

Seasonality of reproduction and production in farm fishes, birds and mammals

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A very large majority of farm animals express seasonal variations in their production traits, thus inducing seasonal availability of fresh derived animal products (meat, milk, cheese and eggs). This pattern is in part the consequence of the farmer's objective to market his products in the most economically favourable period. It may also be imposed by the season-dependent access to feed resources, as in ruminants, or by the specific requirements derived from adaptation to environmental conditions such as water temperature in fish. But seasonal variations in animal products are also the consequence of constraints resulting from the occurrence of a more or less marked seasonal reproductive season in most farm animal species including fish, poultry and mammals. Like their wild counterparts, at mid and high latitudes, most farm animals normally give birth at the end of winter-early spring, the most favourable period for the progeny to survive and thus promote the next generation. As a consequence, most species show seasonal variations in their ovulation frequency (mammals and fish: presence or absence of ovulation; birds: variations or suppression of laying rates), spermatogenic activity (from moderate to complete absence of sperm production), gamete quality (variations in fertilisation rates and embryo survival), and also sexual behaviour. Among species of interest for animal production, fishes and birds are generally considered as more directly sensitive to external factors (mainly temperature in fish, photoperiod in birds). In all species, it is therefore advisable that artificial photoperiodic treatments consisting of extra-light during natural short days (in chickens, turkeys, guinea fowl, sheep and goats) or melatonin during long days (in goats, sheep) be extensively used to either adjust the breeding season to animal producer needs and/or to completely overcome seasonal variations of sperm production in artificial insemination centres (mammals) and breeder flock operations (poultry, fish farming). Pure light treatments (without melatonin), especially when applied in open barns, could be considered as non invasive ones which fully respect animal welfare.

Keywords: birds, fish, mammals, photoperiod, reproduction, seasonality

Seasonal variations in marketed products of animal origin

Seasonal availability of animal products for human consumption has been common long before domestication. In farm animals this pattern has led to the development of breeding stocks aimed at providing animal products all the year round. Despite the fact that domestication processes, which reduce the dependency of farm animals on natural conditions, generally reduce seasonality of reproduction compared with their wild counterparts, a majority of animal-derived products remain accessible only seasonally. This is a consequence of the cycles of reproduction and

production which are themselves seasonal as domestic stock have inherited the characteristics of the natural populations from which they originate (see below and Ortavant *et al.* (1985) also Bronson (1989)).

From an economic standpoint, mass distribution controls large portions of the market in animal products with a long-lasting evolution, such as with poultry, towards further-processed rather than fresh products. This has boosted the demand for more standardised products, a trend now shared by distributors and consumers who are increasingly becoming far distant, culturally, from agricultural constraints, and demand access to most types of animal products, in quantity and quality, throughout the year. As a consequence products like goat cheese, lamb meat, eggs and fish filets have become available year round.

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In recent years, European animal production systems have changed dramatically. This has led to two alternative strategies which can be defined schematically as (a) intensive systems in which farm animals are expected to be less dependent on their environment and (b) extensive systems in which animals are subjected to the natural variations of their environment. These rapid changes have meant the control of seasonal production and reproduction in farm animals have become major research goals. Moreover, the increased knowledge on physiological and genomic control of these traits will facilitate inter-species comparisons regarding adaptative strategies. This will help in choosing the best breeding periods and will also provide useful information to adapt current and develop new control reproduction techniques (Malpaux *et al.*, 2001; Malpaux, 2006).

Under temperate climates, a large majority of marketable animal products show quantitative and qualitative seasonal variations. These include the quantity of lambs and kids, the quality of dairy cattle milk and the collection of sheep and goat milk which greatly vary throughout the year. That induces high variations in the price paid to producers and/or in the ability of these different products to be processed by the food industry. For example in cow milk, fat and protein contents are low in spring and summer but high in autumn and winter (Figure 1). In France, goat milk production is highly seasonal, ranging from over 30 millions litres in May to about 10 millions in November (Figure 2). That induces wide variations in prices paid to the producer (53%). Similarly, monthly mean production of lambs is low in October and high in April, causing significant changes to the market price of lamb meat (Figure 3). In extensive poultry systems of production, which constitute a minority of farmers in Europe and other developed countries, availability of meat and eggs is also seasonal with large variations between species. Thus in France, the

'natural' hatching period for free-range chickens extends from early March to mid October while in guinea fowl it is from late April to mid September. Similarly, fish farming products may also be marketed in a very seasonal way according to species and production systems.

The reasons of such variations will be discussed below. The milk industry has long been able to adapt technically to remedy these variations in order to provide a regular product to the consumer but this requires expensive technological processing. Thus in recent years the food industry has put pressure on milk producers to adapt their production systems to give a more constant final product (see section below: **Using artificial photoperiodic treatments**).

However, a significant number of the above cited variations in milk production (quantity and quality) are, for various reasons, due to pre-determined adjustments of the lactation period by milk producers. Such adjustments may have significant impact on milk quality especially in dairy cows for which producers schedule fertilisations in order to synchronise calvings and therefore milk production with the period of maximum food availability. In dairy cattle, in which ovulations occur all year round, it is the breeder's decision rather than occurrence of a rest season, which determines the dates of conceptions. In contrast, in a majority of seasonal breeding species, including sheep and goats, induced ovulations are generally required if farmers want to fertilise females for a specific season, out of the breeding season.

Thus, seasonality of animal product availability is the result of several intricate factors which link breeder's decisions to the underlying physiological mechanisms of the adaptation of farm animals to local environmental conditions. We will focus here on the basic mechanisms involved in the seasonal variations of reproductive activity which we consider as one of the main remaining constraints within some domestic animal

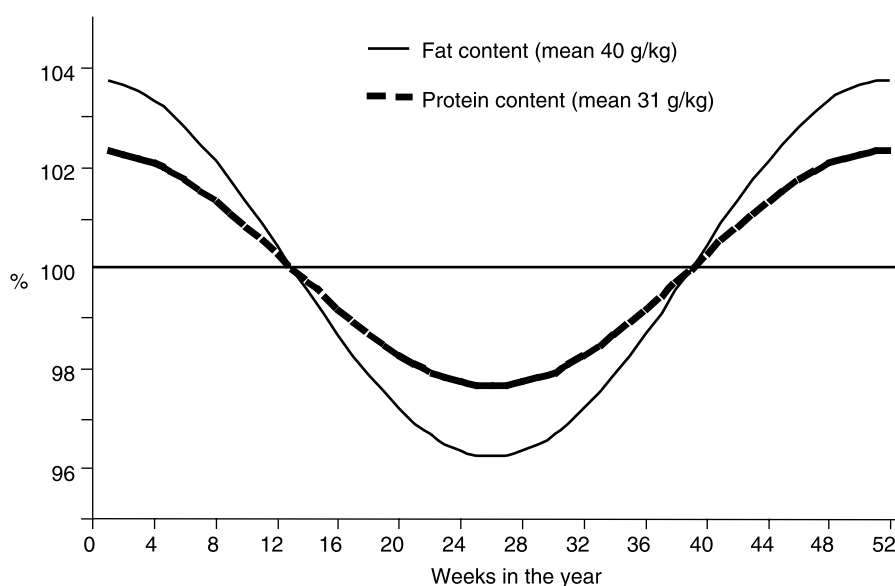


Figure 1 Seasonal variations (% of the annual mean) in dairy cattle milk composition in France (adapted from Coulon *et al.* (1991)).

