REVIEW [REVISIÓN]

A FORESIGHT REFLECTION ON SUSTAINABLE METHODS FOR CONTROLLING MAMMALIAN FARM ANIMAL REPRODUCTION.

[UNA REFLEXIÓN PROSPECTIVA SOBRE TÉCNICAS SUSTENTABLES PARA CONTROLAR LA REPRODUCCIÓN EN MAMÍFEROS DOMÉSTICOS]

Philippe Chemineau

INRA, DEPE, 147 rue de l'Université, 75007 Paris France
E-mail: Philippe.Chemineau@paris.inra.fr
** Corresponding author*

SUMMARY

Controlling farm animal reproduction was/is one of the essential tools for domestication of species. It is still of high interest for genetic improvement, adjustment of production to feed availability, to market and reduction of unproductive periods. Detection of oestrous behaviour in cyclic females, synchronization of conceptions and increase of the potency of diffusion of sires are three common objectives among species. The various situations of reproductive systems, which are reviewed here, are very different among the various livestock systems in the world, because of intrinsic properties of species, but also because of the various degrees of intensification of the livestock systems themselves. A clear tendency appears to continue increasing productivity by improving reproductive efficiency, developing new and sustainable techniques without hormones, and continuing to develop AI and reproductive biotechnologies. Future areas of investment in research could be, first, the physiological and ethological bases of the socio-sexual inter-relationships between animals, second the genetic control of reproductive traits, third increasing the efficiency of classical and new reproductive biotechnologies and fourth engineering new and innovative reproductive techniques to be used in farm conditions. These reproductive techniques should be developed respecting the three pillars of sustainability: environment, economy and society. Thus, they should be included within the livestock systems in which they are supposed to be applied and which should be assessed for sustainability.

Key-words: Mammals; Reproduction; Sustainability.

RESUMEN

El control de la reproducción animal era/es una de las herramientas de la domesticación de las especies. Este control es aún interesante para el mejoramiento genético, la elección de la producción ajustada a la disponibilidad alimenticia, al mercado y a la reducción de los períodos improductivos. La detección del comportamiento de estro en hembras cíclicas, la sincronización de las fertilizaciones y el incremento del poder de difusión de los reproductores, constituyen objetivos communes a las diferentes especies. Las situaciones variables de los sistemas de reproducción, que se revisan aquí, son muy diferentes entre los sistemas de crianza en el mundo, debido a propiedades que difieren entre especies, y al nivel de intensificación de los sistemas mismos. Existe una tendencia clara para continuar el incremento de productividad con el mejoramiento de la eficiencia reproductiva, desarrollando nuevas y sustentables técnicas sin uso de hormonas y continuando con el desarrollo de la IA y de las biotecnologías reproductivas. Las futuras áreas de investigación podrían ser, en primer lugar, las bases fisiológicas y etológicas de las relaciones socio-sexuales entre animales, en segundo el control genético de los caracteres reproductivos, en tercero el incremento de la eficiencia de las técnicas clásicas y de las nuevas biotecnologías reproductivas, y, en cuarto la ingeniería de nuevas e innovadoras técnicas reproductivas que pueden ser aplicables en los diferentes sistemas de producción. Estas técnicas reproductivas deben ser desarrolladas respetando los tres pilares de la sustentabilidad: medio ambiente, economía y sociedad. En consecuencia, deben ser incluídas dentro de los sistemas de producción en los cuales se supone deberán ser aplicadas y probadas por su sustentabilidad.

Palabras claves: Mamíferos; Reproducción; Sustentabilidad.

INTRODUCTION

Controlling farm animal reproduction, in association with the link between animals and humans, is probably one of the key elements that have allowed the domestication of animals. After identification of a specific individual which bears interesting traits, control of reproduction allows to maintain them over the progeny, and to associate them with other useful traits. Very early during the history of domestication a change in the proportion males/females and in the age of animals was observed and this shows that the control of reproduction was used as tool for improvement (Zeder, 2001). Since that time, and especially over the last 50 years, the scientific progress in the area of estimating the genetic value of farm animals and in the development of artificial insemination with deep-frozen semen and other reproductive techniques, especially in the dairy cattle, have together allowed a dramatic increase in the rate of the genetic progress. However, one may question whether we have reached a limit in the application of these techniques of reproductive control and it appears interesting to focus on their sustainability in farm conditions. These are the objectives of the present paper.

