Animal, page 1 of 8 © The Animal Consortium 2010
doi:10.1017/S1751731110001400

Environmental and social cues can be used in combination to develop sustainable breeding techniques for goat reproduction in the subtropics

J. A. Delgadillo†

Centro de Investigación en Reproducción Caprina, Departamento de Ciencias Médico Veterinarias, Universidad Autónoma Agraria Antonio Narro, Periférico Raúl López Sánchez y Carretera a Santa Fe, C.P. 27054, Torreón, Coahuila, Mexico

(Received 19 January 2010; Accepted 7 May 2010)

Goat breeds from subtropical latitudes show different annual reproductive cycles. Some of them display large seasonal variations in their annual breeding season, while others display a moderate seasonality or sexual activity all year round. This reproductive seasonality causes seasonality of milk, cheese and meat productions and, as a consequence, induces wide variation in producer incomes. To solve this problem and provide methods allowing producers to breed animals during the anestrous period and stabilize production all year round, it is necessary to have a deep knowledge of their annual sexual activity and to identify the environmental factors controlling the timing of the annual reproductive cycle. Then, it is possible to build on these knowledge sustainable breeding techniques adapted to the environmental, economic and social characteristics of the local breeding system. In this review, I will illustrate this strategy through the example of our experiments in subtropical goats. First, we determined the characteristics of the annual breeding season in both male and female goats. Second, we identified the photoperiod as the major environmental factor controlling the timing of this annual breeding season. Third, we used the photoperiod to stimulate indirectly the sexual behavior of does. Indeed, we used photoperiodic treatments to stimulate the sexual activity of bucks during the non-breeding season. These sexually active male goats were then used to induce and synchronize the estrous behavior and ovulatory activity of anestrous females in confined or grazing conditions by using the 'male effect'. Under subtropical conditions, these results constitute an original manner to control the reproductive activity of local goats using the photoperiod combined with the 'male effect.'

Keywords: caprine, reproductive seasonality, photoperiod, melatonin, male effect

Implications

The current review describes the development of sustainable techniques to breed goats during the non-breeding season to avoid seasonality of milk, cheese and meat production. The use of these techniques to control goat reproduction can stabilize production all year round, reducing the wide variations in the producer incomes and allowing a continuous availability of fresh goat products to consumers.

Introduction

Goats are found in different ecological zones ranging from tropical to arctic latitudes and from humid to dry areas, and these animals have developed different reproductive strategies to reach a maximal survival of offspring. Under temperate latitudes (>40°), all breeds show marked reproductive seasonality (Mohammad *et al.*, 1984; Amoah *et al.*, 1996). By contrast, under subtropical latitudes (23° to 40°), local or adapted breeds of goats showed different annual rhythm in their sexual activity. Some breeds display large seasonal variations in their sexual activity, while others show a weak seasonality or no seasonality at all as they display sexual activity all year round (Walkden-Brown and Restall, 1996). The reproductive seasonality causes a seasonal availability of the goat-derived products (such as milk, cheese or meat), which affects both producers and consumers. Indeed, prices of goat products decrease during the natural production period, reducing markedly the incomes of producers. By contrasts, fresh products are not available for consumers during the anestrous season (Chemineau *et al.*, 2007). Therefore, a good knowledge of the reproductive strategies of goats, and the identification of the main environmental factor responsible for the annual breeding season in males and females, is necessary to manipulate their reproductive activity and to have the opportunity to produce goat products all year round. In this paper, I will describe studies conducted on local goats from subtropical

† E-mail: joaldesa@yahoo.com

Mexico to determine their annual breeding season and to identify the role of the environmental cues on the development of the annual reproductive rhythm. Then, I will describe how the photoperiod was used in combination with the 'male effect' to develop sustainable breeding techniques for goat reproduction in a subtropical environment.

Subtropical climatic conditions and description of the goat management system in northern Mexico

Subtropical latitudes are geographical regions bounded by the Tropic of Cancer (23.5°N) and the Tropic of Capricorn (23.5°S). These subtropical latitudes are characterized by at least 8 months with a mean temperature of 10°C or above, and the rainfall patterns are highly variable ranging from hot deserts to humid forests. The studies described in this review were conducted using local goats from the semiarid Comarca Lagunera region in the State of Coahuila, Mexico (Latitude, 26°23′N and Longitude, 104°47′W). In this subtropical latitude, the photoperiod varies from 1336 h of light at the summer solstice to 1024 h of light at the winter solstice. This area is characterized by dry climate with a mean annual temperature of 21°C, ranging from 37°C between May and August to 6°C in December and January. The average annual rainfall is 266 mm (range: 163 to 504 mm) and the dry period lasts from November to May.

Mexico has a goat population of about 10 million spread under both subtropical and tropical (<23.5°N) latitudes. The Comarca Lagunera region is an important caprine production area with about 500 000 animals. The local goats are derived from the Spanish Granadina, Murciana and Malagueña breeds. These animals were crossed with Alpine, Saanen, Toggenbourg and Anglo-Nubian breeds during the last 60 years to improve milk and meat production. Kids are nursed by their mothers and are weaned and sold between 4 and 6 weeks of age. However, the sale of the female's milk is the most important income source for producers. Females are usually kept with males in natural grazing conditions, eating only available natural vegetation without supplementary feed in the pen. From June to January, food availability (%) and the nutrient content of diets selected by goats decrease (June: 9.1% CP; 1.7 Mcal/kg; January: 7.4% CP; 0.9 Mcal/kg; Figure 1; Sáenz-Escárcega *et al.*, 1991; Ramírez *et al.*, 1991). At night, animals remain in outdoor pens (Sáenz-Escárcega *et al.*, 1991).

