SEASONAL AND SOCIAL FACTORS AFFECTING REPRODUCTION

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Contents

1. Introduction
2. Environmental regulation of reproduction in mammals
2.2 Seasonal reproductive strategies
2.3. Extrinsic and intrinsic factors and ultimate and proximate factors influencing seasonal reproduction
2.3.1. Ultimate factors
2.3.2. Energy balance
2.3.3. Nutrients
2.3.4. Competence for food and predation pressure
2.3.2. Proximate factors:
2.4. Mechanisms regulating seasonal reproduction with photoperiod as a predictor
2.5. Seasonal reproduction in livestock species
2.5.1. Sheep
2.5.2. Goats
2.5.3. Cattle
2.5.4. Swine
3. Socio-sexual signals
3.1. The ram effect
3.1.1. Managing the ram effect
3.1.2. The ram effect in cyclic ewes
4. Socio-sexual signals and seasonal reproductive patterns
5. General overview

Summary

The present chapter summarizes the current information on how some environmental factors, mainly seasonality and socio-sexual signals, interact with the endogenous mechanisms that control reproductive activity in domestic ruminants and swine. Ultimate factors such as latitude and seasonality, energy balance, nutrients, competence for food and predation pressure, as well as proximate factors such as nutrition, temperature, and socio-sexual influences are explained in relation to the main predictor:

photoperiod. The main seasonal patterns of the domestic species included in the chapter are presented. This review also includes an update on socio-sexual signals, with sheep as reference model (the ram effect), and how these signals can be included in field practices to induce out-of-season births. Although still scarce, information on the use of the ram effect in cyclic ewes is updated. Lastly, the information on how socio-sexual signals can alter seasonal reproductive patterns is presented.

1. Introduction

The reproductive patterns of an animal are a consequence of the interaction of the endogenous regulatory mechanisms – mainly endocrine– and environmental signals. These signals may affect reproductive mechanisms deeply, i.e., females can stop cycling in some periods of the year, or due to the presence of a dominant individual on the group, or can ovulate and come into estrus during the seasonal non-cycling period due to the acute stimulus of male presence.

2. Environmental Regulation of Reproduction in Mammals

It is well known that the expression of a given trait (phenotype) in an animal depends on the combined influence of both, genetic factors (genotype) and environmental factors. The main environmental factors influencing animal reproduction are temperature, humidity, amount and distribution of rainfall, solar radiation and photoperiod, nutrition, productive system management, social interactions among individuals within the same population, predator-prey interactions, parasite- and pathogen- host interactions (Sadleir, 1968; Giwercman and Giwercman, 2011, Taberlet et al., 2011, Burns et al., 2010).

Most wild mammals, especially those of greater size and longevity, are to some extent, seasonal breeders (Goldman et al., 2004). Such animals limit their mating activity and offspring births to well defined seasons of the year. However, some domestic species such as cattle, pigs and rabbits exhibit no seasonal breeding if they are raised in environments with mild climatic changes throughout the year.

2.2 Seasonal Reproductive Strategies

Reproduction is a metabolically highly demanding process, and generally offspring are quite more sensitive to deleterious environmental factors than their parents (Foster and Nagatani, 1999). Reproductive strategies vary with the genetic background of different animal species, and the most important environmental factors are those having greater influence on offspring survival. Many mammalian wild species inhabiting temperate zones adjust their reproductive season so that offspring births are concentrated during spring. Available resources are most scarce in winter, and offspring being born in spring have better chances of survival the older and heavier they are when they will be forced to face wintertime conditions. On the other hand, it seems to be easier, from an evolutionary perspective, to change the timing of the mating season than to change the duration of gestation or lactation.

The degree of reproductive seasonality expressed by any animal can vary markedly in intensity and timing. Variations are driven according to the above mentioned environmental factors, the species to which it belongs, its gender, its particular genotype. However, variations are also driven accordingly to many factors pertaining to the individuals' life history, especially their reproductive status, and amount of body energetic stores.