Thus, after a rapid overview of the interest of controlling animal reproduction in farms, we will review rapidly the major reproductive systems existing in the different mammalian farm animal species and what could be the tendencies, weak signals and potential ruptures existing in these systems. We will end by examining the research areas in which to invest in the future and the necessity of developing an integrative approach in order to insert the reproductive technologies within livestock systems to enable them to be efficient and sustainable.

WHAT IS THE INTEREST IN CONTROLLING ANIMAL REPRODUCTION?

Controlling animal reproduction presents three major interests

Genetic progress

The first interest is clearly to increase the speed of genetic progress. Very early during the process of domestication of farm animal species, the interest of controlling animal reproduction appeared. Once the choice is made of selecting a male or a female with specific and interesting traits, the farmer wishes to spread these traits as widely as possible into their progeny. Thus, the first and still applied way of controlling reproduction is to choose the females to which a specific chosen male should be mated, in order to be sure that its progeny is identified and bred as an adult producing animal.

Since more than 50 years now, the extensive use of artificial insemination (AI) with deep-frozen semen in the bovine species (the « male side ») has led to a dramatic increase of the speed of selection, because of mainly three crucial advantages (van Arendonk, 2011). The first one is the possibility, given by progeny testing in farms, to evaluate the genetic value of young bulls, then to accurately select the best ones before their death. The second one is to largely spread the semen and favourable alleles of these best bulls over space and time to improve the genetic value of the entire flock, even though it has not participated in the progeny-testing scheme. The third advantage comes from the possibility, given by putting in place the progeny of the same bulls in different farms, of connecting herds and, so, being able to compare their genetic value without confounding it with the effects of the environment.

This is true for nearly all farm animal species, even if the amount of sperm produced by males and the minimum number of sperm cells required for AI, which determine the number of females which can be artificially inseminated per sire, varies very much between species (Chemineau et al., 2001). The difference between species also appears in the relative ability to deep-freeze semen, then to use it in farms at a reasonable cost compared to the income of the farmer. Thus, in intensive dairy cattle systems, a large number of females for a single sire are artificially inseminated with deep-frozen semen, while, in sheep, a much fewer number of ewes per ram are inseminated with liquid semen.

The same rationale can be applied for the « female side » using embryo transfer or, more recently, in vitro fertilisation with ovum-pick-up. But, obviously, it is much more difficult and costly to increase substantially the female progeny than the male progeny.

Choice of the periods of parturitions

The choice of the periods of parturition provides a way to cope with feed availability, livestock system or consumer’s demand. The concentration of parturitions over a few weeks or a few days limits the time spent on them, reducing the costs and allowing improved care which limits early mortality. Thereafter, the presence of homogeneous groups of animals allows them to be fed more adequately to meet their needs thus providing less variable growth rate curves and more homogeneous groups for slaughter and the market. The social impact of controlling reproduction for farming family is also important in that it allows available time for other activities, or leisure. Thus, controlling reproduction is a way for the farmer to better find an adequate equilibrium between productivity, adaptation to the market and family life.

Reduction of unproductive periods

In a majority of farm animal species, advancing female puberty increases their lifetime productivity (swine, beef cattle, sheep), and also allows synchronizing their breeding period with that of adults (swine, sheep and goats). Reducing the duration of annual sexual rest (sheep and goats) may allow increasing productivity over the year, which may increase their productivity.

Common features among species for the objectives of controlling reproduction

In spite of large differences between species, there are common features among them concerning the objectives for controlling reproduction.

The first one is the detection of oestrous behaviour, and/or, eventually, associated ovulation(s), in cyclic females. This can be done simply through observation of animals by the farmer, or by automatic detection using the help of robotics.

The second one is the synchronisation of fertile oestrus and ovulations at a precise timing in the year. The « wish » of synchronization could be very precise (ovulations spread over less than 24 hours) in order to perform AI at fixed time(s) without oestrus detection, or more weak (over days) if synchronisation of parturitions is only wanted. Synchronization is associated, especially in sheep, to a moderate increase of ovulation rate to provide two lambs per lambing, but not more.