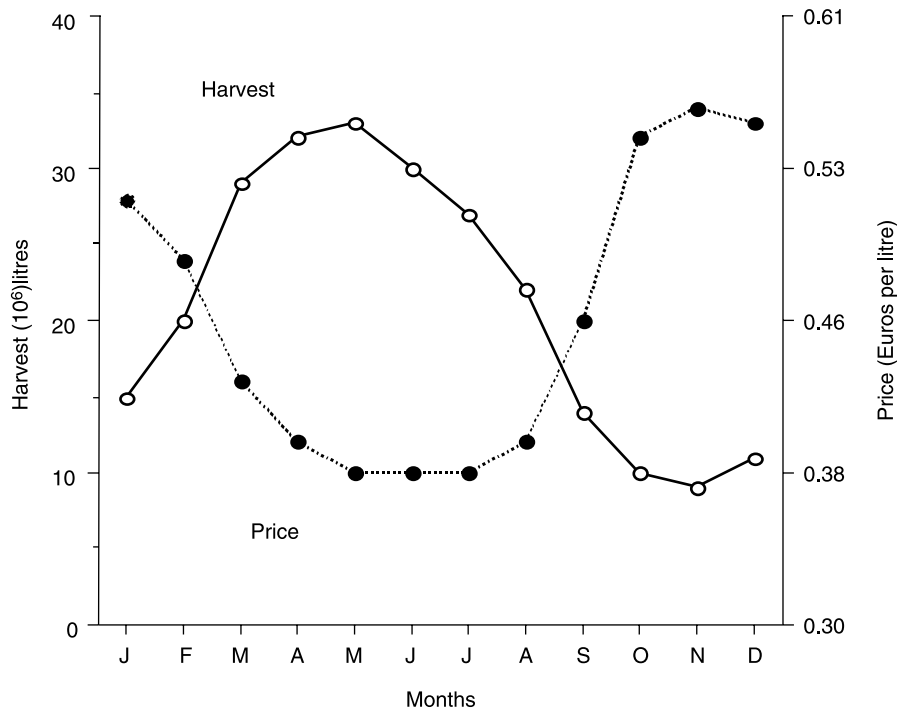


Figure 2 Seasonal variations in the harvest and farm price of goat milk in France (year 1992; adapted from Chemineau *et al.* (1996)).

populations. As our domestic animals are, with the exception of certain new fish species, the result of a very long process of domestication from wild populations, it is worth exploring whether the ancestors of domestic animals and their wildlife equivalents show natural seasonality of reproductive activity.

Seasonality of reproductive activity is an old story first shown by wild species

The occurrence of a specific lambing season in sheep of the Late Stone Age (end of 2nd millennium BC) was shown in South Africa by monitoring the ratio of several stable oxygen isotopes in tooth enamel (Balasse *et al.*,

2003). More recently, using the same technique in sheep teeth collected in the north of Scotland and in the extreme west of Brittany, Balasse *et al.* (2006) demonstrated the existence of a more intense expression of seasonality (lambing season) in sheep originating from Scotland compared with Brittany. Despite thousands of generations of human-controlled selection the results indicate that seasonality has not been bred out of the majority of 'modern' domestic species.

Authors having described the occurrence of a seasonal dependence of reproductive activity in wild mammalian species living in temperate zones are numerous with time of littering being taken as the main reference in most reports. In a majority of cases, the littering season occurs

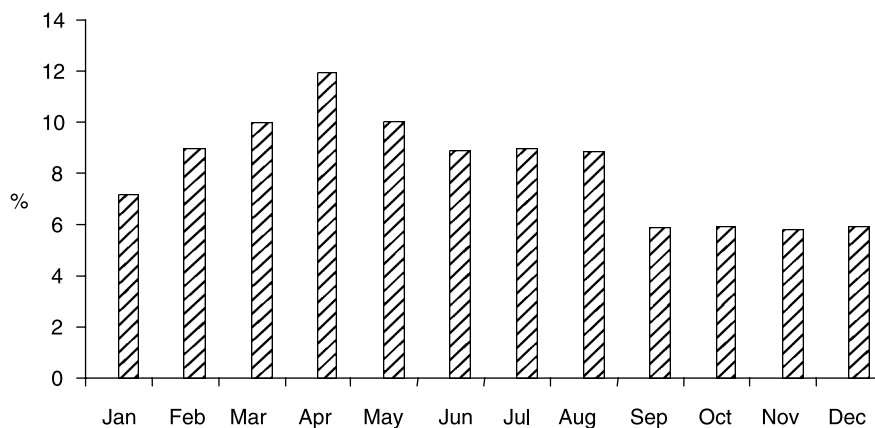


Figure 3 Seasonal variations (% of the total annual production) in ovine meat production in 2004 (4.4×10^6 head) in France (source: Groupe d'économie du bétail (2006)).

from late winter to early spring. This ensures maximal survival rate of the progeny in mammals because this period provides high food availability in these species (Ortavant *et al.*, 1985). Similarly in many feral birds (partridge, quail, granivore birds), the nesting season starts in spring as it also corresponds to the period when food becomes available (onset of the reproductive or hatching season in insects, which are the main source of proteins for recently hatched chicks; period at which plant-derived feed becomes available; Sauveur (1988 and 1996)). In fish which are much more directly dependent on water temperature and to a lesser extent on photoperiodic conditions, spring is also the most commonly observed period for production of first-feeding fry in temperate zones as it corresponds to the period of increasing temperature and day length (Bromage *et al.*, 2001). Young fry have increasing quantities of phytoplankton and zooplankton available for feeding during spring and the juveniles will benefit from a long period of growth during summer and thus be stronger for their first winter of life (Conover, 1992). This is the case of salmonids, which are extensively used in aquaculture. However, variability between fish species appears really very high as alevins, from other species reared under temperate climate, may be naturally released in winter as seen with Mediterranean seabass or seabream (Zohar *et al.*, 1984), or in summer, with cyprinids (Billard, 1995) or turbot (Mugnier *et al.*, 2000).

