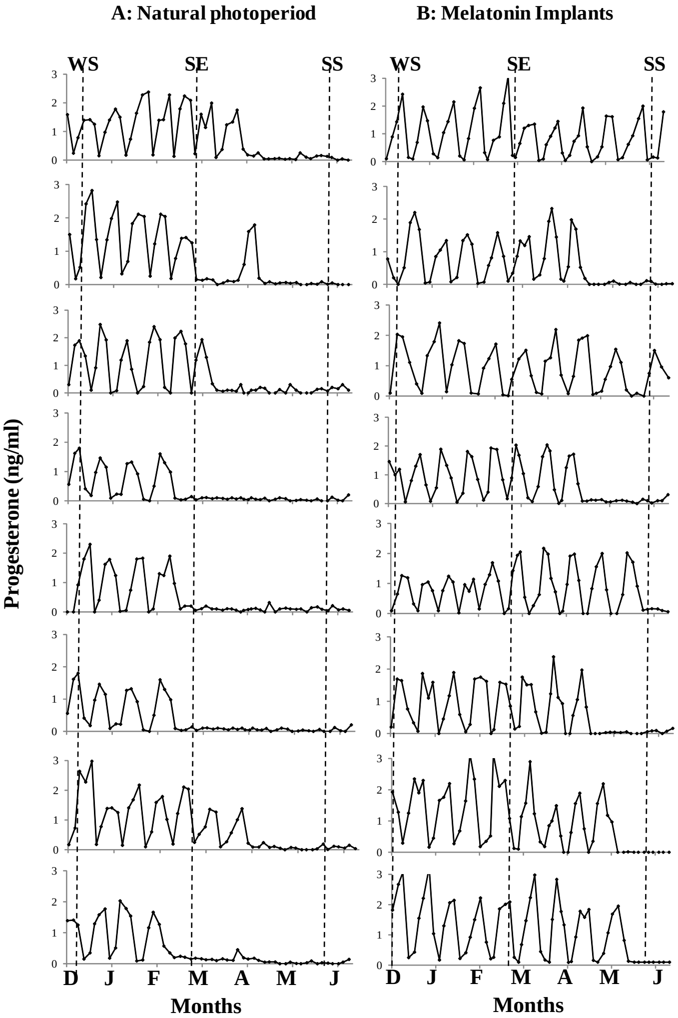


Figure 5. Ovulatory activity of Manchega ewes raised at latitude 40º 25'N and maintained under the natural photoperiod (A) or implanted with melatonin (to simulate a short day photoperiod) between December 23 and June 30. WS = winter solstice; SS = summer solstice; AE: autumn equinox (Adapted from Gómez-Brunet et al., 2001).

In contrast to ewes, which show important variations in their seasonality depending on breed and latitude of origin, most goat breeds are strongly seasonal irrespective of their origin. In the Mediterranean area, differences exist between sheep and goats in terms of the timing and duration of the seasonal reproductive cycle, with a more restricted breeding season seen in does (Mascarenhas *et al.*, 1995; Gomez-Brunet *et al.*, 2003; Zarazaga *et al.*, 2005) than sheep (Forcada *et al.*, 1992; Avdi *et al.*, 1993; Gómez-Brunet *et al.*, 2008). Although studies on the physiological mechanisms underlying the photoperiodic control of seasonal breeding activity in does have been limited (BonDurant *et al.*, 1981; Gebbie *et al.*, 1999), it is likely that, under natural environmental conditions, each reproductive transition is generated endogenously as the reflection of a circannual reproductive rhythm synchronised by photoperiod in a fashion similar to that seen in ewes. To identify the mechanisms involved in the photoperiodic control of the seasonal cycle of ovulatory activity in Spanish goat breeds, cyclicity was determined in Malagueña does exposed to the same artificial photoperiod conditions as described above for Manchega ewes. In an initial study to determine whether the onset of the breeding season results from refractoriness to the inhibitory effects of LDs, and to determine whether the end of the breeding season results from refractoriness to the stimulatory effects of the SDs, does at 40ºN were maintained under NP conditions, or exposed to artificial constant LDs (16 h light/day) from June to December, or received a series of subcutaneous melatonin implants (MI) from December to June to mimic an SD signal. The results showed that the onset of seasonal cyclical ovulatory activity in intact does maintained under constant LD at the summer solstice did not prevent the onset of the breeding season, which occurred at the same time as in the goats kept under the NP conditions (October 3 and September 23 respectively; Figure 7). Further, treatment with melatonin implants from the winter solstice onward did not prevent the end of the breeding season; these SD does became anoestrous at the same time as their counterparts under NP conditions (March 1 and February 23 respectively; Figure 8). Thus, the onset of cyclic ovulatory activity in Malagueña goats is not driven by decreasing day length from the summer solstice onward, and increasing day length after the winter solstice is not the signal required for the end of ovulatory cyclicity (onset of anoestrus). These data support the idea that, as in goat breeds originating from or adapted to either northerly (52ºN) or subtropical (26ºN) latitudes (Gebbie *et al*., 1999; Delgadillo *et al*., 2011), refractoriness to LDs and SDs regulates the transition between breeding and anoestrus in Spanish goats (Gómez-Brunet *et al*., 2010c).