The third one is the increase of the potency of diffusion of favourable alleles of specific male and/or female sires. This objective can be reached in males by an improvement of sperm production, of semen technology, but also by better synchronization of ovulations and of AI conditions in females, which allow a reduction in the number of sperm inseminated to produce a progeny. In females, this objective, as stated earlier, is more complicated to reach because they produce fewer oocytes per ova shedding and because these oocytes are of more difficult access than sperm in males. Superovulation, ovum pick-up associated with in vitro fertilisation, are the main steps to improve for a better diffusion of female alleles.

WHAT IS THE ACTUAL SITUATION OF BREEDING SYSTEMS IN LIVESTOCK?

Reasons for the high variability among species regarding reproductive control.

The situation among farm animal species is extremely variable for four main reasons. The first one comes from the biological differences between species regarding their characteristics of reproduction. As it is an important trait for speciation, firstly in the wild, but also in our favourite farm animals, every species has developed differing oestrous cycle characteristics in terms of duration, presence all the year round and ovulation rate.

The second one comes from the more or less ability of their gametes (sperm and oocytes) to support the in vitro « survival » required mainly to provoke an increase in the diffusion rate or an ability to be artificially inseminated easily. For example, the techniques used for deep-freeze bull semen do not work as well in other species. In sheep, goats and boars, it is necessary to separate the seminal plasma before freezing (goats (Nunes et al., 1982)). In boars, it is necessary to increase sperm concentration of the ejaculate (Martinat-Botte et al., 2009). In sheep, the only way to get a high fertility rate when using deep-frozen semen is to inseminate directly into the uterine horns (Vallet et al., 1992).

The third one is due to the fact that some species of major economic importance (i.e. dairy cattle), have received a lot of attention in terms of research since 50 years, while some other ones remain explored only by a small set of scientists.

The fourth one is that, within one single species, there is a huge variability among livestock breeding systems over the world (De Roest, 2011). Regarding the number of farms or the number of animals, which use techniques for controlling reproduction, it is very obvious that the majority do not use sophisticated ones or do not use even a single one, but rather natural mating.

In spite of this difficult context, we have attempted to draw a very crude description of the major reproductive systems and fertility problems or questions, within species and within the type of production (i.e. meat or milk, essentially).

Cattle

In intensive dairy cattle, the most common system is represented by Holstein cows in which reproduction is done by AI with frozen semen after detection of natural oestrus. In this system, the intense selection for milk production is associated with increasing fertility problems (Dobson et al., 2008). Fertility, expressed in terms of non-return rates after first AI has decreased since more than 15 years and is now below 40% in most cases. These difficulties can be either increased by local conditions (heat stress, use of exogenous hormones to increase milk production), or decreased by adequate selection and/or more friendly management. In the more intensive units, the replacement rate is not even provided, which clearly shows that this system is not sustainable in the medium term. The first problem existing regarding reproduction in this system concerns oestrous detection, which needs to be automatized either at milking (by measuring hormones in milk (Asmussen, 2010)) or by watching behavioural activity. The second problem concerns fertility itself, as, even after good heat detection, conception rates are low and unpredictable. These two areas are the subjects of active research programs in various countries at the moment (Garnsworthy et al., 2008; Royal et al., 2008; Wathes et al., 2008).

In beef cattle, the situation is much more dependant on local feeding conditions (i.e. forage availability) and, as a consequence, the reproductive system is highly dependant on forage availability and on the management of body reserves of cows over the annual cycle (Blanc and Agabriel, 2008). The very large majority of conceptions are achieved by natural mating with a very low control of reproduction, hormonal treatments are used in a limited number of systems of developed countries. In most systems, the priority is to synchronise oestrus and ovulations at a period chosen so that calving will occur when forage availability is at maximum. The economic objective of obtaining one calf per year and per cow is probably not reached in many systems, especially those of the tropics or subtropics in which the rainy season is not well-defined from one year to another.

The situation of dual-purpose cattle is interesting because the farmer needs to find an equilibrium between the two above systems and because he can use the interactions between food availability, milk production and calf presence to drive reproductive activity of the cows (Alejandrino et al., 1999; Gonzalez-Stagnaro, 2008). Except in very harsh conditions when food availability limits the reconstitution of body reserves, the control of reproduction seems generally easier than in the two above systems. In this system, the farmer is generally close to the dairy females and better able to easily detect oestrus behaviour and then to organize mating or use AI.

