World Rabbit Sci. 2007, 15: 61 - 80

PREPARATION OF THE RABBIT DOE TO INSEMINATION: A REVIEW

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Abstract: This review analyses the main factors of success of insemination as well as the methods suitable for oestrus induction in order to improve reproductive efficiency of rabbit does in term of fecundity (combining fertility and prolificacy). Parity, lactation status, pseudopregnancy as well as sexual receptivity at the time of insemination highly influence reproductive performance. Pseudopregnancy (ovulation non-induced by GnRH or mating) strongly depresses fertility, but its cause is still unknown. The routine use of eCG (or PMSG) on lactating does consistently increases the proportion of receptive does at the time of AI and, therefore, their long-term productivity, without any important side-effect. Applied just before insemination, different alternative methods have been studied: animal manipulation (a change of cage, does gathering), "buck" effect, short dam-litter separation, feeding programmes and light stimulations. Some of these methods improve the fecundity, but they sometimes also decrease kits growth (dam-litter separation, lighting programmes...). Consequently, for an optimal application in farms, it is important to consider long-term effects, such as global productivity and persistency of the effects. However, a better knowledge of the underlying physiological mechanisms would allow a better control of reproduction in rabbit farms.

Key words: Rabbit, insemination, oestrus induction, pseudopregnancy, eCG, biostimulations.

INTRODUCTION

Artificial insemination (AI) of rabbit does appeared on European farms in the late 1980s. This reproductive technology allowed the development of a new cycled production system and a better organisation of farms. In France, for example, the farmers generally buy heterospermic pools from one of the 20 production centres and they do the inseminations themselves. More than 80% of French farms are led in «single batch» with most of them maintaining 42 day intervals between two inseminations.

Research of factors responsible for successful AI has been the object of numerous studies, recently. Even though rabbit does can be inseminated right after kindling, their reproduction performance varies considerably with parity (rank of the litter), physiological state (lactating or not, stage of lactation), and sexual receptivity at insemination. In France, today, the fertility (kindling rate) is high (77% on average), but farmers use different hormonal treatments, sometimes combined with other methods not yet validated, such as feed flushing, a short separation between the mother and her litter, vitamin supplements in the drinking water or in food, lighting programmes.

Thus, the aim of this review is to discuss the current knowledge of successful insemination factors and the methods that are susceptible to induce receptivity of does at insemination in order to improve their fecundity (combining fertility and prolificacy).

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Received *September 2006* - Accepted *February 2007*.

FACTORS OF AI SUCCESS RELATED TO THE DOE

A doe is fertile if she is able to ovulate, be fertilised, and carry embryos and foetuses to term. An endoscopy examination performed soon after a negative abdominal palpation allows direct observation of the genital tract. This observation allows to discriminate whether the pregnancy failure was due to the lack of ovulation or not, so implying a failure of fertilisation or total early embryo mortality. Thus, the two components of fertility examined in this review are the *ovulation ability* and the *failure of pregnancy independent of ovulation*. The prolificacy components include the *ovulation rate*, *fertilization rate*, and *embryo survival* which are estimated by the number of *corpora lutea*/number of ovulating does ×100, number of fertilised eggs/number of *corpora lutea* ×100, and the number of alive embryos or foetuses/number of *corpora lutea* ×100, respectively (International Rabbit Reproduction Group, 2005).

Parity

In AI, nulliparous does, which are usually very receptive, are characterised by higher fertility (70%), but lower prolificacy (8.8 born alive), than does of higher parity (at least 10.5 born alive for the same genotype, Perrier *et al*., 1998). Primiparous does inseminated during their first lactation are generally less receptive and fertile (below 70%), but have greater litter size than that of nulliparous does (Chmitelin *et al*., 1990; Davoust *et al*., 1994; Parigi Bini and Xiccato, 1993; Szendro *et al*., 1999; Perrier *et al*., 2000, Rebollar *et al*., 2006). Parigi Bini and Xiccato (1993) reported high energy losses, with a 28% difference between food supply and maintenance plus lactation , during the first lactation as a consequence of the high needs for lactation, pregnancy, and yet unfinished growth.