In a second study, variations in the ovulatory activity of Malagueña goats subjected to either a constant LD photoperiod or the NP conditions at 40ºN for two years, were examined to evaluate whether, as in sheep, an endogenous circannual rhythm is involved in regulating seasonal changes in reproductive activity. As expected, the NP Malagueña goats showed marked seasonality in their ovulatory activity (Figure 9A), which lasted from September to February as preoviusly recorded (Gómez- Brunet *et al*., 2003; 2010c). The LD experimental goats also expressed alternating periods of ovulatory/anovulatoy activity over the course of the study, but these periods varied greatly with respect to those seen in the NP goats (Figure 9B; Gómez Brunet *et al*., unpublished). Therefore, in Malagueña goats also an endogenous rhythm that, irrespective of the photoperiod, appears to be responsible for reproductive transitions under natural conditions, thus allowing them to initiate their reproductive rhythm in the early autumn and finish in winter.

The results of our studies on the role of photoperiod in regulating seasonal reproduction in Spanish Mediterranean sheep and goats, which show marked species-specific differences in their seasonal reproductive patterns (ewes begin their ovarian cycles three months earlier than goats), suggest that both possess an endogenous rhythm responsible for reproductive transitions that does not rely of the natural photoperiod. However, these rhythms are differently expressed in the two species..

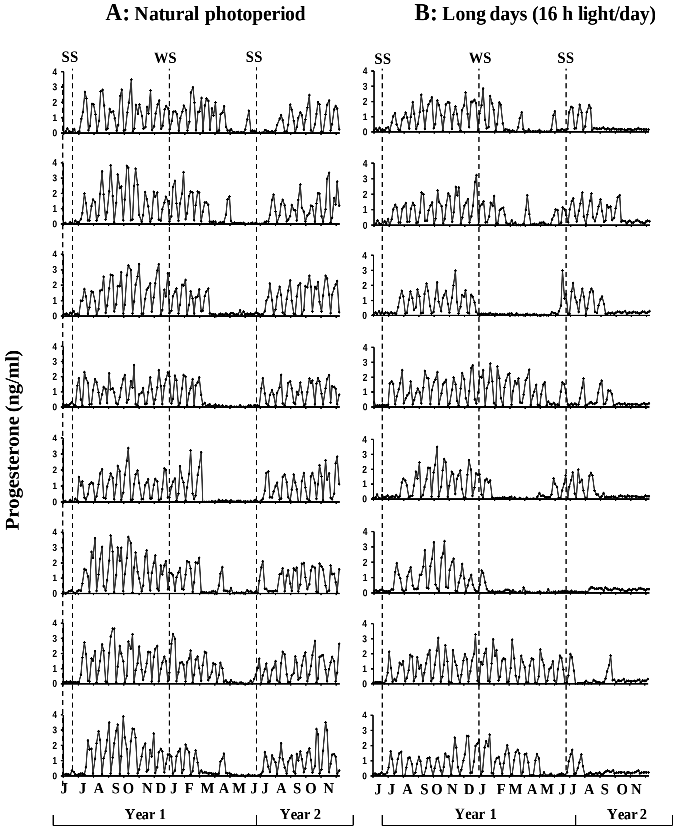


Figure 6. Ovulatory activity of Manchega ewes raised at latitude 40º 25’N and maintained under natural (A) or long days (16 h light/day) (B) for 16 months between June 22 (Year 1) and October 31 (Year 2). WS = winter solstice; SS = summer solstice. (Adapted from Gómez-Brunet et al., 2008).