Thus, this highly adaptive reproductive activity is in many species part of the species-specific mechanism developed over millenariums to produce life strategies adapted to local geographic and climatic environments at the time of parturition. Examples of species-specific strategies include the very short breeding season of the mouflon (Santiago-Moreno *et al.*, 2001), or the delayed implantation of fertilised ova in the roe deer, ferret and bison (in roe deer: fertilisation in July, implantation in December;

Thimonier and Semperé (1989)) and hibernation in the European hamster, European bear and hedgehog (Bronson, 1989, Canguilhem *et al.*, 1988; Saboureau *et al.*, 1991). While it is highly likely that many other strategies remain, at least in part, unknown, those expressed in mammalian species raised for meat and milk production have appeared, despite domestication, as highly predictive of the seasonal variations of their environment. One of the most striking adaptive mechanisms expressed in domesticated mammalian species is the adjustment of the reproductive period (ovulatory activity, sperm production) with the length of gestation so that a given species develops the best possible strategy to provide its progeny with optimal conditions for feed availability and climatic environment at the time of parturition. Thus, horses and sheep litter in spring but whilst mares present their maximum ovulatory activity during late winter and spring, in ewes it occurs during late summer and autumn (Figure 4). In fish pike, spawning occurs during the early spring in shallow weedy water that warms rapidly during the day, while cyprinids will spawn later in the year in already warm deeper ponds. It is obvious that these different predictive strategies, in which the timing of reproduction is precisely adjusted to the environment in order that births coincide with a favourable season for the progeny, constitute a key element of the adaptive mechanisms developed over time and so allow species to survive and proliferate under harsh conditions, i.e. when climatic variations of the environment (light, temperature, food availability) are very variable.

Although seasonality in reproduction is found in all vertebrate classes, some biological specificities may involve various seasonal requirements of energy for reproduction. Firstly, homeothermic mammals and birds require more energy for their basal metabolism than poikilothermic fish. Secondly, oviparous birds and fish need more energy than mammals during gametogenesis for oocyte vitellogenesis.

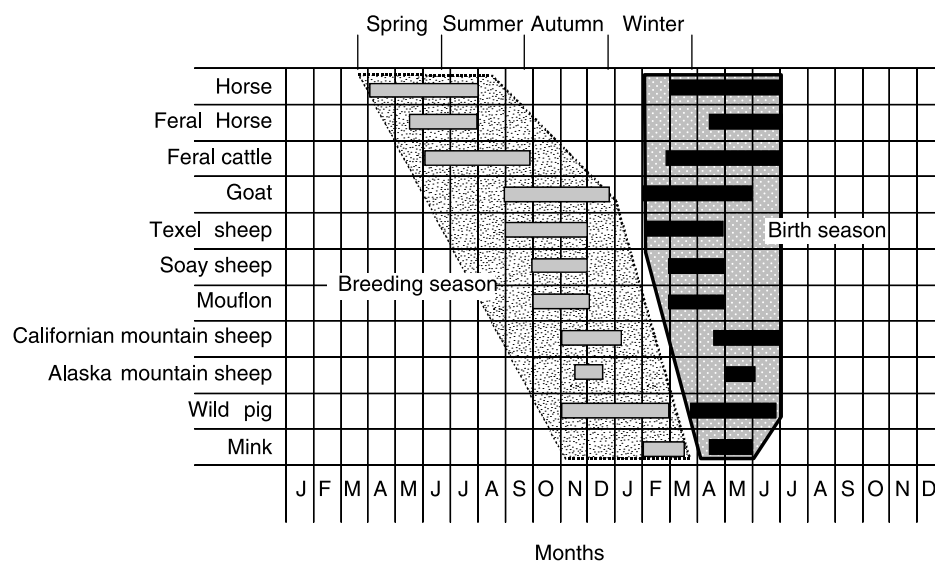


Figure 4 Timing of the annual reproductive cycle of some seasonal breeders. (adapted from Ortavant *et al.* (1985)).

This is especially so in fish which release a large quantity of eggs because youth survival is very low in the natural aquatic environment. Finally, gestation (mammals) and parental care and feeding (mammals and birds), require more energy although this is not the case with farmed bony fish (except in some tilapias). These specific needs have different consequences in the timing of energy requirement and mobilisation for the success of reproduction.

Seasonal variations of gonadal activity, sexual behaviour and littering in farm animals

Alterations in reproductive activity are associated with alterations in gonadal activity and, as such, large species specific differences in both the timing and duration of gonadal activity can be seen. For example, the frequency of ovulations in unmated Alpine and Saanen dairy goats, even when maintained in excellent body condition, varies dramatically from 0 (March to September) to 100% (October to January) which means a long period of sexual rest, the anoestrous season (Figure 5). Oestrous behaviour is strongly associated with ovulatory activity in these breeds (Chemineau *et al.*, 1992). Ile-de-France ewes behave in the same way but, during the anoestrous season, some females show isolated ovulations without associated behaviour (Thimonier and Mauléon, 1969), and in horses a majority of mares stop ovulations from December to May (Palmer and Driancourt, 1983).

In contrast to sheep and goats, dairy or beef cows, when not mated, do not stop ovulatory activity, an indication that they are potentially able to breed year round. Despite this, factors including the interactions

between body condition and nutrition, the presence of a calf (if calving in winter) and photoperiodic rhythm synergistically converge to induce a strong seasonal pattern of the post-partum ovulatory activity in beef cattle characterised by a limited period of time for ovulations (Ingrand *et al.*, 2003; Agabriel *et al.*, 2004).

In males from the seasonal species cited above, spermatogenic activity and sexual behaviour do not stop but are also highly dependent on season. Thus in Soay rams, a primitive breed from north Scotland, testicular size (which reflects spermatogenic activity), plasma FSH and testosterone concentrations as well as sexual 'flush' and aggressive behaviour reach their maximum between August and November, the 'rut' season in this breed (Lincoln, 1979). In Ile-de-France rams, testicular weight and sperm production per testis (directly measured at its output) vary from less than 200 g and 1 billion per day in March, to more than 300 g and 5 billion per day in September, respectively (Ortavant *et al.*, 1985). Similarly, Alpine bucks display dramatic variations in sexual behaviour (0 to 1.5 matings in 10 min), sperm individual motility (2.5 to 3.5 over 5) and fertilizing ability (20 to 70% of kiddings after AI) between the spring-summer and autumn-winter periods (Delgadillo *et al.*, 1992). These variations are associated with deep changes in ejaculate volume and sperm concentration which, in this species showing a deleterious effect of seminal plasma on *in vitro* sperm survival, have important implications on semen technology. Stallions also show seasonal variations in sexual behaviour and sperm quality, the lowest season being in winter and the highest in spring-summer (Magistrini *et al.*, 1987).