Reproductive seasonality in subtropical male and female goats

Male goats

Interbreed differences in the length and the timing of the breeding season are found in subtropical male goats. For example, Angora bucks show marked seasonal variations in their libido and testicular size with a peak in autumn (Ritar, 1991). By contrast, Australian cashmere, Damascus and Rayini male goats display a moderate reproductive seasonality (Walkden-Brown *et al.*, 1994; Zamiri and Heidari, 2006; Ramadan *et al.*, 2009). In cashmere goats, the breeding season, characterized by high levels of LH and testosterone, as well as the emission of a strong odor, begins in late spring and ends in late autumn (Walkden-Brown *et al.*, 1994). Finally, in native Korean bucks, sperm production did not vary between seasons (Chang-Yong *et al.*, 2006).

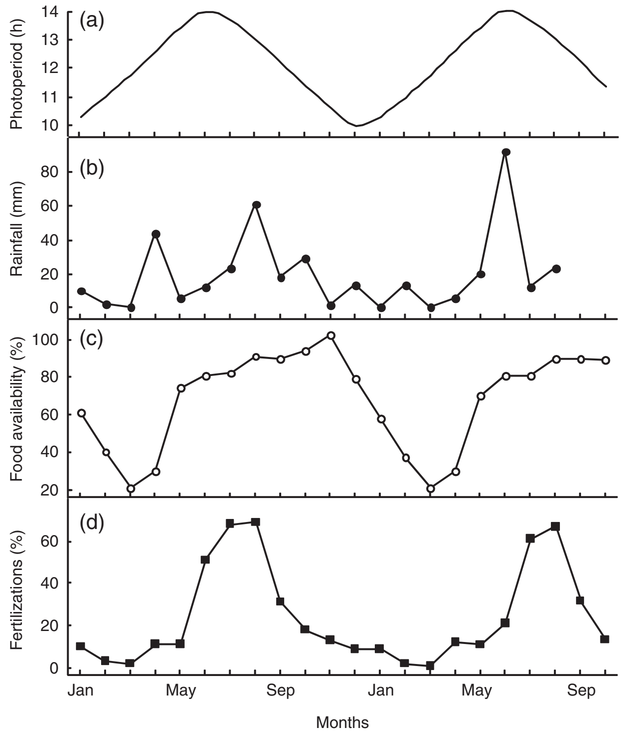

Figure 1 Annual changes in the photoperiod (a), rainfall (b), food availability (c) and fertilizations (d) of local female goats from subtropical Mexico maintained in contact with males under natural grazing conditions (adapted from Sáenz-Escárcega *et al.* (1991)).

In local males from subtropical Mexico, a decrease in sexual behavior was reported in March and April. However, the annual sexual and endocrine activities (testosterone secretion, sexual behavior, quantitative and qualitative sperm production) were never evaluated in the same animals in these early studies (Sáenz-Escárcega *et al.*, 1991). As the rest season coincided with the dry season and consequently with a marked reduction in the quantity and quality of natural food availability in our location, it was hypothesized that undernutrition was the factor responsible for the decrease in male sexual activity during this period of the year, as reported previously in other subtropical breeds (Walkden-Brown *et al.*, 1994; Pérez-Clariget *et al.*, 1998). To test if undernutrition causes the seasonal decrease in sexual activity during the non-breeding season, testicular weight, testosterone secretion and sperm production were determined in male goats fed with alfalfa *ad libitum* and 200 g of a commercial concentrate when maintained in a shaded open pen under natural photoperiodic and temperature changes. In these males, testicular weight, plasma testosterone concentrations and quantitative as well as qualitative semen

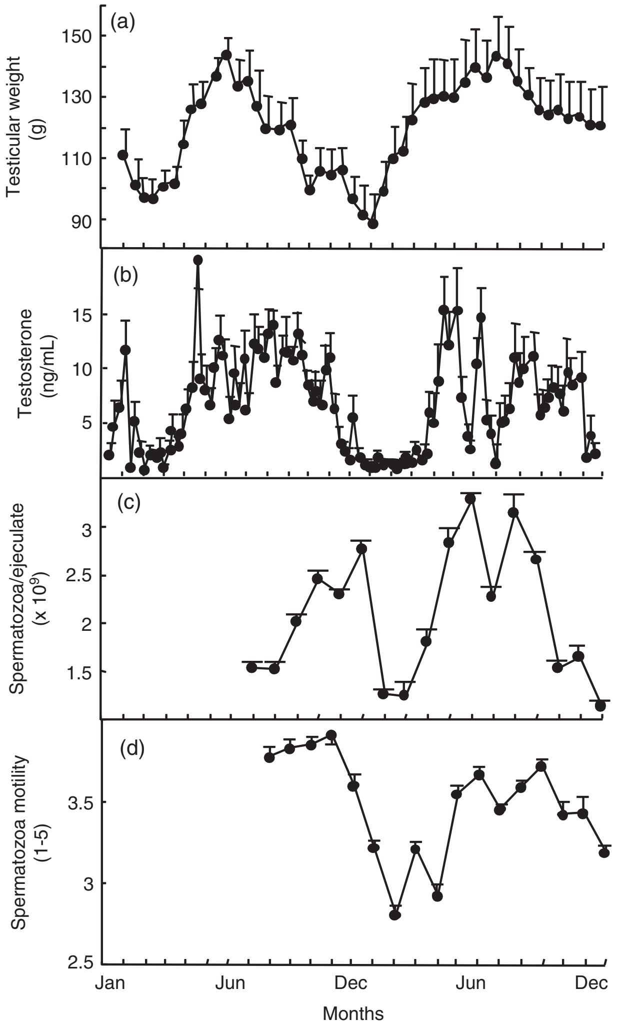

Figure 2 Seasonal variations (mean ± s.e.m.) in testicular weight (a), plasma testosterone concentrations (b), total number of spermatozoa per ejaculate (c) and progressive spermatozoa motility (d) in confined well-nourished local male goats from subtropical Mexico maintained in an open pen and subjected to natural photoperiodic and temperature changes (adapted from Delgadillo *et al.* (1999)).

production varied seasonally and were higher during the breeding season, which lasts from late spring (May to June) to late autumn (December to January), than during the non-breeding season (Figure 2; Delgadillo *et al.*, 1999). These results showed that our male goats exhibited seasonal variation in their sexual activity even if they were housed indoors and received a nutritional level to meet their requirements, thus suggesting that the reduction in food availability observed during the rest season period is not the factor responsible for the reduction in the sexual and endocrine activities in these subtropical males. These results are in contradiction with the initial hypothesis of Sáenz-Escárcega *et al.* (1991) and suggest that male reproductive seasonality is an obligatory phenomenon controlled by other environmental factor(s) than nutrition. In addition, they indicated that Mexican bucks displayed a moderate reproductive seasonality, similar to that reported in other subtropical sheep and goat breeds (Walkden-Brown *et al.*, 1994; Pérez-Clariget *et al.*, 1998).