Reproductive biotechnologies (embryo freezing and transfer, in vitro fertilization after ovum pick-up or oocyte maturation) could be used in both dairy and beef cattle, to be included in selection schemes to improve the speed of genetic progress. They are also useful to exchange genotypes with a high sanitary security from one country to another (exchange of living sires is generally prohibited nowadays)(Thibier, 2006).

Sheep

The majority of sheep breeds are reared for meat in extensive systems in which rams could be in permanent contact with ewes all over the year in less controlled ones. In the systems of temperate and subtropical areas, reproductive activity is driven by photoperiodic changes which impose the presence of an anoestrus season and lead animals to conceive only in autumn-winter, and lamb in winter-spring (Hafez, 1952). In tropical areas the driver is immediate food availability which induces more disperse and less predictable periods of lambing which can, then, be discordant with forage availability (Chemineau et al., 2007). In intensive meat systems, hormonal synchronisation using a sequence progestagens-gonadotropins, allows a precise timing in ovulation time after progestagen withdrawal, then the use of a single AI with liquid semen at a fixed time on a large number of females. In these systems, fertility after AI is generally higher than 55 lambing per cent, with a litter size between 1.5 and 2 .0. This allows a good productivity rate when females lamb thrice over two years (Benoit et al., 2009). In less intensive systems, or in organic farms, and especially in the less seasonal breeds, such as the breeds originating from the Mediterranean Basin, the « male-effect » (re-introduction of active rams among anoestrous ewes to induce synchronised and fertile ovulations) is used (Girard, 1813; Thimonier et al., 2000). But, to our knowledge, probably because of the less precise synchrony of ovulations, the male-effect is rarely associated with AI.

Milk sheep are more or less in the same reproductive situation as intensive meat sheep systems, but the objective of farmers is to get one lambing per year, not more. These breeds are generally reared in temperate or Mediterranean areas, thus submitted to photoperiodic variations, which induces seasonality of ovulatory and oestrous activities as in meat sheep. When AI is used, which is the case in the more intensive breeding schemes for milk production, hormonal synchronisation of oestrous behaviour and ovulations is largely used for getting a very precise timing of ovulations, then the insemination of liquid semen (Lagriffoul et al., 2010).

Reproductive biotechnologies (embryo freezing and transfer, in vitro fertilization after ovum pick-up or oocyte maturation) (Cognie et al., 2004; Lagriffoul et al., 2010) could also be used in sheep for the same purposes as cattle, but, to our knowledge, they are not extensively used at a commercial level, except for exchanges of genotypes and management of nucleus flocks.

Goats

The majority of world goat flocks are reared for meat and, as in sheep; goat-bucks are generally present all over the year with females. Photoperiodic driving of reproductive seasonality (i.e. conceptions from

September to January in the Northern hemisphere) is also very strong in temperate and subtropical breeds which experience a deep anoestrous season in spring and summer. As in sheep, an opportunistic strategy of reproduction based on response to feed availability is developed in tropical breeds (Chemineau et al., 2007). Dairy goats or dual-purpose breeds follow the same reproductive pattern as meat goats and, as in sheep, in intensive systems, could be managed using hormonal treatments with a single AI with deep-frozen semen at a fixed time after progestin withdrawal (Gonzalez-Stagnaro, 1984). This deep-frozen semen could come from buck sires maintained under accelerated light-rhythms, which allow all the year round a permanently very high semen production of exceptional quality for deep-freezing (Delgadillo et al., 1991; 1992; 1993). Under these conditions, fertility rates of intensive dairy goats are generally about 60 kidding per cent (Leboeuf et al., 2008). Liquid semen could also be used if photoperiodic treatments are applied to the sires in order to prevent the seasonal decrease in sperm fertilizing ability.

The buck-effect appears to be very efficient for inducing fertile oestrus and ovulations (Chemineau, 1983; Chemineau et al., 2006), especially when males are light-treated so that they are sexually active when females are in anoestrus (and untreated males in sexual rest)(Delgadillo and Velez, 2010; Delgadillo, 2011).
Reproductive biotechnologies (embryo freezing and transfer, in vitro fertilization after ovum pick-up or oocyte maturation) (Ali Al Ahmad et al., 2008) could also be used in goats for the same purposes as cattle and sheep, but, to our knowledge, they are not extensively used at commercial level, except for exchanges of genotypes and very exceptional situations (« cleaning » a flock from a disease, for example).