Multiparous does have high fertility levels and litter sizes (78.6% and 11.2 live born alive for does of the INRA 0067 genotype, Perrier *et al*., 2000). However, in the particular case of the *post partum* rhythm (AI within 2 days after kindling), Szendro *et al*. (1999a) underlined that the decrease in fertility of primiparous does may be extended to secondiparous does, whereas the litter size no longer varies after the second litter.

State of lactation at insemination

The rabbit, a pluriparous species, the cow and the mare, monoparous species, are the only animals of zootechnical interest for which man requires simultaneous management of lactation and gestation. Thus, the lactation effect can be added to the parity effect at insemination.

Receptivity. At insemination, lactating does are generally less receptive than non-lactating does (Beyer and Rivaud, 1969; Garcia and Perez, 1989; Rodriguez *et al*., 1989; Theau-Clément *et al*., 1990b; Alabiso *et al*., 1996). In addition, lactating does that nurse large litters (≥8 kits) are less receptive than those that nurse smaller litters (Diaz *et al*., 1988; Garcia and Perez, 1989; Theau-Clément *et al*., 1990b; Rodriguez de Lara and Fallas, 1999). The sexual behaviour of does also varies with lactation stage (Ubilla and Rebollar, 1995). The percentage of does that accept to mate is very high (generally around 90%) on the day of birth (Beyer and Rivaud, 1969; Harned and Casida, 1969; Delaveau 1978; Maertens and Okerman, 1987; Diaz *et al*., 1988; Roustan and Maillot, 1990). It decreases at day 4 *post partum* (Diaz *et al*., 1988: 47.2%; Theau-Clément *et al*, 1990b: 54.2%), then increases at day 11 *post partum* (Theau-Clément *et al*., 1998b: 88.7%), and returns to the highest level after weaning (Prud'hon *et al*., 1969; Fortun Lamothe and Bolet, 1995). The dynamic of sexual receptivity from kindling to weaning has been confirmed by Theau-Clément *et al*. (2000).

Fertility. In AI, the difference in fertility due to lactating stage is systematic, being 10-20% in favour of non-lactating does (Lange and Scholaut, 1988; Rodriguez de Lara and Fallas, 1999; Rebollar *et al*., 1992a; Theau-Clément and Lebas, 1996; Perrier *et al*., 2000). On one hand, these differences are likely associated to the depressing effect of lactation on the ovulation ability (68 *vs.* 91.5% for non-lactating does), despite the injection of the hypothalamic hormone GnRH at the time of insemination. On the other hand, they are also associated with the increased percentage of gestation failures independent of ovulation (34.0 *vs.* 5.0%, Theau-Clément *et al.*, 1990a). However, lactating does at 10-11 days *post partum* are more fertile than does at 3-4 days (70.7 *vs.* 39.9% respectively, Theau-Clément, 1996). The fertility measured 24 hours after insemination (percentage of does having at least one segmented egg) is high the day after kindling, it decreases at day 4 *post partum* to increase again until right after weaning (96.4%; Theau-Clément *et al.*, 2000). The depressive effect of lactation stage on fertility is the combined consequence of a decrease in ovulation ability (50.7 and 78.5%, respectively at days 4 and 11 of lactation, Theau-Clément, 1996) and of an increase of the pregnancy failures independent of ovulation (11.7% at 11 days *vs.* 21.6% at day 4 of lactation) corresponding to the lack of fertilisation or total embryonic mortality.