Female goats

In females from subtropical latitudes, there is also an inter-breed difference in the length and timing of the breeding season. In female goats from the subtropical latitudes of Australia and Argentina, estrous behavior and ovarian activity start in autumn and finish in winter (Restall, 1992; Rivera *et al.*, 2003). In contrast, local goats from Chile show only 3 months of anestrus in late spring and early summer (Santa Maria *et al.*, 1990), while Boer goats in South Africa display estrous activity all year round, with the highest percentage of estrus in autumn (Greyling, 2000). In Mexican female goats, it was assumed that an anestrous period existed from March to May considering the marked reduction or absence of parturitions 5 months later, a duration corresponding to the gestation length in goats (Sáenz-Escárcega *et al.*, 1991). However, the annual sexual activity (estrous behavior and ovulatory activity) was never evaluated in the same non-pregnant females. As the anestrous period coincided with the dry season and, as a consequence, with a marked reduction in the quantity and quality of natural food availability in our location, it was hypothesized that undernutrition could be the factor responsible for the changes in their annual sexual activity, as reported previously in other subtropical breeds (Sáenz-Escárcega *et al.*, 1991; Walkden-Brown and Bocquier, 2000). However, in our location, the non-breeding season also coincides with an increase in day-length and a period of intense nursing of the kids (Figure 1). These environmental factors could be also involved in the expression of the anestrous period (Peters and Lamming, 1990; McNeilly, 1994; Malpaux *et al.*, 2001). To test if undernutrition was the factor responsible for the anestrous period, estrous behavior and ovulatory activity were determined in intact female goats fed with 2.7 kg of alfalfa and 200 g of commercial concentrate when maintained in a shaded open pen under natural photoperiodic and temperature changes. In addition, the influence of the management system (nutrition, temperature, socio-sexual relationships, etc.) on the annual breeding season was determined in ovariectomized does bearing a subcutaneous implant constantly releasing estradiol 17β (OVX + E). In these OVX + E females, LH secretion, an index of the ovulatory activity in intact females (Henniawati *et al.*, 1995), was determined. One group of OVX + E females fed with 2.7 kg of alfalfa and 200 g of commercial concentrate was kept in a shaded open pen under natural photoperiodic and temperature changes. The other group of OVX + E females was kept in a local flock of intact females that included four males under extensive conditions eating only the spontaneously available natural vegetation. Intact does displayed large seasonal variations in their sexual activity (Figure 3). During the breeding season, which lasted from September to February, females showed regular estrous and ovulatory cycles (Duarte *et al.*, 2008). In OVX + E females, seasonal variations in LH secretion were also observed regardless of

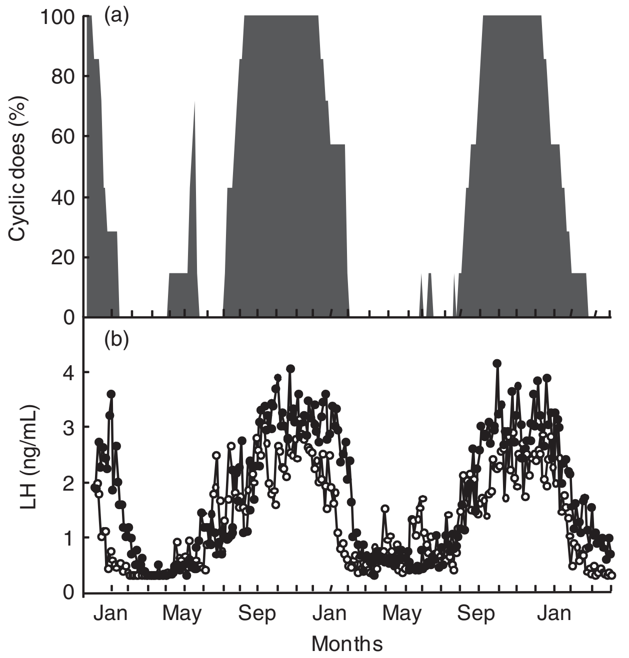

Figure 3 Seasonal variations in the percentage of female goats showing cyclic ovulatory activity (a), or LH secretion (b; mean ± s.e.m.) in ovariectomized estradiol-treated local female goats from subtropical Mexico maintained in open pens (●) or natural grazing conditions (○) and subjected to natural variations of photoperiodic and temperature changes (adapted from Duarte *et al.* (2008)).