Pigs

The rhythm of intensive pig production is governed by the reproductive rate of sows, which ovulate at a fixed time after weaning of the piglets (Soede et al., 2011). This allows the farmer to get a natural synchronisation of a group of females and the opportunity of using semen for AI. Liquid semen is used on a large scale because of the ability of boar sperm to survive up to five days without significant decrease in fertility rate (Fantinati et al., 2009). These conditions have led to the development of reproductive systems with an exceptional efficiency at a relatively low cost, thus allowing rapid and efficient breeding schemes (Tribout et al., 2010). Hormonal treatments are rarely used but could be applied to young sows to synchronise the first fertile oestrus, then allowing a good first synchronisation of the herd (van Leeuwen et al., 2011). AI with frozen semen and/or embryo transfer are still in their infancy and not used more than experimentally nowadays.

« Extensive » (familial) pig production is done in small units, where animals are close to the farmer which allows an efficient oestrus detection after weaning, then natural mating.

WHAT ARE THE TENDENCIES, WEAK SIGNALS AND POSSIBLE BREAKDOWNS?

Livestock systems are expected to follow a clear tendency of more and more intensification to follow the expected strong demand of animal products linked to the increase of a world population with higher incomes, especially in emerging countries (De Roest, 2011). However, it is also very clear that the majority of our intensive systems, developed over the last 50 years have reached (even passed) certain limits in terms of foot-print on the global environment (for example nitrate and phosphate in the water, green house gases emitted by enteric fermentation of ruminants and/or by the manure of pigs) or the welfare of animals (group housing of animals or wider space allowance). We need to modify these intensive systems in order to orient their production towards more sustainability and more friendliness to animals and environment.

Even though, for health reasons (overweight and cardiovascular diseases), it would be necessary to reduce our animal product consumption at a world-wide level (especially in industrialised countries), this will not probably be sufficient to cover the needs in animal products (Karl-Heinz, 2009; Paillard and Treyer, 2010; Paillard S., 2010; Ronzon T., 2011). Thus, the livestock industry is facing the challenge of increasing its production and, at the same time, reducing its impact on the environment.

Reproduction is concerned in three ways in this challenge: (a) to improve reproductive efficiency per producing female, which allows a better productivity thus reducing the impact per kg of animal product, (b) to develop new, innovative and efficient breeding technologies without hormones for controlling reproduction (Martin et al., 2004) (c) to develop AI and reproductive biotechnologies to be used in full association with genomic selection.

i. Increasing reproductive efficiency should be pursued as in the past, but not as a single trait to improve and not for increasing the average without taking into account the variability. For dairy species (cattle and goats), the purpose is still to get maximum fertility (i.e. the ratio between the number of females giving birth over the number of females inseminated). This is especially true, as we mentioned above, for intensive dairy cattle where fertility after AI is close to 40 calving per cent. Even if selection for fertility could be done while continuing selection on milk production (Barbat et al., 2010), we should focus on a better management of the whole lifetime of the female career by trying to find an optimization between milk production and fertility (Coyral-Castel et al., 2011). In beef cattle, a better management of body reserves and of their reconstitution at crucial times during the reproductive cycle may be an objective in order to get one calf per year and per cow (Blanc et al., 2006). For polytoquous species raised for meat production, such as sheep and pigs, prolificacy will still be a major component of farmer income, thus still being an objective to improve when possible (i.e. when prolificacy is low). However, in the most intensive systems, a precise control of the variability of litter size would be a reasonable objective to impair birth of small newborn, which have low chances for survival. In all livestock systems, increasing the reproductive efficiency is a very strong contributor to a decrease of environmental foot-print per kg of animal product provided to the consumer. However, this will need to be calculated at the system of production level, not only at the producing-female level, as it was generally done in the past.