2.3. Extrinsic and Intrinsic Factors and Ultimate and Proximate Factors Influencing Seasonal Reproduction

Factors having an influence on seasonal reproduction in any animal can be classified as intrinsic and extrinsic factors (Bronson, 1989). While intrinsic factors are related to genotype, and belong to the individual itself, extrinsic factors are related to the animal's environment. An example of intrinsic factor is life expectancy, as related to annual environmental variations: in an animal having a life expectancy of approximately one year or less, seasonality will be barely expressed, and the animal will develop opportunistic breeding strategies. Alternatively, an animal having a life expectancy of several years will have more chances of giving birth to viable offspring when restricting births to the most favorable seasons of the year. Similarly, the bigger the body size, the higher the chances of expressing seasonal reproduction, since a bigger animal has bigger energetic body stores, and can postpone easily its breeding activity to seasons more favorable for the newborn. Body size is, however, less important than both life expectancy and diet flexibility: an animal depending on a reduced spectrum of food will generally breed much more seasonally than an animal of similar traits but which is able to feed on a more flexible and varied diet. Another relevant intrinsic factor is gender. Generally speaking, males will tend to have longer breeding seasons than their female counterparts, since spermatogenesis commonly requires significantly more time to complete than ovarian follicle maturation and ovulation (Simpson et al., 1982, Schlatt et al., 1995), and masculine earlier recrudescence of breeding activity may facilitate intrasexual competition for mates (Prendergast, 2005).

Environmental (extrinsic) factors which are decisive on reproductive activity can be classified as ultimate and proximate factors, according to the time when they act on breeding activity. Ultimate factors are important in the long term, from an evolutionary point of view. Generally, the most important ultimate factor is food availability and its influence on energetic balance (Bronson, 2009), as reproduction is energetically highly demanding. The costlier period in mammals extends from late gestation to the first part of lactation. These breeding activities will suffer a strong selective pressure to occur in seasons of the year when most food is available, generally in spring and summer. Other ultimate factors which might be of importance are intra- and inter-species competition for resources, as well as strategies aiming at avoiding or limiting predation on offspring.

2.3.1. Ultimate Factors

2.3.1.1. Latitude and Seasonality

High latitudes display great annual variations in photoperiod and ambient temperature. Most animals adapted to such climates have short, well-defined breeding seasons, whereas tropical latitudes, where photoperiod and temperature vary little along the year, are inhabited by many more animals with long breeding seasons, and many tropical animals breed all year round (Bronson, 1988). Thus, for any given species, the breeding season generally prolongs as latitude diminishes. The latitude at which reproduction becomes annual diminishes as the animal's life expectancy increases. Furthermore, climatic conditions do vary annually. Animals with short life expectancy vary more or less markedly their seasonal reproductive cycles annually, according to prevalent conditions. Conversely, inter-annual variations in reproductive activity tend to be smaller in animals with long life expectancy.

2.3.2. Energy Balance

Generally speaking, the periods of the year when food availability becomes a bottleneck are very important as driving forces for seasonal reproduction. This is the ultimate cause of seasonal reproduction in all mammals and the proximate cause in many other species (review: Bronson, 2009). Interestingly, the smaller the size of the mammal, the more important tends to be the lactational bottleneck, whereas as body size increases, post weaning food availability generally becomes the main bottleneck. In most ancestors of livestock species, weaning food availability was very important.

2.3.3. Nutrients

Besides energetic balance, availability of different key nutrients varies throughout the year. This fact can become, for some species, an important limiting factor to seasonal reproduction.

2.3.4. Competence for Food and Predation Pressure

Several species which are competing totally or partially for the same resource (i.e. pasture) can be strongly selected for desynchronization of their breeding seasons. Such a situation has been well documented for herbivorous ungulates in the African savanna (Mossman & Mossman, 1962).

2.3.2. Proximate Factors:

Proximate factors are responsible for immediate influences on breeding activity.