whether they were constantly fed indoors or kept under grazing conditions (Figure 3). Variations in LH secretion in OVX + E females were consistent with the ovulatory activity in intact ones with high LH levels coinciding with ovulatory activity and low levels with anovulation. The increase in LH secretion was similar in does maintained indoors or under grazing conditions and occurred in August. By contrast, the seasonal decline in LH secretion occurred earlier in females kept in grazing conditions (January) than in those kept indoors on a high level of nutrition (February; Duarte *et al.*, 2008). Taken together, these results showed that female goats exhibited seasonal variation in their sexual and endocrine activity even if they received a nutritional level to meet their requirements. Thus, the seasonal reduction in food availability does not appear as the factor responsible for the seasonal variations in the reproductive activity of females. It seems that, similar to what is observed in males of the same breed, reproductive seasonality of Mexican female goats is an obligatory phenomenon controlled by other environmental factor(s) than food availability. The difference of 1 month in the decline in LH secretion between OVX + E females maintained indoors or in extensive conditions was probably due to the drastic reduction in food availability observed at the beginning of each year in our subtropical location (Sáenz-Escárcega *et al.*, 1991). The delay in LH secretion observed in indoor OVX + E females suggests that nutrition could be a modulatory factor in the timing of the breeding season. Indeed, the ovulatory activity in intact highly and constantly fed goats and ewes is longer than in undernourished ones (Forcada and Abecia, 2006; De Santiago-Miramontes *et al.*, 2009). The pattern of the reproductive seasonality observed in this study agrees with those reported in breeds from subtropical and temperate latitudes in which the natural breeding season occurs in autumn and winter (Chemineau *et al.*, 1992; Restall, 1992).

Taken together, these results demonstrate that local male and female goats in subtropical Mexico display seasonal variations in their sexual and endocrine activities. Nutrition levels do not appear to be the main factor controlling the sexual activity in this subtropical breed.

Photoperiod is the major environmental cue that triggers the annual breeding season in subtropical goats

The year-to-year repeatability of the annual reproductive cycle in highly and constantly fed does and bucks from subtropical Mexico suggests that these animals use the photoperiod to synchronize their breeding season. To test this hypothesis, female and male goats were submitted to alternations between short and long days mimicking, respectively, the winter and summer solstice day-length.

Male goats

In subtropical Merino rams, it was clearly shown that the reproductive axis is driven by photoperiodic changes. Indeed, testosterone secretion increases during artificial short days and decreases during artificial long days (Poulton and Robinson, 1987). In Angora bucks adapted to a subtropical latitude, rapid changes between long and short days modified the reproductive seasonality observed in natural conditions suggesting an important role of the photoperiod in the synchronization of their annual breeding season (Morello *et al.*, 2004). To test if the photoperiod was the factor responsible for the annual reproductive rhythm observed in our subtropical male goats, testosterone secretion was determined in bucks exposed, in a light-proof building, to alternations between 3 months of subtropical long days (14 h of light/day) and 3 months of subtropical short days (10 h of light/day). Control male goats remained in a shaded open pen under natural photoperiodic and temperature variations. As expected, in the control group, plasma testosterone concentrations showed large seasonal variations increasing in May to June and decreasing in November to December. By contrast, in the experimental group, testosterone secretion increased invariably during short days and decreased during long days (Figure 4; Delgadillo *et al.*, 2004). These results showed that in male goats from subtropical Mexico, the photoperiod is the major environmental factor that controls the annual breeding season. In the experimental group, the photoperiodic rhythm modified the seasonality of testosterone secretion observed in control animals exposed to natural light variations as reported in Alpine bucks and Soay rams (Lincoln and Short, 1980; Delgadillo and Chemineau, 1992).

Female goats

In subtropical sheep and female goats, a role of photoperiod on the annual reproductive rhythm was suggested. Indeed,

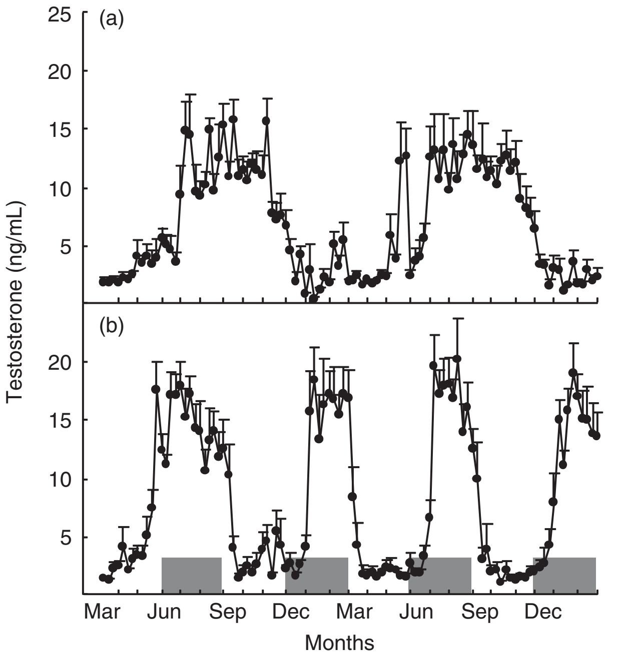

Figure 4 Changes (mean ± s.e.m.) in plasma testosterone concentrations in local male goats from subtropical Mexico subjected to natural photoperiodic variations (a) or to alternations between 3 months of long days (14 h of light/day) and 3 months of short days (10 h of light/day; b). Gray areas indicate the months of short days (adapted from Delgadillo *et al.* (2004)).

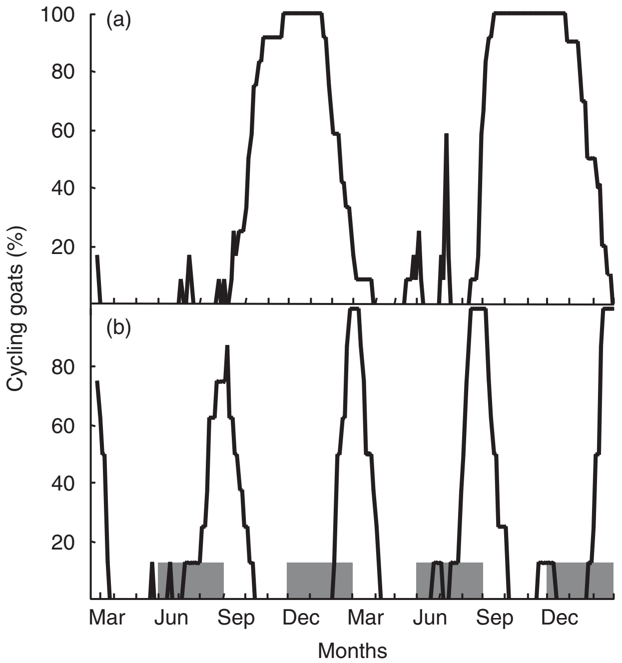

Figure 5 Changes in cyclic ovulatory activity in local female goats from subtropical Mexico subjected to natural photoperiodic variations (a) or to alternations between 3 months of long days (14 h of light/day) and 3 months of short days (10 h of light/day; b). Gray areas indicate the months of short days (adapted from Duarte *et al.* (2010)).