As previously mentioned, the intensity of seasonality of reproductive activity is highly variable between and within

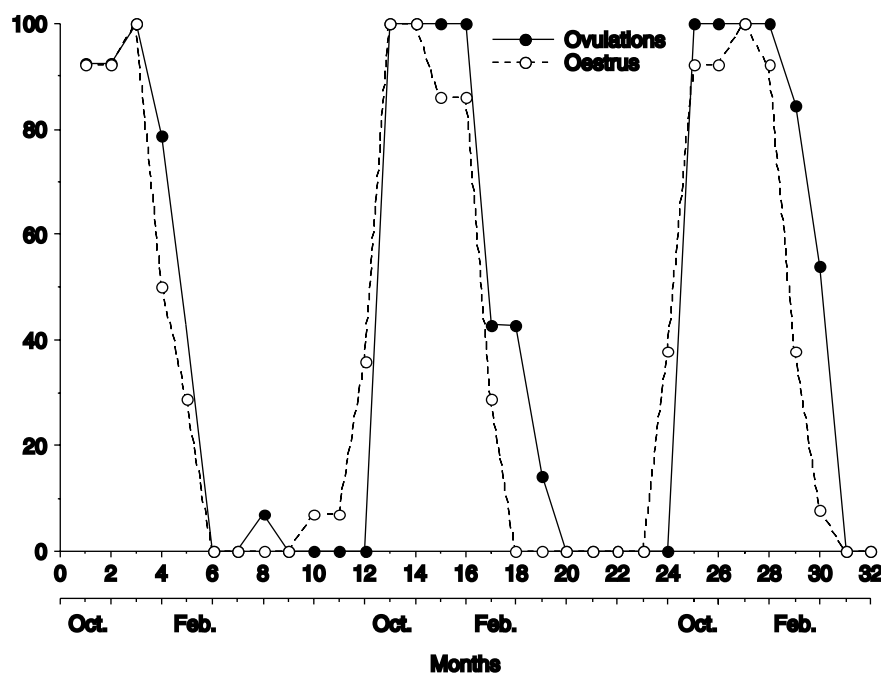


Figure 5 Seasonal variations of the occurrence of ovulations and oestrous behaviour in Alpine goats (adapted from Chemineau *et al.* (1992)).

species. Thus, in fish, which are found at all latitudes, opportunistic strategists are more common in tropical latitudes and periodic strategists are more common in temperate and Arctic latitudes (Vila-Gispert *et al.*, 2002).

In the Bovidae family, cows do not stop their ovulatory activity over the year while goats are in anoestrus for, depending on their genetic origin, 250 days or more. Similarly, domestic sows present moderate seasonal variations of their reproductive activity while wild sows completely stop completely in spring-summer.

Within a given species, it has long been established that the various breeds may express variable degrees of seasonality. For example, Texel and Soay ewes are highly seasonal, while Merino and Manchega ewes present more discrete expression of seasonality (Hafez, 1952; Santiago-Moreno *et al.*, 2000). Breeds raised in more southern areas, especially in the subtropics and the tropics (north Africa, west Africa, West Indies, tropical Asia and the Americas) generally present low seasonality or cycle all the year round with no anovulatory period (Gonzalez-Stagnaro, 1983; Khaldi, 1984; Yenikoye, 1984; Chemineau, 1986; Mahieu *et al.*, 1989). This is an interesting trait of these breeds for local farmers who can then organise the breeding season of their flock without expensive hormonal treatments. Unfortunately, a marked seasonality is expressed in these breeds when subjected to the wide photoperiodic variations and temperate climates of septentrional countries, thus constituting a major limitation to their extensive use in animal production systems in these countries (Chemineau *et al.*, 2004).

However, in temperate breeds maintained under environmental conditions similar from which they originate, an intra-breed variability may also exist. In some species (sheep, goat), some reproductive traits including the onset,

offset and duration of the breeding season were found heritable, therefore becoming candidates for genetic selection (Ricordeau, 1982; Quirke *et al.*, 1986; Hanrahan, 1987; Smith *et al.*, 1992; Al Shorepy and Notter, 1997). However these traits are quite difficult to measure at farm level because of their strong link with the female production cycle. An alternative approach could be to use more indirect traits such as the presence or absence of ovulatory activity in spring, a trait found to be heritable in Merino ewes (Hanocq *et al.*, 1999).

The existence of a genetic basis for seasonality of reproduction also suggests control by a polymorphism of specific genes. In the Landaise grey goose, laying intensity (i.e. number of eggs laid per week by 100 females) varies from zero in January to 50% in April-May (Figure 6), and could also be genetically selected (Basso *et al.*, 2006). The existence of a relationship between intensity of anovulation (presence/absence of ovulations) and the relative frequency of precise alleles of the melatonin receptor MT1 in Merino sheep was shown and suggests that it could be used for selecting animals on the presence of favourable alleles (Pelletier *et al.*, 2000; Notter *et al.*, 2003; Notter and Cockett, 2005). However, the genetic variability of seasonality, as it occurs for many other traits, is not dependent on the polymorphism of a single gene but on a variety of genes most of which still remain to be identified and assessed prior to any possible application in selection.

Fish show a very large diversity of reproductive strategies within many of their species (Jalabert, 2005). However, as a large quantity of energy is required during vitellogenesis to produce the millions of eggs containing the reserves for embryos, this process lasts several months under temperate climates (Jalabert, 2005). Thus, seasonal species of fish

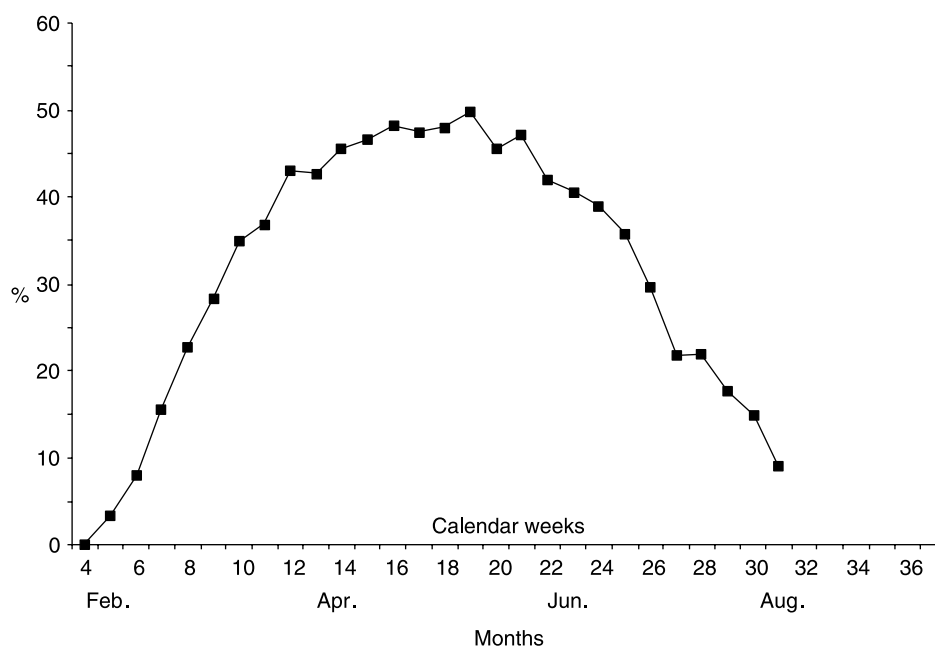


Figure 6 Laying intensity (= number of eggs laid per week per 100 females) in the Landaise grey goose (adapted from Mialon-Richard *et al.* (2004)).