2.3.2.1. Nutrition

Nutrition is a very important factor. It can act not only as a paramount ultimate factor, but as a proximate factor as well in many cases. Furthermore, if food availability falls below a threshold that may vary according to species and populations, an animal will not breed. Moreover, changes in food availability can influence seasonal breeding patterns. This effect has been extensively studied in sheep, and marked differences in sensitivity to food availability have been described. Generally speaking, the effect of food availability on seasonal breeding is much stronger in breeds originated from Mediterranean or tropical climates than in breeds originated from temperate latitudes (Martin and Walkden-Brown, 1995, Boukhliq et al., 1996, Bielli et al, 1999, Zarazaga et al, 2005). Conversely, food availability or even some increase in nutrient availability can be the proximate factor triggering breeding activity.

2.3.2.2. Temperature

Ambient temperature can also be a proximate factor, since warmer temperatures could trigger reproductive activity. Conversely, too high temperatures could limit reproductive activity (Haim et al., 2005).

2.3.2.3. Social Factors

The reproductive activity of fellow individuals can trigger reproductive activity of others within the same population. This is going to be dealt with in the second part of the present chapter.

2.3.2.4. Predictors: Photoperiod

The most widespread proximate factor timing seasonal reproduction is the annual photoperiodic variation (Ortavant et al., 1988). It is well known that due to the inclination of the Earth's rotation axis and Earth's translation along its orbit, the duration of daylight (photoperiod) varies along the year, and that such variation is more marked nearer the poles than near the Equator. Photoperiod is a very reliable predictor of future environmental conditions, since it is a very constant environmental clue. Furthermore, it predicts seasonal changes in climate and food availability (Bradshaw and Holzapfel, 2007). Some species (i.e., sheep, goat, deer) are known as 'short-day breeders' because their breeding season occurs mainly when days are getting shorter (summer and autumn). Such species normally have gestation lengths of 5-6 months. Thus, their offspring are usually born in spring. On the other hand, other species having either short gestation lengths (1-2 months, i.e., hamster, mink) or long gestation lengths (horse) are 'long-day breeders', and breed in late winter or spring, with their offspring also being born mainly in spring.

2.4. Mechanisms Regulating Seasonal Reproduction with Photoperiod as a Predictor

Most seasonal breeding mammals studied have been shown to possess a self-sustained endogenous rhythm of seasonal reproductive activity (circannual biological clock, reviews: Rensing et al., 2001; Lincoln et al., 2006), which is either synchronized or entrained by photoperiod (review: Kumar, 1997). Daylight is perceived essentially by the eyes. The retina of the eye is stimulated by light and transmits neural information through the optic nerve to the suprachiasmatic nucleus (a group of neurons located in the ventral side of the encephalon). The information is transmitted to the stellate ganglion (anterior cervical ganglion) and then to the pineal gland (Bittman et al., 1983). The pineal gland is a small endocrine gland in the brain. Its shape is similar to a pine cone (hence its name). The pineal gland apparently evolved from a photoreceptor organ which used to be situated on the roof of the brain in primitive vertebrates (Ekström and Meissl, 2003). It is pivotal in mediating the effects of photoperiod on reproduction, as it translates neural stimuli mediating photoperiod into hormonal stimuli. The hormone secreted by the pineal gland is melatonin (N-acetyl-5-methoxytryptamine).

Melatonin is a small indole compound (chemically related to aminoacids) secreted by the pineal gland when the animal is in a dark environment. Melatonin secretion is inhibited by daylight. High melatonin concentrations in blood transmit the information that the animal is in a dark environment to the animal's organs and tissues. Thus, melatonin can either inhibit ('long day breeders') or stimulate ('short day breeders') reproductive activity (Figure 1).