on the four Merino ewes subjected to alternations between subtropical long and short days, only one responded to the treatment (Poulton and Robinson, 1987). In addition, in subtropical Egyptian ewes, annual sexual activity was modified by a long-day and melatonin treatment (Aboul-Naga *et al.*, 1992). To test whether the photoperiod was the factor responsible for the annual reproductive rhythm observed in our subtropical female goats, ovarian activity was determined in does exposed to the same experimental conditions described above in males. As expected, the control group displayed large seasonal variations in their ovulatory activity, which lasted from September to February, as in other subtropical and temperate breeds of sheep and goats (Chemineau *et al.*, 1992; Restall, 1992; Rivera *et al.*, 2003). The experimental group also displayed changes in their ovulatory activity, but the timing of these changes was profoundly modified by photoperiodic treatment. In the experimental group, the ovulations started during short days and ended during long days (Figure 5; Duarte *et al.*, 2010). These results showed that in female goats from subtropical Mexico, the photoperiod is a major environmental factor that controls the annual ovulatory activity. In the experimental group, the photoperiodic rhythm modified the seasonal pattern of ovulations observed in the control group exposed to natural light, a result consistent with those reported in Alpine does and Suffolk ewes (Karsch *et al.*, 1984; Gebbie *et al.*, 1999).

These results clearly showed that the local male and female goats from subtropical Mexico were sensitive to the photoperiod and suggested that this environmental factor was important in the timing of the annual reproductive rhythm. In addition, they suggested that the photoperiod could be used to induce sexual activity in both males and females during the non-breeding season as in goat breeds from temperate latitudes (Chemineau *et al.*, 2007).

Control of the sexual activity of male and female goats

In goat and sheep breeds from temperate latitudes, the sexual activity of males and females can be induced during the non-breeding season using long days followed by short days or melatonin treatment, a pineal hormone that can mimic the effects of short days (Hanif and Williams, 1991; Donovan *et al.*, 1994; Sweeney *et al.*, 1997). We tested different photoperiodic treatments to stimulate the sexual activity of males during the non-breeding season. We did not test the effect of these treatments in females because, in subtropical Mexico, most local goats remain in precarious open pens at night, making it difficult to expose them to photoperiodic treatment. In females, it was rather decided to stimulate their sexual activity by acute exposure to males, a technique known as the 'male effect' (Chemineau *et al.*, 2006; Delgadillo *et al.*, 2009; Bedos *et al.*, 2010). Indeed, exposure of anestrous does or ewes to rams or bucks, respectively, induces the rapid activation of LH secretion leading to estrous behavior and ovulation. Several factors can modify the ovulation and estrous responses of females exposed to males, including the intensity of the sexual behavior. In fact, a major limitation of the 'male effect' is that the sexual response of females is weak or absent when it is performed during mid-seasonal anestrus, probably because of the low sexual behavior of males, which are also in rest season at this time (Restall, 1992; Flores *et al.*, 2000; Delgadillo *et al.*, 2006). Therefore, it was tested if this limitation of the 'male effect' could be circumvented by the use of males rendered sexually active by a previous exposure to photoperiodic treatments.

Long days, melatonin and the 'male effect'
Males from the control group were exposed to natural day-length, while another group of males was exposed to long days (16 h of light/day) from November 1 to January 15. On January 16, males of the experimental group received two subcutaneous ear melatonin implants and were then exposed to natural photoperiodic changes. This light-treatment during the non-breeding season stimulated LH and testosterone secretion, sexual behavior and sperm production from the end of February to the end of April (Delgadillo *et al.*, 2001). Then, we tested whether these photoperiod-treated bucks could stimulate the sexual activity of anestrous goats. For this purpose, three treated and three control bucks were placed with anovulatory goats maintained in open pens. The photoperiod-treated males induced estrous behavior in all females (40/40) in the first 11 days after their introduction. By contrast, no behavioral activity was observed in females exposed to the light-untreated males during the same period (Flores *et al.*, 2000). These were our first results showing that the photoperiod could be used indirectly to stimulate the sexual activity of anovulatory goats.

Long days and the 'male effect'
To simplify the photoperiodic treatment used in males, we first tested whether melatonin implants were necessary to stimulate the sexual activity of our local bucks. Indeed, during long-day treatments, animals are exposed to 16 h of light/day. When long-day treatment was stopped in January, males were exposed to natural photoperiodic changes, that is, about 11 h of light/day, and this day-length was shorter than the previous artificial long days. This reduction in day-length may provide a sufficient stimulatory signal (Robinson and Karsch, 1987). Thus, two groups of males were kept in two shaded open pens and exposed to artificial long days (16 h of light/day) from November 1 to January 15. On January 16, the light treatment was stopped and one group of bucks received two subcutaneous ear melatonin implants while the second group did not. Control males remained in a shaded open pen under a natural photoperiod throughout the experiment. In both long-day treated groups, plasma testosterone concentrations did not differ and were higher than in controls from February to April, during the non-breeding season, indicating that the long-day treatment stimulated the endocrine testes activity, and that melatonin was not necessary for this stimulation (Figure 6; Delgadillo *et al.*, 2002). Then, we tested the efficiency of the only long-day treated bucks to stimulate the sexual activity of the anestrous goats. For this purpose, two light-treated and two control bucks were placed with anovulatory goats maintained in open pens. The proportion of females that displayed estrous behavior was greater in those exposed to the light-treated bucks (19/19) than in those exposed to light-untreated ones (2/20; Delgadillo *et al.*, 2002). Interestingly, the light-treated males could also stimulate the estrous behavior of female goats maintained under extensive conditions. In fact, the proportion (18/20) of females that displayed estrous behavior was higher when they were left permanently in pens and grasslands with sexually active males than with sexually inactive ones (9/20; Rivas-Muñoz *et al.*, 2007). In addition, a high behavioral response (>90%) was also obtained when males remained in the open pen during the day while females grazed in open range (Rivas-Muñoz *et al.*, 2007; De Santiago-Miramontes *et al.*, 2008; Fitz-Rodríguez *et al.*, 2009).