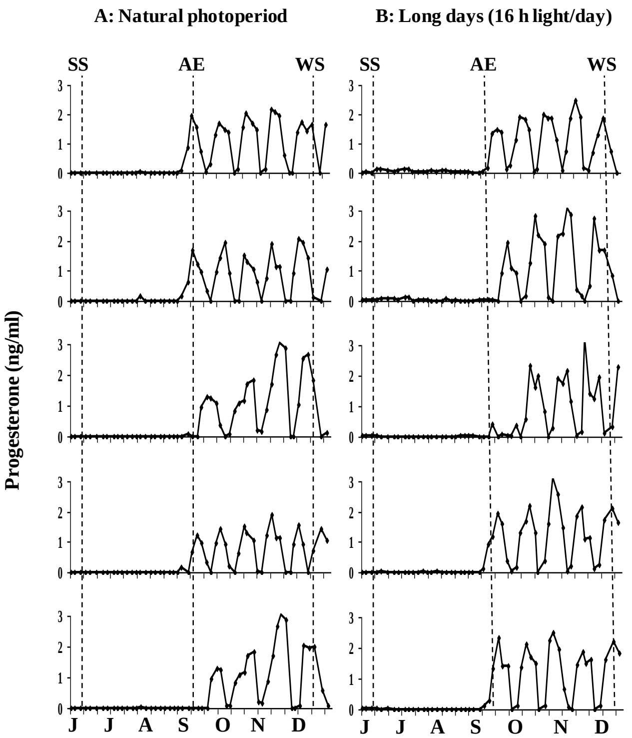


Figure 7. Ovulatory activity of Malagueña does raised at 40º25’N and maintained either under the natural photoperiod (A) or long days (16 h light/day) (B) between June 22 and December 31. WS = winter solstice; SS = summer solstice; AE: autumn equinox (Adapted from Gómez-Brunet et al., 2010c).

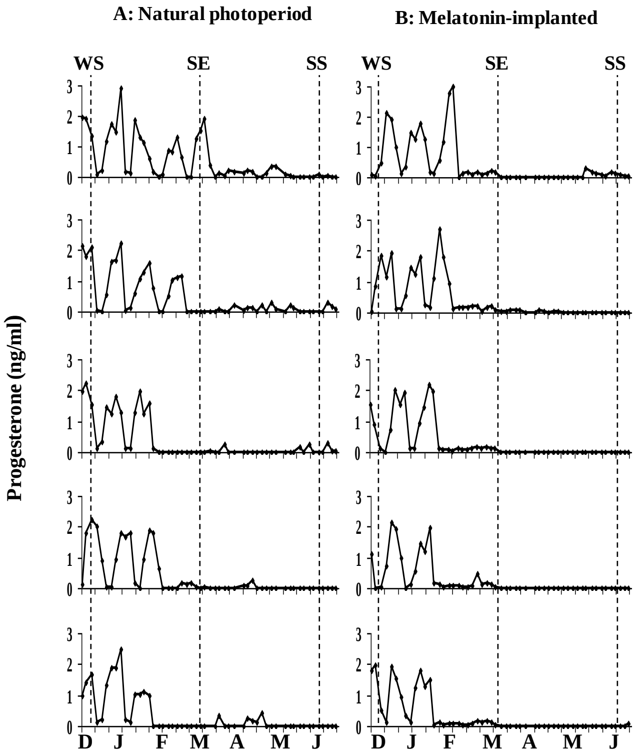


Figure 8. Ovulatory activity of Malagueña does raised at 40º 25’N and maintained under the natural photoperiod (A) or implanted with melatonin (to simulate a short day photoperiod) between December 23 and June 30. WS = winter solstice; SS = summer solstice; SE = spring equinox (adapted from Gómez-Brunet et al., 2010c).