usually show an annual sexual cycle where their spawning period occurs only once a year. During this period salmon, trout and carp spawn all their eggs at once. Other commercial fish species females are multi-spawners however, like common perch, turbot, halibut or cod. Here the reproductive period may last several weeks (McEvoy and McEvoy, 1992). In contrast to what is observed in domestic mammals, spermatogenic activity is usually completely stopped, for a vast majority of the year and starts at a specific season, producing synchronous waves of germinal cells (Maisse and Breton, 1996; Gomez *et al.*, 1998). Breeders produce sperm during a long part of the spawning season and can be used several times for *in vitro* fertilisation. However the quality of the sperm may vary (Billard, 1986). Secondary sexual characters are not always well marked in fish, and they may only appear shortly before the breeding period. Pheromones, which regulate sexual behaviour, originate from hormones (prostaglandins and steroids; Stacey (2003)) involved in the regulation of the last stages of gametogenesis and of gametes release, and are thus only released into water during the breeding season.

Diversity in fish reproductive strategy involves diversity in the timing of fish spawning (Webb and McLay, 1996). Thus, it occurs in late autumn to winter in salmonids (Bromage *et al.*, 1992), late winter to early spring in European sea bass, gilthead seabream (Zohar *et al.*, 1984) and cod (Hansen *et al.*, 2001), spring in Eurasian perch, (Migaud *et al.*, 2002), red porgy (Kokokiris *et al.*, 2001) and Atlantic halibut (Björnsson *et al.*, 1998), or late spring to summer in turbot, (Mugnier *et al.*, 2000) and carp (Billard, 1995). Embryonic development up to first-feeding fry depends on egg size and water temperature. Usually, this period is shorter in spring-summer spawning species than in autumn-winter ones. Thus, eggs develop within several weeks in salmonids and only a few days in cyprinids. However, eggs from the European sea bass, which spawns during the cold season, develop within 8 days at 13°C (Saillant *et al.*, 2001). Slowing down or speeding up the embryonic development and the growth of juveniles by adjusting water temperature and/or feeding, can be one way for fish farmers to partly schedule their production. Genetic selection may also be used in some cases to extend the reproductive period: a high heritability has been found in rainbow trout for the date of spawning ($h^2 = 0.65$; Su *et al.* (1997)) and several strains spawning at different seasons already exist for experimental or aquaculture purposes.

Seasonality is a combination of endogenous circannual rhythms with the entraining effects of photoperiodic and temperature variations

Thus a large proportion of farm vertebrates raised under temperate climates show seasonal variations in their gonadal activity and a precise timing in the year when females shed eggs to be fertilised by male spermatozoa. Within a specific species or breed, the so-called 'breeding season'

appears very stable from one year to another, with fixed dates of onset and offset of female ovulatory activity and a period of maximum quantitative and qualitative sperm production. Even within-species or within-breed variability in these dates exists, the average timing of the breeding season in a calendar year is always the same from one year to another, thus allowing a maximum fit with the variations in the environment. This timing is due to complex but highly precise underlying physiological mechanisms which allow animals to 'locate' their breeding season over the year and express their sexual activity at the right time, synchronously between sexes and with external environmental factors.

In some species of mammals, birds and fishes, similarly to the circadian 'clock' (i.e. with a free-running period close to 24 h) which generates endogenous circadian rhythms, a circannual 'rhythm', endogenous to animals, is likely to generate alternate periods of sexual activity with periods of sexual rest throughout the year. These alternate periods can be observed when animals are kept experimentally under constant photoperiodic regimens (constant short days, for example), over at least two consecutive years (mammals: Jansen and Jackson, 1993; Malpoux *et al.*, 2001; Malpoux, 2006; birds: Gwinner, 2003; fish: Bromage *et al.*, 2001). The physiological mechanisms underlying this circannual system remain largely unknown. Some information has been identified in two experimental models, rodents (Larkin *et al.*, 2002) and domestic sheep (Lehman *et al.*, 2002). The main part of the mechanism resides in the central nervous system and probably involves successive ability to alternately inhibit or stimulate the LH-RH neurons of the hypothalamus. Thyroid hormone T4 must be present at a constantly low plasma level for the expression of the endogenous rhythm (Billings *et al.*, 2002). It probably acts in the pre-mammillary area of the posterior hypothalamus in ewes. Associated changes in neuronal plasticity, identified by changes in PSA-NCAM, have been demonstrated (Lehman *et al.*, 2002). Similarly, changes in the expression and binding capacity of serotonergic receptor 5HT2A were observed in association with opposite stages of the endogenous rhythm (Chemineau *et al.*, 2003). In ewes, this endogenous rhythm is timed by discrete signals given by external changes in photoperiod (Barrell *et al.*, 2000).

The specific role of long days (LD) and short days (SD) in timing reproductive activity depends on species. In short-day breeders (i.e. animals which are fully sexually active during SD) like sheep and goats, SD are stimulatory and LD inhibitory of sexual activity. In contrast, SD inhibit while LD stimulate sexual activity in species sensitive to LD such as horses, mice and most poultry. These unique properties of the duration and variations of photoperiod to control reproductive activity in both sexes have, in practice, been of extensive use in farm animals (see below). However in mammals and birds subjected to a constant, normally gonado-stimulatory photoperiod, the day length-specific effect is not permanent. Animals «escape» and