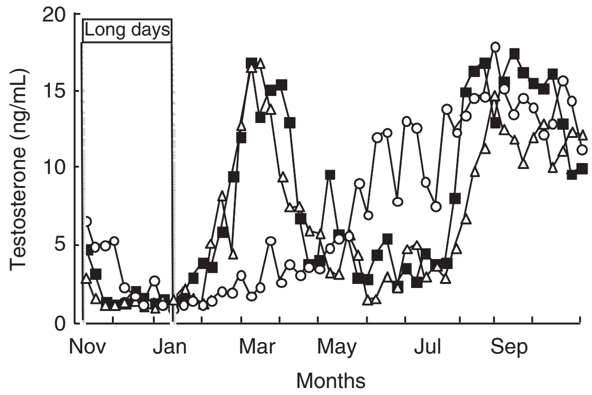

Figure 6 Changes (mean ± s.e.m.) in plasma testosterone concentrations in local male goats from subtropical Mexico subjected to natural photoperiodic variations (○, or to 2.5 months of artificial long days (16 h of light/day) from November 1, and then treated with two s.c. melatonin implants (△) or exposed to natural short days (■) (adapted from Delgadillo *et al.* (2002)).

These results showed that artificial long days followed or not by melatonin implants stimulate the sexual behavior of bucks during the non-breeding season. These photoperiodic treatments can be applied in open pens, making them easy to use in semiarid subtropical conditions. In addition, and more importantly, the photoperiodically treated males can stimulate the sexual activity of anestrous goats raised in confined or extensive conditions. These data showed that in our subtropical breed, females do not need to be submitted to photoperiodic treatment to obtain a high sexual response when exposed to the light-treated males as reported in the Alpine breed raised in temperate latitudes (Chemineau *et al.*, 1986; Pellicer-Rubio *et al.*, 2007). The indirect use of a photoperiod to control the sexual activity of females by means of sexually active males is a sustainable breeding technique for goat reproduction in the subtropics. The high response induced by the light-treated males could be due to the fact that photoperiodic treatment stimulates testosterone secretion, the odor of males and their sexual behavior, improving the quality of signals provided by the males to does during the 'male effect' (Delgadillo *et al.*, 2006; Murata *et al.*, 2009). Indeed, it was recently shown that the sexual behavior displayed by the sexually active males contributes to the maintenance of high LH secretion, allowing a higher rate of ovulations in does exposed to these light-treated males (Vielma *et al.*, 2009).

Conclusion

This review indicates that knowledge of the reproductive characteristics of both male and female goats and the characterization of the role of environmental cues is a useful tool to develop relevant techniques to manipulate the sexual activity of animals. In our case, the identification of the photoperiod as the main environmental cue controlling the annual breeding season in our subtropical goats allowed us to develop original techniques to control the reproductive activity of does. Indeed, the manipulation of the photoperiodic environment stimulates the sexual activity of males, which in turn was used to induce and synchronize the estrous behavior and ovulations in anovulatory goats by the phenomenon called the 'male effect'. In addition, the sexually active males improve the sexual response of does, even in conditions in which the male effect had been previously described as poorly efficient. The manipulation of the photoperiod as well as social relationships are two strategies to ensure a sustainable control of goat reproduction in the subtropics.

Acknowledgments

I express my deepest thanks to Philippe Chemineau for giving me the opportunity to do my PhD in his laboratory and allowing me to discover the fascinating world of caprine reproduction. My warmest thanks goes also to Benoît Malpaux for his unconditional friendship during all these years of collaboration; I much appreciate the comments, advice and support that he gave me during this time. I also very much appreciate the friendship of Pascal Poindron who introduced me to the fascinating study of the maternal and sexual behavior of goats; his decision to participate in the development of our goat program of reproduction contributed to its success. I am also grateful to Dolores López for her great contribution and friendship in the development of our research program by her infallible secretarial and administrative assistance during all these years. You all will find in this review the results of the great support you provided to me to initiate this fantastic goat reproduction history and to build the Centro de Investigación en Reproducción Caprina (CIRCA). I also thank the past and present members of the CIRCA for their dedicated participation in the experiments described in this review, especially G. Duarte, J. A. Flores, H. Hernández, J. Vielma, G. Fitz-Rodríguez and I. G. Fernández. I appreciate very much the comments of M. Keller that improved this manuscript and for his kind help in the correction of the English. J. A. Delgadillo was supported by the International Foundation of Science (grant B/2071-3F) and the exchange program between Mexico (ANUIES, SEP, CONACYT) and France (ECOS; M02-A04 and M95-B05 grants) in carrying out the described experiments.

References

Aboul-Naga AM, Aboul-Ela MB and Hassan F 1992. Manipulation of reproductive activity in subtropical sheep. Small Ruminant Research 7, 151–160.

Amoah EA, Gelaye S, Guthrie P and Rexroad CE Jr 1996. Breeding season and aspects of reproduction of female goats. Journal of Animal Science 74, 723–728.

Bedos M, Flores JA, Fitz-Rodríguez G, Keller M, Malpaux B, Poindron P and Delgadillo JA 2010. Four hours of daily contact with sexually active males is sufficient to induce fertile ovulation in anestrous goats. Hormones and Behavior, doi:10.1016/j.yhbeh.2010.05.002.