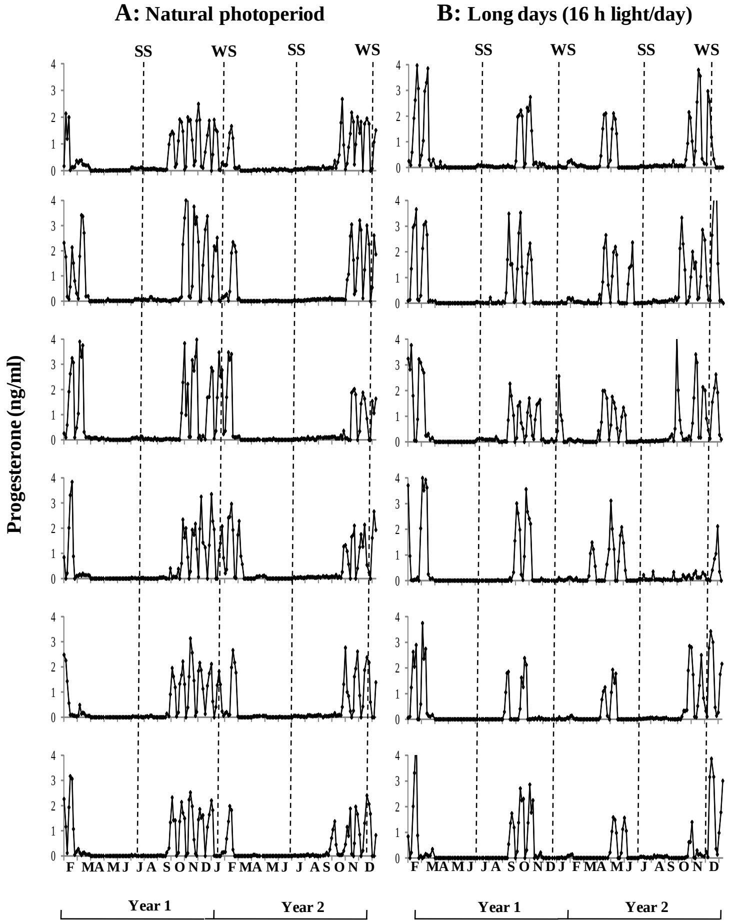


Figure 9. Ovulatory activity of Malagueña does raised at latitude 40º25’N and maintained under natural (A) or long days (16 h light/day) (B) for 23 months between February 12 (Year 1) and December 31 (Year 2). WS = winter solstice; SS = summer solstice. (Gómez-Brunet et al., unpublished data).

CONTROLLING OVULATORY ACTIVITY IN SHEEP AND GOATS OUTSIDE OF THE BREEDING SEASON

Over the last few decades, a number of ways of achieving reproductive activity outside of the normal breeding season have been developed for use with sheep and goats. Some are based on the administration of exogenous hormones (progesterone/progestagen, equine chorionic gonadotropin (eCG), and/or prostaglandin $F_{2\alpha}$ ($PGF_{2\alpha}$) or its analogues, while others involve environmental manipulation (e.g., day length control) or exposures to males (the male effect).

The most commonly used hormonal treatment involves the administration of a synthetic progestagen (FGA: fluorogestone acetate), eCG (equine chorionic gonadotropin), hCG (human chorionic gonadotropin) and cloprostenol (a $PGF_{2\alpha}$ analogue) (Corteel *et al.*, 1988: Gómez-Brunet *et al*., 2007). This induces and synchronises ovulations rapidly, ensuring high fertility (60% lambing/kidding) with just one round of AI performed 46-48 h after treatment.

Since the seasonality of reproduction in sheep and goats is controlled by day length, out of season reproduction can also be achieved using strategies based on changing the length of the photoperiod. Treatments based on the alternation of LDs and SDs can be used in either closed or open barns by imposing an artificial light regimen (Chemineau *et al*., 2008). Under field conditions, SD effects are easily provided by melatonin implants. This advances the onset of the breeding season and induces ovulatory activity in females throughout seasonal anoestrus (Chemineau *et al.,* 1988; 1992b), but it does not synchronise it well enough to be able to use AI.