Prolificacy. The results of prolificacy are generally little different between non-lactating and lactating does on day 11 *post partum* at the time of AI (8.2 *vs.* 7.7 born alive, respectively). However, they are higher than those of does inseminated at day 4 (4.5 born alive, Theau-Clément, 1996). Rodriguez de Lara and Fallas (1999) and Szendrö and Biro-Nemeth (1991) found no effect of the number of suckling kits at the moment of insemination on prolificacy. The intensity of ovulation increases when the interval between kindling and insemination enlarges (Theau-Clément *et al.*, 1990a, 1994). In identical experimental conditions, 24 hours after AI, Theau-Clément *et al.* (2000) observed 9.7, 10.1, 14.4, 14.7, and 14.8 *corpora lutea* when the does were inseminated 1, 4, 12, 19 days *post partum* respectively and 2 days after weaning. The fertilisation rate (number of segmented eggs/number of *corpora lutea*) has been little studied. Indeed, this measurement requires a laparatomy or sacrifice of the animals, 24-48 hours after insemination and perfusion of the oviducts in order to verify whether the oocytes have been fertilised (ovules) or not. The fertilisation rate is influenced by the lactation stage. It is high in the 24 hours following kindling (73.4%), but falls on the 4th day *post partum* (66.9%) and then increases until just after weaning (90.7%). In addition, Theau-Clément *et al.* (1990a) observed, during the week following implantation, 14.5% mortality for 11-day lactating does at the moment of AI, as compared to only 4.8% for non-lactating does. Lactation, on the one hand, depresses the receptivity of the does at the moment of AI and, on the other hand, the reproduction performances and its components: fertility (ovulation ability, pregnancy failures not associated with ovulation), and prolificacy (ovulation intensity, fertilisation rate, embryo survival). Lactation and its intensity (number of suckling kits) depress fertility, in particular the percent of ovulating does (despite the injection of GnRH) and the frequency of pregnancy failures not associated with ovulation. The stage at 4 days post partum is particularly unfavourable to induction of ovulation, pregnancy establishment and its maintenance in the beginning of the development. The depressed effect of lactation on prolificacy is closely related to lactation stage. Ovulation intensity increases with an increase in the interval between kindling and insemination whereas the fertilisation rate is variable. However as Foxcroft and Hasnain (1973) early suggested, the moment of mating after birth has a more important effect on behaviour and reproduction performances than lactation.

Sexual receptivity at insemination

Artificial insemination is a technique that aims to induce pregnancy also in those females that would have refused the mating, if mated naturally. Thus, in AI, parity and lactating effects add to the receptivity effect. Receptivity, measured by a test in the presence of a male or by observation of the colour and turgescence of the vulva, reflects the state of oestrus or dioestrus of does at insemination (Moret, 1980; Gosalvez *et al.*, 1985).

Fertility. In AI, fertility is strongly related to sexual receptivity of does (Theau and Roustan, 1980; Battaglini *et al.*, 1986). Indeed, fertility is significantly higher (>75%) in receptive does than in non-receptive does (25 to 55%, Theau-Clément and Poujardieu, 1994; Alabiso *et al* 1996; Theau-Clément, 1996; Rodriguez de Lara and Fallas, 1999; Theau-Clément, 2001). The slightest fertility of non-receptive does at insemination is partially due to ovulation failures (Rodriguez and Ubilla, 1988; Theau-Clément *et al.*, 1990a; Theau-Clément and Poujardieu, 1994) and pregnancy failures of ovulating does (27.1% *vs.* 11.7% respectively, Theau-Clément *et al.*, 1990a). However, in a recent study, Theau-Clément (2001) showed that pregnancy failures independent of ovulation also depend on parity (primiparous: 33 *vs.* 8%; multiparous: 15 *vs.* 0%, respectively for non-receptive and receptive does).