Chang-yong C, Jung-Gon K, Sang-Rae C, Dong-Soo S, Young-Keun K, Balasubramanian S, Sang-Yong C and Gyu-Jin R 2006. Influence of season, extenders, slow and rapid freezing on seminal characters in Korean native bucks. Reproduction in Domestic Animals 41, 55–60.

Chemineau P, Normant E, Ravault JP and Thimonier J 1986. Induction and persistence of pituitary and ovarian activity in the out-of-season lactating dairy goats after a treatment combining a skeleton photoperiod, melatonin and the male effect. Journal of Reproduction and Fertility 78, 497–504.

Chemineau P, Daveau A, Maurice F and Delgadillo JA 1992. Seasonality of estrus and ovulation is not modified by subjecting female Alpine goats to a tropical photoperiod. Small Ruminant Research 8, 299–312.

Chemineau P, Malpaux B, Brillard JP and Fostier A 2007. Seasonality of reproduction and production in farm fishes, birds and mammals. Animal 1, 419–432.

Chemineau P, Pellicer-Rubio MT, Lassoued N, Khaldi G and Monniaux D 2006. Male-induced short oestrous and ovarian cycles in sheep and goats: a working hypothesis. Reproduction, Nutrition and Development 46, 417–429.

Delgadillo JA and Chemineau P 1992. Abolition of seasonal release of luteinizing hormone and testosterone in Alpine male goats (Capra hircus) by short photoperiodic cycles. Journal of Reproduction and Fertility 94, 45–55.

Delgadillo JA, Canedo GA, Chemineau P, Guillaume D and Malpaux B 1999. Evidence for an annual reproductive rhythm independent of food availability in male Creole goats in subtropical northern Mexico. Theriogenology 52, 727–737.

Delgadillo JA, Cortez ME, Duarte G, Chemineau P and Malpaux B 2004. Evidence that the photoperiod controls the annual changes in testosterone secretion, testicular and body weight in subtropical male goats. Reproduction, Nutrition and Development 44, 183–193.

Delgadillo JA, Gelez H, Ungerfeld R, Hawken PAR and Martin GB 2009. The "male effect" in sheep and goats: revisiting the dogmas. Behavioural Brain Research 200, 304–314.

Delgadillo JA, Carrillo E, Morán J, Duarte G, Chemineau P and Malpaux B 2001. Induction of sexual activity of male creole goats in subtropical northern Mexico using long days and melatonin. Journal of Animal Science 79, 2245–2252.

Delgadillo JA, Flores JA, Véliz FG, Duarte G, Vielma J, Hernandez H and Fernandez IG 2006. Importance of the signals provided by the buck for the success of the male effect in goats. Reproduction, Nutrition and Development 44, 391–400.

Delgadillo JA, Flores JA, Véliz FG, Hernández HF, Duarte G, Vielma J, Poindron P, Chemineau P and Malpaux B 2002. Induction of sexual activity of lactating anovulatory female goats using male goats treated only with artificial long days. Journal of Animal Science 80, 2780–2786.

De Santiago-Miramontes MA, Malpaux B and Delgadillo JA 2009. Body condition is associated with a shorter breeding season and reduced ovulation rate in subtropical goats. Animal Reproduction Science 114, 175–182.

De Santiago-Miramontes MA, Rivas-Muñoz R, Muñoz-Gutiérrez M, Malpaux B, Scaramuzzi RJ and Delgadillo JA 2008. The ovulation rate in anoestrous female goats managed under grazing conditions and exposed to the male effect is increased by nutritional supplementation. Animal Reproduction Science 105, 409–416.

Donovan A, Boland MP, Roche JF and O'Callaghan D 1994. The effect of supplementary long days, a subcutaneous melatonin implant and exposure to a ram on the onset of the breeding season in ewes. Animal Reproduction Science 34, 231–240.

Duarte G, Flores JA, Malpaux B and Delgadillo JA 2008. Reproductive seasonality in female goats adapted to a subtropical environment persists independently of food availability. Domestic Animal Endocrinology 35, 362–370.

Duarte G, Nava-Hernández MP, Malpaux B and Delgadillo JA 2010. Ovulatory activity of female goats adapted to the subtropics is responsive to photoperiod. Animal Reproduction Science 120, 65–70.

Fitz-Rodríguez G, De Santiago-Miramontes MA, Scaramuzzi RJ, Malpaux B and Delgadillo JA 2009. Nutritional supplementation improves ovulation and pregnancy rates in female goats managed under natural grazing conditions and exposed to the male effect. Animal Reproduction Science 116, 85–94.

Flores JA, Véliz FG, Pérez-Villanueva JA, Martínez de la Escalera G, Chemineau P, Poindron P, Malpaux B and Delgadillo JA 2000. Male reproductive condition is the limiting factor of efficiency in the male effect during seasonal anestrus in female goats. Biology of Reproduction 62, 1409–1414.

Forcada F and Abecia JA 2006. The effect of nutrition on the seasonality of reproduction in ewes. Reproduction, Nutrition and Development 46, 355–365.

Gebbie FE, Forsyth IA and Arendt J 1999. Effects of maintaining solstice light and temperature on reproductive activity, coat growth, plasma prolactin and melatonin in goats. Journal of Reproduction and Fertility 116, 25–33.

Greyling JPC 2000. Reproduction traits in Boer goat doe. Small Ruminant Research 36, 171–177.

Hanif M and Williams HL 1991. The effect of melatonin and light treatment on the reproductive performance of yearling Suffolk rams. British Veterinary Journal 147, 49–56.

Henniawati, Restall BJ and Scaramuzzi RJ 1995. Effect of season on LH secretion in ovariectomized Australian cashmere does. Journal of Reproduction and Fertility 103, 349–356.

Karsch FJ, Bittman EL, Foster DL, Goodman RL, Legan SJ and Robinson JE 1984. Neuroendocrine basis of seasonal reproduction. Recent Progress in Hormone Research 40, 185–232.