become 'refractory' to the prevailing photoperiod: SD are no longer stimulatory in sheep or inhibitory in mares, LD are no longer inhibitory in goats or stimulatory in mares, chicken and turkey. In fish, in which both photoperiod and temperature may interact to regulate seasonality, occurrence of refractoriness has also been reported, for example, from the middle of autumn to early winter, gonads do not develop in mummichog, even under adequate temperature and long day-length conditions (Shimizu, 2003). This refractoriness could conceptually be considered as merely expression of the circannual endogenous rhythm. It can be 'broken' by transferring animals into the opposite photoperiod: refractoriness to SD, which occurs naturally in sheep in late winter, is broken by 2 months of exposure to LD in December-January, allowing the efficiency of stimulatory SD to be restored. Thus, by subjecting animals to opposite photoperiods, it is possible to control seasonality of reproduction. This property is now commonly used in photoperiodic treatments applied on farms and/or in AI centres. The definition of what is really LD and SD is not straightforward. For example, it is possible to define a threshold of photosensitivity based on the number of light hours per day, under which LD are stimulatory and below which SD are inhibitory (see reviews Malpaux *et al.* (1996) and Chemineau *et al.* (1996)). For example, in male turkeys, recent observations indicated that the threshold of sensitivity to photoperiod occurs between 0930 (non stimulatory) and 1030 (stimulatory hours of light/day; Blackault *et al.* (2006a and b)). In mammals and birds, the photoperiodic history of each individual should also be taken into account. Thus, it is now commonly accepted that SD are days shorter than the preceding ones, and that LD are days longer than the preceding ones. This property is interesting under field conditions: following a period of artificial long days, animals perceive SD even though natural day length is longer than 12 h of light per day. Another interesting property can be used under farm conditions to apply long days: the illumination of a specific phase of the night, the so-called 'photosensitive phase', generally situated 14 to 16 h after dawn, allows animals to perceive LD even though real LD are not applied (see reviews of Aupinel and Bonnet (1996) in snail, Sauveur (1988 and 1996) and De Reviers (1996) in birds, Maise and Breton (1996) in fish, Malpaux *et al.* (1996) and Chemineau *et al.* (1996) in sheep and goats, and Guillaume (1996) in mares).

More generally, photoperiod, which entrains the endogenous circannual rhythms of reproduction, exerts its action through two different but complementary and dependent pathways by (a) synchronising the reproductive period between individuals of the same species and (b) by adjusting the phases of gonadal development with external natural conditions. It is noteworthy that circannual rhythms of photoperiod affect avian migrations by controlling the migratory direction in a seasonal manner (see review by Gwinner (2001)). In mammals, all the photoperiodic input is perceived exclusively through the eyes then transmitted via a synaptic pathway to

the pineal gland, which transduces the photic signal into a chemical one by synthesising and secreting melatonin. Synthesised at night, mainly in the pineal gland in mammals, melatonin is delivered to the brain via the cerebrospinal fluid and to peripheral tissues by general circulation. To control reproductive activity in sheep, melatonin acts on the pre-mammillary hypothalamus in which it binds to specific receptors which stimulates, about 45 days after the onset of daily impregnation, the pulsatile activity of LHRH-LH which in turn will drive gonadal and behavioural sexual activities (review by Malpaux *et al.* (2001)). External melatonin can be given to 'mimic' SD and has been of practical use in sheep and goats to stimulate reproduction in spring. The situation is more complicated in fishes and birds which, at an impubertal stage, may directly perceive light through photoreceptors located in the brain and/or the pineal gland, for which the role of melatonin is not well understood because it probably acts on various parts of the organism (Sauveur, 1988 and 1996; Ekström and Meissl, 1997). In birds, the mechanisms involved in the processes of photoperiodic time measurement and of light transmission to the brain remains, in part, unexplained. Since the early observations of Rowan (1925), several hypotheses have been proposed to describe the precise and highly repeatable mechanism by which avian species perceive and measure the duration and variations of photoperiod to regulate their reproductive season. While extensive research has demonstrated that photoperiodic time measurement in mammals and birds is perceived through the circadian system (Benoît, 1935), indications now exist in birds that the median basal hypothalamus contains several major components involved in a specific response to photoperiod (Ball and Balthazart, 2003). In these species, light reaches encephalic receptors through several pathways including a direct transmission to the hypothalamus *via* the eye and the optic nerve or *via* the pineal gland or, perhaps also, *via* the Harderian gland. In addition, light which penetrates the skull to the extra-retinal photoreceptors is received by a photo-pigment (hypothetically rhodopsin) prior to its chemical transduction towards the hypothalamus (see review by Lewis and Perry (1995)). Even though not yet fully understood, the mechanisms involved in the processes of light transmission in birds do appear quite specific, perhaps due to the necessity, in many species, to adjust precisely their migratory behaviour to the onset and duration of their reproductive season.

Although, melatonin receptors have been reported in pike pituitary (Gaildrat and Falcón, 2000), the role of melatonin is more confusing in birds and fish, probably because, as stated earlier, it acts on various parts of the organism in these species. Not only sun but also moon light changes may be perceived by some coral fish species (Park *et al.*, 2006). Besides in fishes, other aspects of reproductive biology such as sexual inversion might involve melatonin (Shi, 2005). It remains, however, that a circadian clock entrains the rhythm of melatonin synthesis at least in part

if not in all non-mammalian vertebrates (Falcón, 1999). Such a circadian clock is itself adjustable by photoperiod (Ceinos *et al.*, 2005).

In addition to photoperiod, temperature may also play an important role in the reproductive seasonality of fishes, birds and, more generally, in a number of other poikilotherm vertebrates. As an example, an adult common carp may spawn four or five times per year if maintained at 20 to 22°C (Horvath, 1986). Besides temperature *per se*, a quite common factor is the occurrence of temperature × photoperiod interactions even in species renowned as photoperiod-dependent (fishes: Breton and Billard, 1977; Bromage *et al.*, 2001; birds: Kato and Konishi, 1968). In some species, like the Eurasian perch, a proper photothermal regime is necessary to obtain a normal gametogenesis (Fontaine *et al.*, 2006).

Important progress has been made in the last few decades to understand the main components of the underlying physiological mechanisms that control seasonality of reproduction in vertebrates. The existence of an endogenous circannual mechanism entrained by photoperiodic variations remains to be proved. It is thought that the retinal photoreceptors modulate pineal melatonin secretion and are the common 'knots' of the network, whatever the species. However, the precise location of this circannual mechanism remains to be discovered, as does whether it is, or is not, a 'clock', and how melatonin acts to drive the LHRH system. Of course, large differences exist between species and in many their specificities remain to be extensively studied.

Nevertheless, the numerous experiments done before entering the 'black box' of the brain, using only photoperiodic variations have led to proposals to farmers and artificial insemination (AI) centres for specific light schemes which may be able to control seasonality of reproduction of their animals.

Using artificial photoperiodic treatments to control seasonality of reproduction and milk production in farm animals

Over the past few decades, photoperiodic treatments have been of practical use in a variety of farm animal species ranging from meat and egg-type poultry (Lewis and Perry, 1995) to mammals (Malpaux *et al.*, 1996) and from fish (Maise and Breton, 1996) to snails (Aupinel and Bonnet, 1996) with the ultimate objective of providing consumer's accessibility to fresh animal products of various origins all year round.