Prolificacy. Receptive does have higher prolificacy than non-receptive does at insemination (Theau-Clément, 1996: +2 kits; Rodriguez de Lara and Fallas, 1999: +1 kit). The relation between the high levels of receptivity and prolificacy can be found whatever the reproductive rhythm. Indeed, receptive does inseminated at 4 or 10 days *post partum* have larger litters at birth than non-receptive does inseminated at the same stages (10.5 and 8.2 *vs.* 8.7 and 6.7 total born, respectively; Theau-Clément *et al.*, 1990b; Theau-Clément and Lebas, 1996). Receptive does have a higher intensity of ovulation (11.0 *vs.* 8.7 *corpora lutea*; Theau-Clément and Poujardieu, 1994), are more frequently fertilised (84.1 *vs.* 44.1% Theau-Clément, 2001), and have better embryo survival (at the 14^{th} day of pregnancy: +2.5 foetuses, Theau-Clément and Poujardieu, 1994). Sexual receptivity of does at insemination, which varies with lactation stage, is associated with a better fertility. Possessing a higher number of preovulatory follicles in the ovaries (Kermabon et al., 1994) and higher plasma oestrogen concentrations (Rebollar et al., 1992b), receptive does ovulate more frequently and have fewer gestation failures independent of ovulation than non receptive does. Sexual receptivity of does at insemination is associated with high prolificacy at birth. This result is the consequence of higher ovulation intensity, fertilisation rate, and embryo survival in receptive does. As a consequence, the productivity of receptive females is three to four times higher than that of non-receptive females (Figure 1).

Physiological state
Parity, stage of lactation, and sexual receptivity of does at insemination influence reproductive performance. However, lactating females are generally less receptive. These effects interact with the reproductive performances. The "physiological state" of does, defined by the combination between lactating stage and sexual receptivity, should therefore be studied. Does may be lactating-receptive, lactating-non-receptive, non-lactating-receptive, and non-lactating-non-receptive.

Fertility. Does that are both lactating and non-receptive present a depressed fertility (<45%) as compared to the three other groups of does (>70%: Theau-Clément and Lebas, 1994; Castellini and Lattaioli, 1999). However, the effect of the physiological state varies with lactation stage (Theau-Clément, 1996). The lactating-non-receptive does at 4 days *post partum* are less fertile than the lactating-non-receptive does at day 11 of lactation (16.2 *vs.* 53.8%). This poor result is the consequence of ovulation and fertility failures, and/or marked embryo mortality, particularly when does are lactating-non-receptive at day 4 *post partum*.

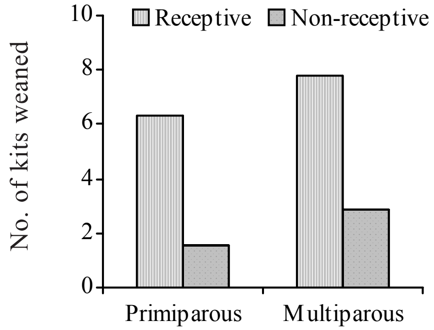

Figure 1: Influence of the receptivity of lactating does (11 days *post partum*) at AI on their productivity at weaning.

Prolificacy. Generally, lactating-non-receptive does are almost systematically the opposite of the three other groups of females and have significantly fewer kits at birth. In addition, as with fertility, the effect of physiological stage varies with the lactation stage of the does. Indeed, at 11 days *post partum*, the lactating-non-receptive does produce 8.2 total kits at birth as compared to 9.8 for the other groups of does (Theau-Clément and Lebas, 1994). At 4 days *post partum*, the lactating-non-receptive does produce only 4.6 total kits against 8.1 on average for the other categories of does (Theau-Clément *et al*., 1990b).