Lincoln GA and Short RV 1980. Seasonal breeding: nature's contraceptive. Recent Progress in Hormone Research 36, 1–52.

Malpaux B, Migaud M, Tricoire H and Chemineau P 2001. Biology of mammalian photoperiodism and the critical role of the pineal gland and melatonin. Journal of Biological Rhythms 16, 336–347.

McNeilly AS 1994. Suckling and control of gonadotrophin secretion. In The physiology of reproduction (ed. E Knobil and JD Neill), pp. 1179–1212. Raven Press Ltd, New York, USA.

Mohammad WA, Grossman M and Vatthauer JL 1984. Seasonal breeding in the United States dairy goats. Journal of Dairy Science 67, 1813–1822.

Morello H, Alvarez H, Medina V, Bogado M, Quintana M, Venturino A and Aisen E 2004. Artificial photoperiodic cycles for semen collection from male Angora goats during the non-breeding season. Reproduction Fertility and Development 16, 503–526.

Murata K, Wakabayashi Y, Kitago M, Ohara H, Watanabe H, Tamogami S, Warita Y, Yamagishi K, Ichikawa M, Takeuchi Y, Okamura H and Mori Y 2009. Modulation of gonadotrophin-releasing hormone pulse generator activity by the pheromone in small ruminants. Journal of Neuroendocrinology 21, 346–350.

Pellicer-Rubio MT, Leboeuf B, Bernelas D, Forgerit Y, Pougnard JL, Bonné JL, Senty E and Chemineau P 2007. Highly synchronous and fertile reproductive activity induced by the male effect during deep anoestrus in lactating goats subjected to treatment with artificially long days followed by natural photoperiod. Animal Reproduction Science 98, 241–258.

Pérez-Clariget R, Forsberg M and Rodríguez-Martínez H 1998. Seasonal variation in live weight, testes size, testosterone, LH secretion, melatonin and thyroxine in Merino and Corriedale rams in a subtropical climate. Acta Veterinaria Scandinavica 39, 35–47.

Peters AR and Lamming GE 1990. Lactational anoestrus in farm animals. Oxford Reviews of Reproductive Biology 12, 245–288.

Poulton AL and Robinson TJ 1987. The response of rams and ewes of three breeds to artificial photoperiod. Journal of Reproduction and Fertility 79, 609–626.

Ramadan TA, Taha TA, Samak MA and Hassan A 2009. Effectiveness of exposure to longday followed by melatonin treatment on semen characteristics of Damascus male goats during breeding and non-breeding seasons. Theriogenology 71, 458–468.

Ramírez RG, Loyo A, Mora R, Sanchez EM and Chaire A 1991. Forage intake and nutrition of range goats in a shrubland in northeastern Mexico. Journal of Animal Science 69, 879–885.

Restall BJ 1992. Seasonal variation in reproductive activity in Australian goats. Animal Reproduction Science 27, 305–318.

Ritar AJ 1991. Seasonal changes in LH, androgens and testes in the male Angora goat. Theriogenology 36, 959–972.

Rivas-Muñoz R, Fitz-Rodríguez G, Poindron P, Malpaux B and Delgadillo JA 2007. Stimulation of estrous behavior in grazing female goats by continuous or discontinuous exposure to males. Journal of Animal Science 85, 1257–1263.

Rivera GM, Alanis GA, Chaves MA, Ferrero SB and Morello HH 2003. Seasonality of estrus and ovulation in Creole goats of Argentina. Small Ruminant Research 48, 109–117.

Robinson JE and Karsch FJ 1987. Photoperiodic history and a changing melatonin pattern can determine the neuroendocrine response of the ewe to daylength. Journal of Reproduction and Fertility 80, 159–165.

Santa Maria A, Cox J, Muñoz E, Rodríguez R and Caldera L 1990. Estudio del ciclo sexual, estacionalidad reproductiva y control del estro en la cabra Criolla en Chile. Final Research Co-ordination Meeting'. FAO, Bogotá, Colombia, 19–23 September 1988, pp. 363–385. International Atomic Energy Agency, Vienna, Austria.

Sáenz-Escárcega P, Hoyos FG, Salinas GH, Espinoza AJ, Guerrero BA and Contreras GE 1991. Establecimiento de módulos caprinos con productores cooperantes. In Evaluación de Módulos Caprinos en la Comarca Lagunera (ed. S Flores), pp. 24–34. Matamoros, Coahuila, México.

Sweeney T, Donovan A, Roche JF and O'Callaghan D 1997. Variation in the ability of a long day followed by a short day photoperiod signal to initiate reproductive activity in ewes at different times of the year. Journal of Reproduction and Fertility 109, 121–127.

Vielma J, Chemineau P, Poindron P, Malpaux B and Delgadillo JA 2009. Male sexual behavior contributes to the maintenance of high LH pulsatility in anestrous female goats. Hormones and Behavior 56, 444–449.

Walkden-Brown SW and Restall BJ 1996. Environmental and social factors affecting reproduction. In 6th International Conference on Goats (ed. PJ Host), vol. 2, pp. 762–775. International Academic Publishers, Beijing, China.

Walkden-Brown SW and Bocquier F 2000. Nutritional regulation of reproduction in goats. In 7th International Conference on Goats (ed. L Gruner and Y Chebert), vol. 1, pp. 389–395. Institut de l'elevage and INRA, Paris, France.

Walkden-Brown SW, Restall BJ, Norton BW, Scaramuzzi RJ and Martin GB 1994. Effect of nutrition on seasonal patterns of LH, FSH and testosterone concentration, testicular mass, sebaceous gland volume and odour in Australian cashmere goats. Journal of Reproduction and Fertility 102, 351–360.

Zamiri MJ and Heidari AH 2006. Reproductive characteristics of Rayani male goats of Kerman province in Iran. Animal Reproduction Science 96, 176–185.