The enormous development of intensive poultry production world-wide is, in part, the consequence of long-defined light regimes applicable to each period of the breeder's life in which the duration and variations of the photoperiod, as well as light intensity and adequate wavelength (through light source), can be adequately controlled from hatching to the end of the reproductive season (Sauveur, 1996; De Reviere, 1996). Over the past 25 to 30

years, the majority of layer-type chickens for table egg production have been subjected to intermittent lighting regimes (i.e. providing more than one light and dark period per day) necessitating dark housing. Such regimes, in which a 24-h cycle is fractioned in several alternate light and dark periods may, depending on the category of programme used (asymmetrical, symmetrical, biomimetic...) result in increased laying performance, egg weight and/or feed consumption (Lewis and Perry, 1995; Sauveur, 1996). In poultry meat-type breeds, a specific adjustment of the external environment (light, temperature) in male and female breeders has also been of prime interest in developing AI programmes. As an example, egg fertility in artificially inseminated flocks depends on the timing of semen deposition with regards to the period of oviposition, itself directly under the control of the photoperiod (Brillard, 2003). Changes currently underway to adjust egg-type production systems to EC regulations along with the rapid evolution of phenotypes in meat-type strains has resulted in the necessary re-appraisal of environmental (light) and nutritional practices to properly adjust to the new requirements necessitated by these changes.

In fishes, where the number of sires is reduced, different photoperiodic schemes can be applied to induce an out-of-season spawning. The principles of these treatments are those described earlier, a succession of LD and SD. In the rainbow trout, for example, the succession of 2 months LD immediately after the usual spawning period followed by 4 months SD, induces a new spawning season about 6 months after the first one (Figure 7). It is also possible to delay the onset of sexual maturation which could be of interest in focusing all the metabolism of the animal on growth and not on reproduction (Maise and Breton, 1996; Bromage *et al.*, 2001). Whatever the photoperiodic treatment, temperature should be adjusted properly. Thus, an off-season spawning of rainbow trout in summer, needs to keep water temperature at least below 15°C (Maise and Breton, 1983). Finally, even though results are globally satisfactory, there is still inter-individual variability in terms of gametes quality, especially when occurrence of malformations are accurately looked for (Bonnet *et al.*, 2006). This variability might be related to the heterogeneity of gametogenic stages within breeders at the beginning of the photoperiodic manipulation.

In mammals, photoperiodic treatments have been of practical interest for controlling seasonal reproduction essentially in sheep, goats and horses.

In sheep and goat AI centres, now equipped with dark housing, alternate light regimes with 1 month LD and 1 month SD allow permanent high semen production in rams and bucks, with no seasonal variations in sperm quality. Currently, all bucks of the French national genetic improvement scheme (about 70 per year) are permanently treated with rapid alternation LD-SD, which allows increased AI dose production (+40%) per buck and per year (Delgadillo *et al.*, 1993) and reduced duration of the breeding period of males (culling after 18 months of

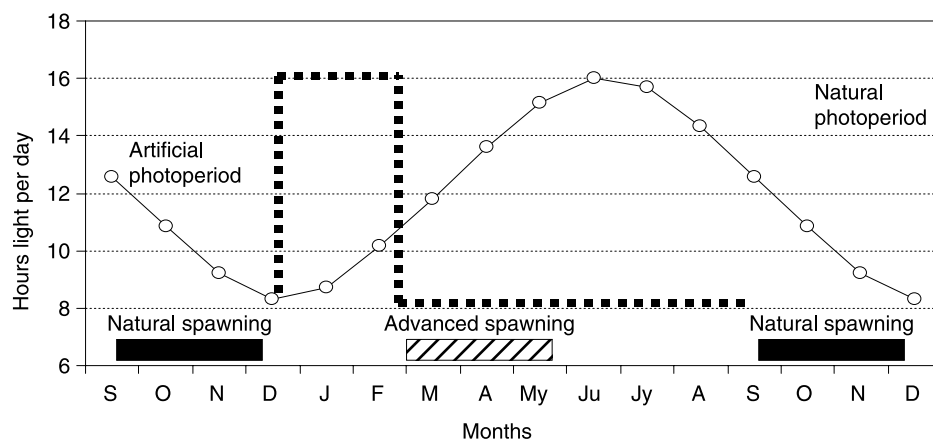


Figure 7 Spawning times of rainbow trout exposed to natural (black bars) or stimulatory long-short (striped bar) photoperiods. (adapted from Maise and Breton (1996)).

production, or about 18 months earlier than those maintained under natural photoperiod). In other AI centres which do not require permanent production of semen doses, rams raised in open barns are subjected to 2 to 3 months extra 'LD' (from December to February) followed either by return to natural photoperiod, or by subcutaneous treatment with melatonin implants to mimic SD ('SD') (Figures 8 and 9). This 'LD'-'SD' treatment stimulates semen output in quantity and quality in spring, thus mimicking the normal sexual season which, itself normally lasts 2 to 3 months (Malpau *et al.*, 1995).

On goat farms, (always equipped with open barns) males and females are subjected to the second type of treatment performed in AI centres ('LD'-'SD'). It is always associated with a 'buck effect' (introduction of treated bucks for 45 days, after 35 to 75 'SD') in order to induce ovulations and oestrous behaviour. Under such conditions, out-of-season fertility and prolificacy can be kept at high levels (>75% kidding rate with about two kids per kidding) (Chemineau *et al.*, 1996). In subtropical conditions and for local breeds of the subtropics where seasonality is less marked than those raised under temperate latitudes, the treatment of females may not be necessary. When the LD treatment is applied only in bucks used for the 'buck-effect', the percentages of females ovulating and fertility after natural mating are high (Delgadillo *et al.*, 2002 and 2004).

In ewes, a majority of out-of-season lambings are still obtained using 'classical' hormonal treatments (FGA sponges + eCG) but the frequency of utilisation of melatonin implants is increasing, especially in Mediterranean countries. Implant use also increases fertility and prolificacy. Overall, an increase of 0.20 lamb per ewe treated per year has been almost always observed, such increase originating from increased proportions of twins rather than triplets (Chemineau *et al.*, 1996).

Photoperiodic treatments are also applied in mares to advance the annual breeding season and to give foals a decisive age-related advance when competing with their

contemporaries born the same year. This is generally performed by exposing mares to LD or pseudo LD during autumn. Such treatments allow mares to be fertilised about 2 months earlier than females kept under a natural photoperiod (Guillaume, 1996).