These results allow to better specify the factors and their interaction that can determine the success of AI, as well as the complexity of the mechanisms involved. The reproduction performance of does simultaneously lactating-non-receptive is largely depressed. Indeed, these does are less fertile, a direct consequence of ovulation lacks (despite the injection of GnRH), fertility failures or early embryo mortality. They also have smaller litters. These observations suggest, especially in non-receptive does, the existence of a partial antagonism between lactation and reproduction, reflecting the corresponding partial hormonal antagonism between prolactin and gonadotropin secretions (Theau-Clément and Roustan, 1992; Fortun-Lamothe and Bolet, 1995; Boiti, 2004). Even though the effects of prolactin on the level of the uterus (deterioration of the migration of the spermatozoa, increase in foetal mortality) and ovary (inhibition of follicular growth and the activation of proteolytic enzymes intervening in the rupture of the follicules of Graaf, inhibition of the expression of LH receptors) seem rather well known, the mechanisms of action of prolactin on the level of the hypothalamo-pituitary axis, are not well identified. The secretions of dopamine and opioids at the hypothalamic level intervening in the release of PRL would be implicated in the reduction in the secretion of gonadotropins.

However, the degradation of reproductive efficiency varies with lactation stage. Concerning the rhythms studied, it is at day 4 of lactation that does are less receptive and that lactating-non-receptive does have the lowest reproductive performances. In terms of productivity, as compared to the other physiological states, the does that are both lactating and non-receptive at the moment of AI, have a very low productivity at weaning (day 4 post partum: 0.9 weaned kits/AI; day 11 post partum: 2.7 weaned kits/AI, Figure 2). The problem is important since in intensive production systems, does are inseminated at the beginning of lactation. It is noteworthy that this effect is not very visible with natural mating, since this antagonism is hidden by the refusal of non-receptive does to mate.

Pseudopregnancy

Ovulation is the result of a neuro-endocrine reflex, induced in the doe by mating. In AI, ovulation is induced by the administration of GnRH. Thus, after kindling, the functional *corpora lutea* (those secreting progesterone) should not be present in the ovaries of a doe that has not been mated or inseminated. However, Boiti *et al.* (1996) have shown that almost 20% of the rabbits have, at insemination, high plasma progesterone concentrations associated with a low sexual receptivity and

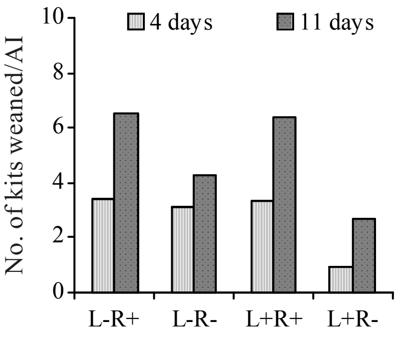

Figure 2: Influence of the physiological state of does at AI on their productivity at weaning in relation to lactation stage according to Theau-Clément *et al* (1990b) and Theau-Clément and Lebas (1994).
L-R+: non-lactating-receptive; L-R-: non-lactating-non-receptive; L+R+: lactating-receptive; L+R-: lactating-non-receptive.

a low fertility. This observation was confirmed by Theau-Clément *et al.* (2000). Indeed, 35 of 170 does observed 24 hours after insemination presented 2 generations of *corpora lutea* (from 11 to 33): a first generation of recent *corpora lutea* (corresponding to the injection of GnRH,) and a second generation of older and prominent *corpora lutea* (Photo 1). These does were characterised by low sexual receptivity (22%), low fertility (3%), but all had ovulated. Blood sampling at insemination showed that these does had a high level of progesterone (9.4 ng/mL); they were thus pseudopregnant. During several experiments, systematic progesterone measurements were realised at insemination (11 days *post partum*). A preliminary analysis (Theau-Clément *et al*., 2005) showed that the frequency of pseudopregnant does (plasma concentration >1 ng/mL) depends on the parity of the does (nulliparous: 16%; primiparous: 32.5%; multiparous: from 4 to 9%). Pseudopregnancy does not seem to affect the receptivity of nulliparous does; however, their fertility is highly reduced (37.5 *vs.* 96.1%) leading to low productivity at birth (3.0 *vs.* 7.4 born alive/AI). In primiparous does, pseudopregnancy affects receptivity (60.0 *vs.* 81.3%), fertility (24.0 *vs.* 82.5%) and as a consequence productivity at birth (2.1 *vs.* 8.3 born alive/AI). In multiparous does, pseudopregnancy depresses fertility (53.8 *vs.* 86.2 %) and to a lower degree productivity (6.1 *vs.* 8.6 born alive). In pseudopregnant does, the plasma concentration of progesterone is higher in primiparous than in nulliparous or multiparous does (7.1 *vs.* 1.9 and 3.3 ng/mL, respectively).