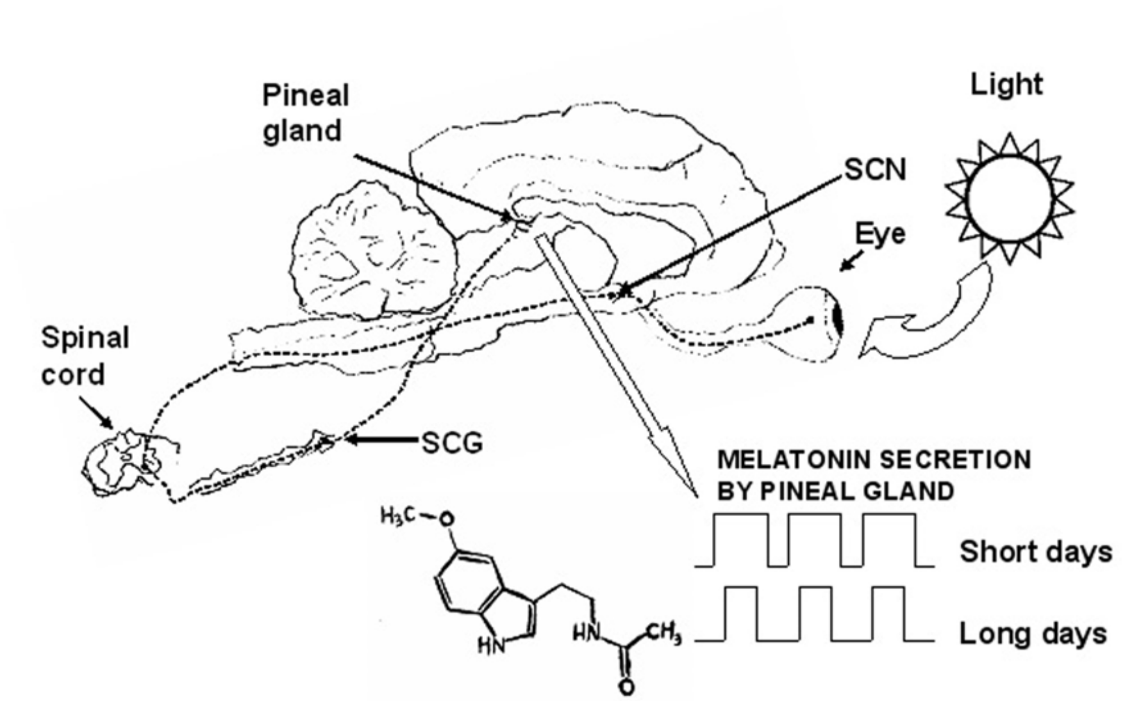

Figure 1. Regulation of pineal gland melatonin secretion by photoperiod: schematic sagittal view of a sheep's eye and brain. Light is perceived by the eye's retina (i.e., photic information is converted into neural information). Neural information generated in the retina is transmitted to the suprachiasmatic nuclei (SCN). Connections from the SCN reach the spinal cord. Spinal neurons send the information to the anterior cervical ganglion (ACG). Postganglionic SCG neurons send neural paths to the pineal gland, where neural information is converted into hormonal information (high melatonin secretion levels during dark hours). The duration of high melatonin blood levels indicates the duration of dark hours to the whole animal's body. Melatonin is a small indole molecule (bottom of figure).

2.5. Seasonal Reproduction in Livestock Species

2.5.1. Sheep

Most sheep breeds show reproductive seasonality, normally breeding in late summer and autumn. Because of genetic differences, different breeds of sheep maintain different levels of photo-responsiveness (Gómez-Brunet et al., 2008). This is one reason why differences of breeding time occur between different breeds of sheep. Seasonal reproduction occurs widely in mid and high-latitude breeds, but is very weak or does not exist at all in breeds originated near the Equator, i.e., most hair sheep breeds.

Both rams and ewes have seasonal variations in breeding activity, but females are more seasonal than males, and ewes' breeding season is normally shorter than rams' one, from the same breed. Temperature, nutrition, social influences, lambing date and lactation period can modulate photo-periodical influences (Scaramuzzi and Martin, 2008; Forcada and Abecia, 2006). It is possible to manipulate breeding season timing by altering the photoperiod with artificial lightning or with melatonin implants that simulate melatonin blood concentrations similar to the breeding season.