Exposing seasonally anovulatory females to a male after a period of isolation has been shown to induce ovulation in both sheep and goats (Ungerfeld *et al*., 2004; Chemineau *et al.*, 2006; Delgadillo *et al*., 2009). In most females this male effect triggers a short ovarian cycle of 5–7 days in length, followed by a second ovulation occurring 7–9 days later associated with oestrus behaviour and the appearance of a corpus luteum (CL) of normal lifespan. The response to the male effect depends of many factors, but the depth of anoestrus and breed are reported the most important. In general, the male effect appears to be more effective (regardless of breed) at the end of the anoestrous period, and can be used to advance the breeding season by about a month. Moreover, while in highly seasonal sheep breeds the response varies widely, especially in mid-anoestrus, in breeds with reduced seasonality the male effect is even positive at the beginning and middle of anoestrus (Chanvallon *et al*., 2009). In Spanish breeds, the male effect not only advances the breeding season and induces ovulation during anoestrus in mature animals, it causes the same in prepuberal ewes (López-Sebastián *et al*., 1985b; Falagan, 1987; Folch, 1990). In goats the response varies within breeds during the seasonal anoestrus period, and among breeds from different latitudes (Walkden-Brown *et al*., 1999). For instance, in highly seasonal breeds, the male effect can only advance the onset of the breeding season by a few weeks; it does not satisfactorily induce full sexual activity in the middle of the anoestrous period. However, in breeds with moderate seasonality, such as the Creole goats of Guadeloupe Island, the introduction of the male induces highly fertile ovarian activity in anovulatory females throughout the year (Walkden-Brown *et al*., 1999). In Spanish goats, continuous exposure to bucks extends the seasonal ovulatory period. In fact, in Malagueña does isolated from males, the onset of seasonal ovulatory activity occurs about one month later than in Payoya goats kept continuously with males (September/October vs. August) (Gómez-Brunet *et al*., 2003, 2010c; Zarazaga *et al*., 2005). Moreover, most Spanish does exposed to males during anoestrous ovulate (87-92%) and eventually kid (85%) (Mateos Rex and Perez Llano, 1993; Folch *et al*., 1993). Nutrition and sociosexual signals are also known to interact. In Spanish ewes, the oestrous response to the male effect during anoestrus, and the fertility obtained as a result of natural breeding, are reduced in those with poor nutritional status (74% and 32% respectively) compared to those with a medium (95% and 67% respectively) or high (95 and 77% respectively) status (Folch, 1990). In goats, the oestrus response to the male effect is reduced in does of low body weight compared to those of medium and heavy body weight (Veliz *et al*., 2006). Further, the proportion of does showing signs of oestrus over the first 15 days after their introduction to sexually active bucks is greater if they receive nutritional supplementation for seven days before the introduction of the bucks (De Santiago-Miramontes *et al*., 2008).

In both species, oestrus induced by a single injected dose (20-25 mg) of progesterone (P4) before allowing the male effect, is limited to a single peak of female sexual activity that occurs three days after exposure to the males, followed by ovulation and the formation of a normal CL (Chemineau, 1985; Pearce *et al*., 1987). Notwithstanding, the degree of synchronisation achieved is again insufficient for successful AI.

The following lines describe three approaches used to control reproductive activity and optimise fertility in local Spanish sheep and goat breeds. The first is based in the use of melatonin implants combined with the male effect, the second uses the male effect in combination with progesterone (P4) and cloprostenol, and the third uses the male effect in combination with cloprostenol alone.

Melatonin implants and the male effect

Subcutaneous melatonin implants containing 18 mg of melatonin (hormone that communicates photoperiodic information from the pineal gland to the neuroendocrine system) induce high plasma concentrations of melatonin over the full 24 h of the day without suppressing the endogenous secretion of the pineal hormone during the night. It therefore provides an SD-like response by lengthening the duration of the melatonin signal (O'Callaghan *et al*., 1991b). Several countries of the European Union (UK, France, Greece, Portugal and Spain) authorise the commercial use of melatonin implants, which are widely used in combination with the male effect to advance the onset of the breeding season in anoestrous ewes and goats, and/or to improve reproductive performance after natural mating.

In sheep breeds from the temperate regions of northern Europe (>45ºN), melatonin implants have been traditionally inserted around the time of the summer solstice in order to advance the breeding season (Haresign *et al*., 1990). In Mediterranean sheep breeds the onset of the breeding season starts earlier than in breeds living at higher latitudes, thus melatonin implants are usually inserted at about the time of the spring equinox (Chemineau *et al*., 1988). The use of melatonin implants in tropical or subtropical latitudes is limited, as most ewes in these areas have a year-long breeding pattern.