In the experiments cited above, the does were raised in individual cages; the last injection of GnRH was done 32 days earlier and the corresponding luteolysis was completed (the end of luteolysis occurs 18 days after ovulation, Browning *et al*., 1980). In addition, no visible stress was noted, and there was no contact with males. The absence of these causes capable of inducing ovulations leads to advance some hypothesis to justify the abnormal status of pseudopregnancy.

Boiti *et al.* (1999) showed that uterine infections increase the life of *corpora lutea* and could partly explain the high levels of progesterone at insemination. In addition, Boiti *et al.* (2005) showed that progesterone could be secreted by the adrenal glands following activation of the adrenalin axis by ACTH or by injection of lipopolysaccharides (constituents of gram – bacteria cell walls). However, in the experiments of Theau-Clément *et al*. (2000), none visible uterine infection had been observed in young slaughtered does, so the unique “pathology” hypothesis cannot be retained. In fact, no doe at 1 day of lactation showed 2 generations of *corpora lutea* at insemination. These observations suggest the emergence of currently unidentified spontaneous ovulation in primiparous does between the first and the fourth day of lactation.

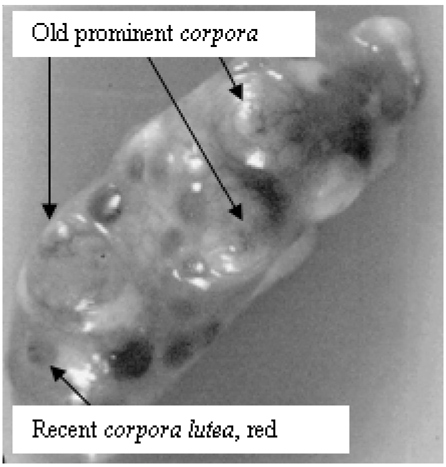

Photo 1: Ovaries of does having 2 generations of *corpora lutea* 24 hours after AI.

Pseudopregnancy is thus susceptible to strongly depress reproduction performances. However, the cause of these ovulations prior to insemination are today unknown. Additional studies are necessary on the one hand to more precisely characterise pseudopregnant does and the level of progesterone beyond which they cannot reproduce and on the other hand, to explain the cause of these ovulations.

Other factors
In order to completely express their reproductive potential, does must have a good sanitary state. When this is not the case, the percent of receptive does at insemination decreases as well as their reproductive performances.

Few studies allow the analysis of the importance of genetic factors in the success of AI. With natural mating, Foxcroft and Hasnain (1973) showed that the incidence of lactation and lactation stage on the aptitude to ovulate and on fertilisation rate depends on the genetic type of the does. Hulot and Matheron (1979, 1981) found complementarity between the INRA “A2066” strain (high ovulation intensity) and the INRA “A1077” strain (high embryo survival). In artificial insemination, Brun *et al* (1999) estimated the evolution of the reproductive performances of does between the F0 and F1 generations of an artificial strain obtained from the INRA “A1601” and INRA “A2066” strains. All the characteristics except foetal and postnatal viability increased between F0 and F1 due to a direct heterosis effect: in particular the receptivity rate (10%). The study and use of genetic variability of the sexual receptivity of does at AI could be a way to improve the insemination results.