ii. We need to develop new, innovative and efficient breeding technologies without hormones for controlling reproduction in the future. Since about 50 years, with the discovery of the very potent effects of steroids (progestagens) and gonadotropins, the industry has been able to develop highly efficient ways for controlling time and rates of conception. But, on the one hand, more and more discussions appear to question the use of such hormones in animal production, at least in Europe, for sanitary and ethical reasons. On the other hand, the producers themselves are tempted to develop new and hormone-free systems of reproduction of their animals. Intensive research in the area of socio-sexual relationships between animals has been done, especially in small ruminant species (sheep and goats) which allow, in a majority of livestock systems, the development of new and innovative systems based on the « male-effect » (Girard, 1813; Underwood, 1944; Shelton, 1960; Chemineau, 1983; Thimonier et al., 2000) to control out-of-season reproductive activity. Advances were also done in cattle to manipulate the post-partum anoestrus duration using temporary calf removal (Stumpf et al., 1992; Soto Belloso et al., 1997; Fagundes et al., 2006; Escrivao et al., 2009), associated or not, with the presence of bulls. This seems an interesting way to follow (Bonavera et al., 1990; Monje et al., 1992; Gazal et al., 1999; Molina et al., 2002; Berardinelli and Joshi, 2005b; a; Berardinelli et al., 2005; 2007; Berardinelli and Tauck, 2007; Miller and Ungerfeld, 2008). In cycling animals, the challenge is to find efficient and low-cost ways of detecting oestrous behaviour. This is clearly a very active area in terms of applied research, at least in cattle and sheep.

iii. Finally, it is still very important to develop AI and reproductive biotechnologies to be used in full association with genomic selection (Merton, 2011). Artificial insemination is still a highly efficient way to perform genetic improvement, as explained above, and it is still necessary to improve its efficiency and enlarge its domains of application in the future. This means that liquid semen could be used in association with deep-frozen semen. Also we need to continue to decrease the minimum number of spermatozoa to be inseminated in a variety of species. But with the new techniques of genomic selection, it will probably be important to continue the investment in basic and applied reproductive biotechnologies for decreasing inter-generation interval, thus getting as soon as possible (embryo) tissue for genomic evaluation, then collecting semen and oocytes from very young animals, once their value known (Merton, 2011). The continuous development of these reproductive biotechnologies should be done in close association with the programs developed simultaneously in genomic selection.

IN WHICH AREAS DO WE NEED TO INVEST IN THE FUTURE?

Research programs in the area of reproductive biology, with the aim of controlling farm animal reproduction, need to be developed into four main directions.

i. The first direction could be a better knowledge of the physiological and ethological bases of the socio-sexual inter-relationships between animals. Recent results obtained in dairy goats using sexually active males to induce out-of-season oestrus and ovulations (Delgadillo et al., 2009) showed the potency of these socio-sexual relationships. They also demonstrated that we have probably underestimated them as a means to develop new and friendly techniques for controlling reproduction. The identification of the relative responsibility of pheromonal communication *versus* behavioural activity in the response to the « male effect » could be of major interest. This could be used to better develop techniques coming from the cue(s) which is (are) mainly responsible in the response to the presence of males (Delgadillo, 2011). Putative pheromones have been identified in goats as potentially being the oxidative products of degradation of the fatty acids synthetized and secreted by sebaceous glands of buck neck (Iwata et al., 2003; Okamura and Mori, 2005). However, to our knowledge, if these compounds have been demonstrated to be involved in male attractiveness, the formal demonstration of their efficiency to stimulate LH secretion and to induce ovulations remains to be done. In beef cattle systems of production, the same observation could be done using temporary removal of calves (Berardinelli and Joshi, 2005a; Kawashima et al., 2008) and bull presence (Zalesky et al., 1984; Larson et al., 1994; Landaeta-Hernandez et al., 2004; Landaeta-Hernandez et al., 2006) to shorten the post-partum anoestrus. This is an area already explored (Custer et al., 1990; Burns and Spitzer, 1992; Fernandez et al., 1996; Fike et al., 1996; Bolanos et al., 1998; Rekwot et al., 2000a; Rekwot et al., 2000b; Ruas et al., 2001; Rekwot et al., 2004; Calegare et al., 2009; Fiol et al., 2010; Tauck et al., 2010), but which need continuous investigation. Attempts to identify putative pheromones were also done in cattle as a basis for the observed effects of bull presence on resumption of post-partum anoestrus (Tauck et al., 2006; Tauck and Berardinelli, 2007; Tauck et al., 2010). In swine, the efficiency of piglet weaning for induction of fertile oestrus could be an interesting model to better understand what are the underlying mechanisms involved in this effect of weaning. In all of these species, it would be of special interest to better know what are the sensory cues involved in the perception of the partner and to better understand the importance of sexual and/or social activity of the partner in eliciting a reproductive response. Finally, the identification of the physiological mechanisms used by responding animals to trigger their reproductive activity would also be interesting.