In Spain, melatonin treatment is largely used with ewes under intensive, semi-extensive and extensive production systems. The treatment is usually given in conjunction with the male effect. The females are isolated from rams at least two months prior to implantation, and then the males introduced about 35 days after implantation. Both sexes remain together for a mating period of 40-45 days. In Spanish Rasa Aragonesa sheep, subcutaneous melatonin implants containing 18 mg of melatonin (Melovine®, CEVA Salud Animal, S.A., Barcelona, Spain), given in early March (spring), influence the ovarian response to the male effect, leading to modifications in the mating pattern and consequently the lambing curve (Abecia *et al*., 2006). The proportion of ewes mated within the first 20 days after introduction to the rams, and the proportion of ewes lambed within the first 17 days of the lambing period (145–161 days after ram introduction), is greater in melatonin-treated than non-treated ewes (Figure. 10A). Others authors have also reported the efficacy of melatonin- implantation in Manchega and Rasa Aragonesa ewes at around the winter solstice (December/January, when most females are cycling) in delaying the onset of anoestrous and advancing the onset of reproductive activity in the absence of males (Gómez-Brunet *et al*., 2001; Forcada *et al*., 2002; Abecia *et al*., 2010). From a practical point of view, melatonin-implantation around the winter solstice is very interesting since it can open up possibilities for developing breeding strategies in Mediterranean ewes showing reduced seasonality.

Numerous studies performed under field conditions with commercial have shown the efficacy of melatonin implants to improve the reproductive variables of Spanish sheep breeds (López-Sebastian and Inskeep, 1991; Folch *et al*., 1991; Gómez-Brunet *et al*., 1995; Martin *et al*., 2002; Palacios *et al*., 2006; Palacin *et al*., 2006; Abecia *et al.*, 2007). For example, the fertility and litter size of treated ewes are improved; in general the number of lambs produced is increased by 15-30%, although this varies depending on the breed, management system and time of melatonin implantation (Table 1). Males treated with melatonin implants during the non-breeding season experience an increase in their scrotal circumference and sexual behaviour, and produce more – and more fertile -sperm (Bravo and Roy *et al*., 2003; Garcia- Pastor *et al*., 2004). Treating Rasa Aragonesa and Manchega rams with melatonin implants increases net lamb production under field conditions (Palacín *et al*., 2008), possibly by increasing sperm progressive motility from days 45-90 after implantation (Casao *et al*., 2010).

Studies on the effects of melatonin implants in Spanish Mediterranean goats have been limited. Although its effectiveness is still not fully established, some studies have shown its efficacy in advancing the breeding season and improving reproductive performance. In Payoya goats, melatonin implants inserted in spring (March) induce cyclicity during the anoestrus period (April/May) in a breeding system in which the bucks remain permanently with the does. However, this effect is not permanent and goats return to ovarian inactivity, before ovarian activity restarts in September (Zarazaga *et al*., 2009a). In Florida goats (Figure 10B), melatonin implantation of the does in March also influences the response to the introduction of the buck, advancing the lambing pattern and improving fertility and prolificacy (Santos *et al*., 2002).

The male effect, progesterone and PGF$_{2\alpha}$

In cycling animals, PGF$_{2a}$ or its analogues (e.g., cloprostenol) causes rapid luteolysis of the CL and achieves well-synchronised behavioural oestrus (Acritopoulou and Haresign., 1980). Thus, the synchronization required for breeding females by natural mounting or AI when using the male effect alone or when combined with a progesterone injection, may be achieved by the administration of cloprostenol during the normal luteal phase induced by the male effect.

A study conducted during the non-breeding season (March-April) with Rasa Aragonesa ewes managed in extensive production flocks (at 42ºN, NE Spain), showed that the male effect combined with an i.m-injection of 25 mg progesterone (P4) at ram introduction, followed by 100 µg of cloprostenol 14 or 16 later, induced oestrus and ovulation, and was associated with lambing rates of about 70% after natural mating (López-Sebastian and Inskeep, 1988).

Table1. Fertility (%), prolificacy and fecundity of different Spanish sheep breeds treated-or not-with melatonin implants

Breed	Aptitude	Melatonin-Treated	N animals		Fertility (%)		Prolificity		Fecundity		Reference
			C	M	C	M	C	M	C	M	
Merino	Meat	January	167	174	56.3	72.4	1.03	1.16	0.57	0.83	Martín et al., 2002
Merino	Meat	March	150	175	51.3	64.5	1.07	1.11	0.55	0.72	Gómez-Brunet et al., 1995
Manchega	Mixta	April	42	42	59.5	69	1.04	1.34	0.62	0.93	Palacin et al., 2006
Churra	Milk	October	17	21	23.5	47.5	1.00	1.00	0.23	0.47	Palacios et al., 2006
Churra	Milk	April	55	48	68	71	1.07	1.20	0.73	0.85	López & Inskeep, 1991
Rasa Aragonesa	Meat	February	486	254	54	63	1.33	1.36	0.71	0.86	Folch et al., 1991
Rasa Aragonesa	Meat	March	100	100	38	53	1.06	1.10	0.40	0.58	López & Inskeep, 1991