Photoperiodic treatments are now used in both sexes of nearly all farm species to control seasonal reproduction. Whatever the species, they use common properties of alternations between inhibitory and stimulatory photoperiods, where durations are adapted to the species and sex. When using pure light treatments (without melatonin), especially when applied in open barns, they could be considered as non-invasive which fully respects animal welfare considerations. It is very probable that these photoperiodic treatments will be used more extensively in the future as livestock production systems strive to be more sustainable.

As explained in the first section of this review, seasonal variations in the quantity (milk yield) and quality (fat and protein content, somatic cell count) of dairy milk production are partly due to direct effects of day length on milk production and composition and/or on the general metabolism of dairy females. Long day length has been shown to stimulate milk production during lactation but to impair milk fat in cattle (Peters *et al.*, 1978 and 1981; Stanisiewsky *et al.*, 1985; Dahl *et al.*, 2000 and Dahl and Petitclerc, 2003), sheep (Bocquier *et al.*, 1984, 1990 and 1997) and goats (Delouis and Mirman, 1984). In contrast, short days, when applied during lactation, have a negative effect on milk production *per se* but increase the fat and protein contents of milk.

Interestingly, dairy heifers subjected to long days during their pre-pubertal period tended to produce more milk during the first lactation when maintained under the natural variations of photoperiod in regions of moderate latitudes in the northern hemisphere (Rius and Dahl, 2006). On the contrary, cows subjected to short days during their dry period, produce more milk during the subsequent lactation when maintained under the natural variations of photoperiod in regions of moderate latitudes in the northern hemisphere

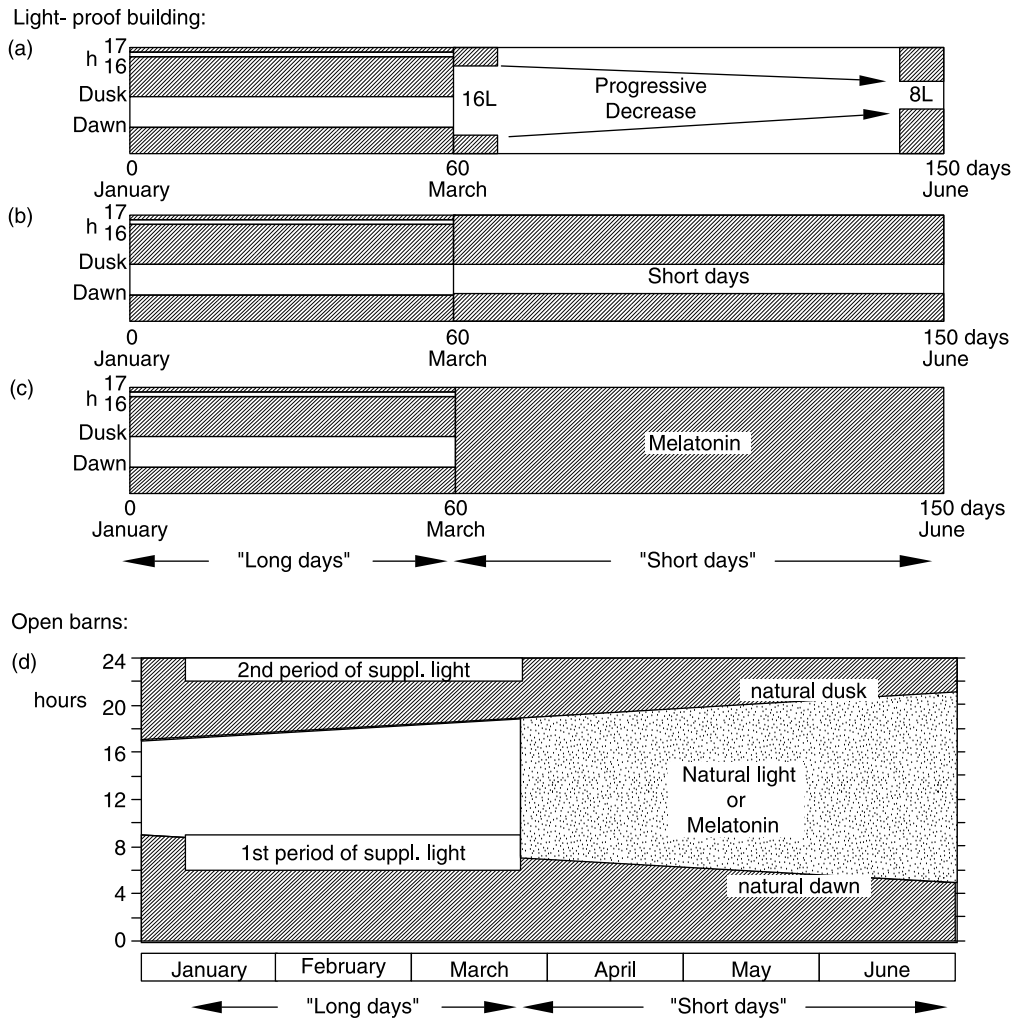


Figure 8 Photoperiodic treatments to control sexual activity in small ruminants raised in closed or open barns (adapted from Chemineau *et al.* (1996)).

(Auchtung *et al.*, 2005). These effects cause a modulation of milk secretion at the mammary gland level, probably via pituitary hormones like prolactin and its associated recep-

tors in the mammary tissue (Auchtung *et al.*, 2005) but also via a general orientation of the metabolic routes under photoperiodic entrainment (Bocquier *et al.*, 1998; Faulconier *et al.*, 2001; Chilliard and Bocquier, 2000; Chilliard *et al.*, 2005). Photoperiod has also been shown to modify the general immune system in dairy cattle (Auchtung *et al.*, 2004). To our knowledge, these photoperiodic manipulations of milk production in dairy cattle are widely used nowadays in USA/Canada, where over 30% of producers consistently report using long days in their herds.



Figure 9 Open barn used for photoperiodic treatment of bucks in the Mexican subtropics (with the courtesy of J.A. Delgadillo, CIRCA Uni. A. Narro, Coahuila, Mexico).

Conclusion

The seasonality of animal products release is more the consequence of interactions between the natural endogenous rhythmicity of animals and environmental constraints than a deliberate choice of the farmer to produce at a definite season. In most seasonal species and breeds involved in these productions, specific photoperiodic treatments derived, at least in part, from the cumulative knowledge of physiological mechanisms involved in the control of the reproductive function, have progressively been proposed to

overcome the problem raised by the seasonal availability of reproduction-derived products. In mammals, such treatments should be taken as an interesting alternative to classical hormonal treatments in a general context of reduction of hormonal utilisation in more sustainable animal production systems.

The existence of strong genetic bases for seasonality of reproductive activity in the main farm animal species should be further explored to propose selection criteria and/or gene markers accessible to primary breeder and producer organisations willing to reduce seasonality in their flocks.

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