In all farm mammalian species, a better knowledge of the mechanisms used by males (or females) to detect the oestrous females could also be of high interest (Delgadillo et al., 2009). Pheromones associated to oestrus have been identified in wild species (elephant;(Lazar et al., 2002; Goodwin et al., 2006)), but, to our knowledge, not in the major farm species. This identification should be a major area to invest as it could be used for developing bio probes able to replace detector males in large bovine farms, especially in dairy cattle (Le Danvic C., 2011).

ii. The second direction could be an important investment in the genetic control of reproductive traits. Since the sequencing of the genomes of our main farm domestic species and with the dramatic development of genomic selection it is now possible to take into account the less heritable traits within programs of genetic improvement. This is the case for fertility traits which are among the lowest heritable ones and which are, moreover, difficult to phenotype. Fertility (i.e. non-return rate) of intensive dairy cows is already taken into account in selection schemes (Berglund, 2008; Barbat et al., 2010). The other different traits described above (seasonality, post-partum duration, oestrous behaviour, superovulation, etc.) could be further explored in terms of their genetic control (AlShorepy and Notter, 1997; Hanocq et al., 1999), then identify the genes and alleles responsible for favourable phenotypes and used in selection schemes.

iii. The third direction is a continuous effort in developing the efficiency of « classical » reproductive biotechnologies (AI, ET, IVF, etc.), simultaneously with an investment in new ones (cloning and homologous recombination)(Merton, 2011). As explained above, the use of genomic selection will probably provoke an renewal of interest for biotechnologies which may allow access to very young animals, even to the embryo itself, on which only a small set of cells could be used to evaluate marker polymorphisms (Le Bourhis et al., 2011). Once known the young animals will be interesting to use for producing progeny as soon as possible.

A renewal of interest is also expected for elite females for which estimation of genomic value will be much easier, and which could be an interesting way to get high value progeny from them. New biotechnologies of reproduction, which are defined here as those that aim to modify genome sequence and/or genome expression, are also an area in which the most advanced laboratories may invest. At least in Europe, because of the reluctance of the society towards these techniques, there is little possibility for using them in field conditions in the near future, but rather to use them as tools for exploring the role of genes suspected to control a specific trait and the importance of epigenetics in building the adult phenotypes.

iv. The fourth direction is clearly directed towards engineering of new and innovative reproductive techniques to be used in farm conditions. The oldest techniques such as the sequence progestagens- PMSG and/or the use of prostaglandins (Macmillan, 2010; Islam, 2011) which are now used on millions of females each year, have required at least ten years and strong efforts to pass from the discovery in the laboratory to a correct use in field conditions. This will be the case for the new and sustainable techniques described above which would require specific engineering for a correct application to farm conditions. This engineering is clearly part of the research and should be done by the laboratories themselves, which simultaneously invest on more basic research.

Engineering for oestrous detection is still an area of much interest in dairy cattle where monitoring the twice-daily endocrine status of milking females was proposed as an automatic technique for detecting the end of a luteal phase and the onset of the following follicular phase associated with oestrus behaviour (Asmussen, 2010). As stated above, the identification of putative pheromones associated to oestrous behaviour (Le Danvic C., 2011) could be the beginning of an engineering program using either olfactory binding proteins or/and pheromone receptor protein able to detect automatically the female status as trained dogs are able to do it (Fischer-Tenhagen et al., 2011). Quantification of animal behaviour could also be attempted automatically either by detecting it visually with video cameras, then estimating the status of females, or by equipping detector females or males with electronic apparatus able to register movements, then estimate their predictive value for oestrous behaviour (Lee et al., 2008). Recently, an electronic apron was developed in sheep to equip detector rams. This counts the number of mounts for a specific female in a given period of time, then calculates a probability for it to be in oestrus (Bocquier et al., 2006).