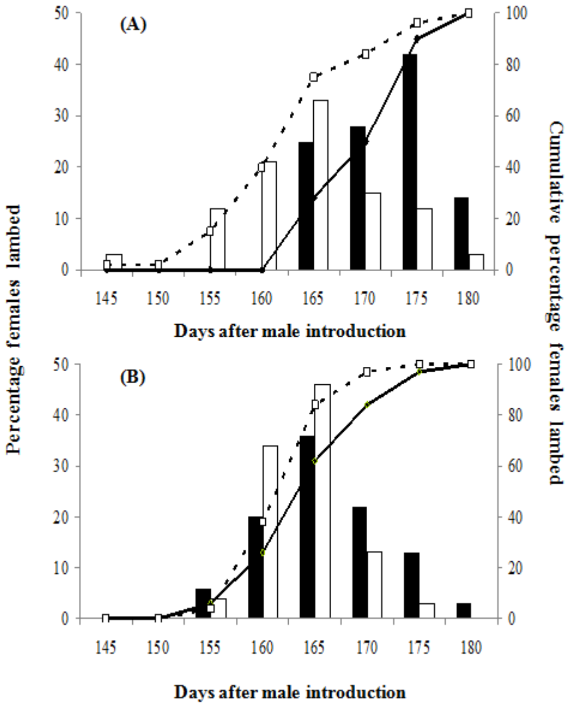


Figure 10. Proportion (%) and cumulative percentage of Melatonin-treated (□ and ---□---) and untreated (■ and——■——) Rasa Aragonesa ewes (A) and Florida goats (B) that lambed after introduction to males. Melatonin implants were administered in March. (Adapted from Santos et al.., 2002 and Abecia et al., 2006).

Monitoring follicular dynamics in goats by ultrasonography has shown that early lysis of the CL (on day 5–6 of the oestrous cycle) leads to ovulation occurring sooner, as well as a more tightly synchronised period of ovulations, than when lysis occurs at a more advanced luteal stage (on days 11–16) (Gonzalez-Bulnes *et al*., 2005). Our group assessed the effectiveness of the IMA.PRO2® method at inducing and synchronizing ovulation in Murciano-Granadina (a high production dairy breed) does during the non-breeding season (April- June). The females were subjected to the male effect plus a single i.m-dose of 25 mg of P4 in olive oil at the time of male introduction, and to early lysis of the induced CL by a single i.m-dose of 75 µg cloprostenol given 9 days after exposure to the bucks (López Sebastián *et al*., 2007). Oestrus behaviour was observed in 87.5% of the does a 37.0 ± 1.4 h ho after the administration of the cloprostenol, with the preovulatory LH surge occurring 40.5 ± 1.6 h after its injection. In addition, the pregnancy rate achieved under field conditions in inseminated does treated via the IMA.PRO2® method, without the need for the detection of oestrus, was higher than in females treated using the conventional method (intravaginal progestagens for 11 days plus 350 IU of eCG and 75 µg of cloprostenol on day 9 after sponge insertion) (65.2 and 49.4% respectively).

In Spain, as in other Mediterranean countries, goat farming for milk and cheese production has become an important industry involving the use of high yielding breeds subjected to selection programmes, with the use of AI an essential part of the production strategy. The degree of oestrus and ovulatory synchronisation obtained with the IMA.PRO2® method, the high fertility rates it achieves, and its allowing systematic timed AI without the need for the detection of oestrus, has led to its becoming extensively employed in intensive and semiextensive dairy flocks in Spain.

Following the recent forbidding of the i.m-injection of P4 in the EU, our group tested the value of P4 intravaginal gelatine capsules as a replacement for P4 injection at buck introduction as part of the IMA.PRO2®method (Gómez- Brunet et al., 2011). During the non-breeding season (April), Murciano-Granadina goats were treated with intravaginal P4 capsules (120 mg in palm oil) or with 25 mg i.m-P4 in olive oil at the time of introduction to the bucks. Oestrus behaviour and the LH surge occurred at 53.5 ± 3.0 h and 58 ±3.9 h respectively after buck introduction in does treated with the intravaginal P4 capsules, and at 63.3 ± 1.7 h and 69.0 ± 2.5 h respectively in those treated with i.m P4 (Figure 11). The pregnancy rate in inseminated does at 50 h after the i.m-injection of 75 µg of cloprostenol, given 9 days after buck introduction, were 60.6% in the IMA-PRO2®-treated goats and 58.5% in those treated with the intravaginal P4 capsules, confirming the effectiveness of the P4 capsules in replacing the i.m. P4 injection in the IMA.PRO2®method.