2.5.2. Goats

Goats are also well known as seasonal breeders. Seasonal patterns are similar to those of sheep. The beginning and duration of the breeding season is dependent on several factors such as latitude, climate, breed, physiological stage, presence of the male (buck effect), breeding system and photoperiod. In temperate regions, goats breeding season occurs in autumn and winter. In tropical regions, goats are normally continuous breeders, but anestrous periods are frequent when food is scarce. Generally speaking, tropical origin breeds are less seasonal or not seasonal at all. Interestingly, melatonin implants are markedly more effective in goats than in sheep breeds of Northern Europe (Chemineau et al., 1992). Photoperiodic treatments coupled with buck effect allow synchronization of ovulation but fertility results are poorer than those of hormonal treatments (Fatet et al., 2011).

2.5.3. Cattle

Cattle breeds originated from temperate climates are normally not seasonal breeders. However, ancestral species of domestic cattle are seasonal breeders, and cows living in very high latitudes do breed seasonally, with calving concentrating in spring (Borisenkov et al., 2004). Furthermore, there are mild seasonal variations in hormone secretion in bulls (Stumpf et al., 1993). Thus, it seems that domestication and selection for all year round breeding has been successful in cattle, but still a hidden endogenous rhythm exists, which can manifest itself under extreme conditions.

2.5.4. Swine

Female pig ancestors (wild European boar) are seasonal polyestrous breeders, with two reproductive periods: the main period extends from November to March in the Northern Hemisphere, and the secondary from April to May (Mauget, 1972; Mauget et al., 1984). Feral pigs adapt easily to seasonal breeding. However, seasonal breeding patterns of domestic pigs are more flexible with the duration and timing of their breeding seasons (Ravault et al., 1982). In the domestic pig seasonal variations in prolificacy still exist. Boars not only show decreased steroid synthesis, sperm counts and libido in summer when compared with the winter but also show a biphasic pattern with a transient increase in spring. In cyclic sows anestrus may appear mainly in summer and occasionally in February/March (Northern Hemisphere) (Claus and Weiler, 1985). Periods of infertility and late pregnancy loss are frequent in both sows and gilts during summer (Bertoldo et al., 2009), and periods of early pregnancy disruption exist along summer and early autumn (Tast et al., 2002). However, swine can normally breed throughout the year if food and housing are adequate (Macchi et al, 2010). Both hormonal melatonin treatments and photoperiod manipulation are effective, but not a sustainable solution to seasonal infertility, mainly because of economic reasons (Bassett et al., 2001).

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Biographical Sketches

Rodolfo Ungerfeld, Biologist (Universidad de la República, Uruguay), Master in Biology-Physiology (Programa de Desarrollo de Ciencias Básicas, PEDECIBA, Uruguay), PhD (Swedish University of Agricultural Sciences, Sweden). Full Professor of Animal Physiology at the Facultad de Veterinaria (Universidad de la República, Uruguay). Author of more than 70 peer-reviewed articles in the field of reproduction, endocrinology and behavior in ruminants, including work with sheep, goats, cattle, and deer. Scientific reviewer for more than 30 international journals, and member of the Editorial Committee of 3 journals. Researcher of PEDECIBA, member of the standing Committee of Posgraduate Studies. Winner of the Prize of the National Academy of Veterinary Science, Uruguay (1997, 2004, and 2009), and of the Caldeyro-Barcia Award (most important scientific award in Uruguay) in 2003.

Alejandro Bielli, graduated in Veterinary Medicine and Technology at the Universidad de la República (Montevideo, Uruguay) in 1992 and took graduate studies (Licenciate in Veterinary Medicine, 1995 and PhD, 1999, both in histophysiology of seasonal testicular activity of rams, and the interaction with nutrition) at the Swedish University of Agricultural Sciences (Uppsala, Sweden). Full Professor at the Facultad de Veterinaria, Universidad de la República (Uruguay). Research interests: nutritional influences on seasonal reproduction, fetal programming and early life nutritional influences on reproductive activity. Author of 25 research papers in international journals, 4 chapter books and numerous presentations in international scientific meetings on animal reproduction and histology. Researcher of PEDECIBA, Uruguay (2003), Member of the standing Committee of Graduate Studies, Veterinary Graduate Studies Program, University of Uruguay (2006-), winner of the Prize of the National Academy of Veterinary Science, Uruguay (1999 and 2010).