The use of new, non-hormonal molecules could be of high interest in controlling farm animal reproduction. The molecules could originate from plants containing native steroids (especially progesterone) or unknown compounds, from plants which are known in the local pharmacopeia to have reproductive effects (in animals or humans). But these molecules can also originate from research discoveries and could be peptides and/or antibodies able to stimulate the endogenous hormones (Hervé et al., 2004).

Engineering in the areas of genetics and biotechnologies is also extremely important in order to develop efficient techniques, which could be applied either in field or applied laboratory conditions. Two points are of special importance: the efficiency of the developed techniques (for example the number of living calves per 100 oocytes collected and fertilized in vitro) and their costs (for example the price of sexing semen or embryos).

NECESSITY OF A SYSTEMIC APPROACH OF REPRODUCTIVE SYSTEMS WITHIN INTEGRATED FARMING SYSTEMS

In addition (or in combination) of being technically efficient, reproductive techniques should be developed respecting the three pillars of sustainability: environment, economy and society. Thus, they should be included within the livestock systems in which they are supposed to be applied, taking into account these three elements. Thus the livestock system itself rather than the reproductive technique, should be assessed for sustainability (Gamborg and Sandoe, 2005; Neeteson-van Nieuwenhoven et al., 2006).

Respecting the environment is the first objective for sustainable reproductive systems. In that sense, it could be considered that reducing the use of exogenous hormones could be one objective to reach, in order to reduce the potential effects on the ecosystems, especially on biodiversity. Reduction of exogenous hormones could come from either a substitution of xenobiotic molecules by natural ones (for example synthetic progestagens replaced by progesterone), or the development of a new technique of induction (for example « male effect » to replace PMSG/eCG). However, as explained above, sustainability should not be only assessed at the level of the technique itself, but rather at the livestock system level, to prevent the adoption of a new technique, which may have positive effects per se, but adverse effects for the whole system (Baxter et al., 2011).

The second pillar is economic and it is obvious that a new technique for controlling farm animal reproduction should have an economic interest for the farmer in order to be adopted on a large scale (Moyo et al., 2009). This economic interest is not easy to estimate as it may include an advantage in terms of labour or in terms of image of the livestock system itself, which may provide an advantage to market the products (for example organic farms which prohibit the use of exogenous hormones for oestrus synchronization). However, as for the environment, the economic sustainability should be appreciated at the level of the livestock system or even larger to appreciate its efficiency (for example the potential exclusion of organic farms from artificial insemination, then genetic progress) (Brocard and Portier, 2008; Pellicer-Rubio et al., 2008; Benoit et al., 2009; Nauta, 2009).

Finally, sustainability should also be social, in order to validate the fact that the considered technique is socially acceptable (for example not going against animal welfare) and could be accepted by the farmers themselves and by the social stakeholders who develop some interest in the area (Costa-Neto, 2000; Cristofori et al., 2005; Mwacharo and Drucker, 2005; Kosgey et al., 2006; Getachew et al., 2010; Murage and Ilatsia, 2011). Finally, in the social acceptance, we could also raise the importance of new paradigms, partly coming from scientific observations of nature and farmers' practices, which may play a role in the development of new techniques for controlling reproduction (Mesa and Machado, 2009).

CONCLUSION

As for many other domains of agriculture, the control of farm mammalian reproduction is facing a new and somewhat contradictory challenge: it should continue to improve productivity (i.e. fecundity of females) in order to reduce the indirect environmental foot-print of livestock by producing more with the same livestock, but, at the same time to reduce the direct impact of the livestock systems on the environment and on welfare of animals. The exploration of new and more friendly ways of controlling animal reproduction is not only a necessity, but seems also feasible, especially by investing in a better knowledge of the ethological and physiological bases of the socio-sexual relationships between animals. The identification of sexual pheromones, associated with a better knowledge of the sensory cues used by females to perceive sexual male activity may lead to engineering of new and sustainable bio techniques able to assess the behavioural or/and endocrine status of the females, and to induce their activity during anoestrus. Replacement of exogenous hormones seems also feasible if an investment is done into the identification of new sources of natural hormones, for example in plants.

However, we should remind ourselves here that sustainability should be assessed at the level of the whole livestock system and not just at the level of the reproductive technique itself. Such an assessment is not trivial and needs a good overview of the considered system to achieve high efficiency.

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