The male effect and PGF$_{2\alpha}$

The size of the response to the male effect is known to depend on the strength of seasonality in both sexes. Depending on the breed (and its latitude of origin) and on the depth of the sexual shutdown that occurs in the anoestrous period, great variation is seen in the response to the male effect during this time (Walkden-Brown *et al*., 1999). In some breeds, photoperiod treatment of the males, females or even of both sexes may be necessary to optimise the response to the male effect (Flores *et al*., 2000; Pellicer-Rubio *et al*., 2007).

In the general context of a more restrictive use of hormone administration, our group is assessing the potential of prostaglandin-AI protocols based on the use of the male effect combined with cloprostenol administration alone at different times of the buck-induced luteal phase (López-Sebastian et al., unpublished data). We have characterised the response of Murciano-Granadina goats to the male effect (using vasectomised males) in terms of the detection of oestrus and variations in daily plasma progesterone from day 0 (male introduction day) to day 21. The results show that 80% of goats responded to the male effect, and of these 73.6% responded with a short P4 cycle followed by a normal P4 cycle, while 26.3% responded with a normal P4 cycle. Regardless of the cycle type induced, fertile ovulation occurred at 7.4 ± 0.3 days.

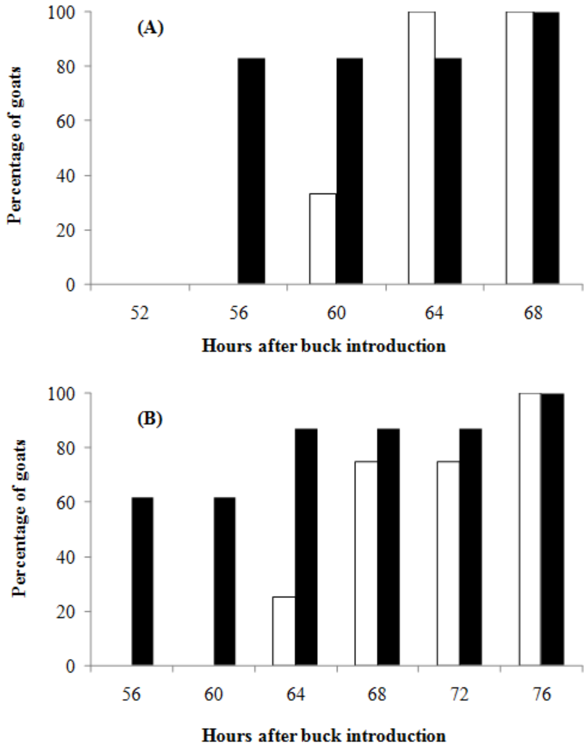


Figure 11. Cumulative percentage of Murciano-Granadina does showing oestrous behaviour (A) and the preovulatory LH surge (B) at different time points after treatment with a single i.m-dose of 25 mg of P4 in olive oil (white bars), or with intravaginal P4 capsules (120 mg in palm oil) (black bars) at the time buck introduction (Adapted from Gómez-Brunet et al., 2011).

CONCLUSIONS

This review indicates that local sheep and goat breeds from mid-high latitudes show reproductive seasonality, mainly regulated by variation in the photoperiod. Spanish sheep breeds are less seasonal than breeds from higher latitudes, but goat breeds show seasonality very similar to that of breeds from higher or even lower latitudes. The manipulation of the photoperiod has provided evidence that, at Spanish Mediterranean latitudes, these two species appear to use an endogenous circannual rhythm to control their reproductive transitions irrespective of the natural photoperiod, although it is differently expressed in each. The good response of Spanish breeds to the male effect in inducing ovulation outside of the normal breeding season has encouraged research into methods based on its use to control reproductive activity. In addition to their simplicity, these methods provide an interesting alternative to classic methods of reproductive control in the general context of reducing the use of hormones in animal production systems.

ACKNOWLEDGEMENTS

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