METHODS OF INDUCTION OF SEXUAL RECEPTIVITY OF DOES

Since in general rabbit does are lactating at insemination, a partial antagonism between lactation and reproduction leads lactating and non-receptive does to have very low performance. The improvement and homogenisation of reproductive performance on farms are conditioned by the choice of reproduction rhythm (today stabilised at 42 days, stage of lactation at AI: 11 days) and by the use of methods allowing the induction and synchronisation of oestrus of lactating does in particular. This concerns hormonal treatments or non-hormonal alternative methods called “biostimulations”.

Hormonal methods
Hormonal treatments have been widely used in recent years. With these treatments, different types and dosages of hormones are administered 2-3 days before insemination.

Pregnant Mare Serum Gonadotropin (PMSG or eCG). This molecule is a glycoprotein with a mass estimated between 45 and 64 kDa (Drion *et al*., 1998). It is extracted from the serum of pregnant mares. It is a dimerous hormone with both an FSH and LH activity. Its major FSH effect was used to induce and multiply the ovulations (superovulation) first in the cow (Avery *et al*., 1962), then in laboratory animals (Chang and Pickworth, 1969), including the rabbit (Kennelly and Foote, 1965). In this review, studies related to superovulation will not be considered.

In small ruminants, the hormonal inducing and synchronising treatments of oestrus and ovulation are a preliminary condition for out-of-season breeding and artificial insemination. However, repeated use of PMSG is generally followed by a decrease in fertility in specific ewes and goats treated by artificial insemination. Some studies have shown that this phenomenon is correlated to the appearance of antibodies in the plasma of certain treated females in both ovines and caprines (Baril *et al*., 1992; Bodin *et al*., 1995; Roy *et al*, 1999). PMSG has been used for about 15 years to induce and synchronise rabbit doe oestrus. However, it could have an important immunogenic nature since it is an exogenous protein with high molecular weight. For this reason, its efficacy may decrease when used over a long period in the doe.

An injection of PMSG made on lactating does at 11 days *post partum* improved the percentage of receptive does at insemination, whatever the dose (10 IU: Bonanno *et al*., 1991; 20 IU: Bonanno *et al*., 1990; Maertens, 1998; 25 IU: Theau-Clément and Lebas, 1996; Theau-Clément *et al*., 1998c; 30 IU : Mirabito *et al*., 1994b; 35 IU: Bourdillon *et al* 1992; 40 IU: Castellini *et al*., 1991). In addition, its positive effect was maintained after several injections during 7 (Boiti *et al*., 1995), 9 (Theau-Clément and Lebas, 1996) or 11 cycles of reproduction (Theau-Clément *et al*., 1998c).

An injection of PMSG before insemination generally increases fertility of does, but its efficacy could depend on the treatment conditions (dosage, way of injection, interval between injection and insemination…). In the same experimental conditions, Alabiso *et al.* (1994) did not show any improvement of fertility when the dose injected increased from 20 to 40 IU.

To our knowledge, the optimal interval between PMSG injection and AI has been little studied. Only Alvariño (2005) evidenced that fertility decreases when the interval reaches 96 hours, within any significant differences of fertility from 24 to 72 hours. However, a bibliographic analysis showed that the injection of 20 IU of PMSG (Bonanno *et al*., 1993; Alabiso *et al*., 1994, 1996) 72 hours before insemination does not lead to an improvement of fertility, whereas such an improvement is often described for a 48 hour interval. Even though Alvariño (2005) showed that the way of injection does not influence fertility (intramuscular or subcutaneous).

The efficacy of the treatment also depends on the physiological state of the does at insemination. Thus, PMSG does not improve the fertility of nulliparous does (Castellini *et al*., 1991; Parez, 1992; Alabiso *et al*., 1994). On the contrary, it increases the fertility of primiparous does (Bourdillon *et al*., 1992; Davoust *et al*., 1994, Maertens, 1998, Rebollar *et al*., 2006) and multiparous lactating does (Davoust *et al*., 1994; Mirabito *et al*., 1994b; Theau-Clément and Lebas, 1996; Theau-Clément *et al*., 1998c). The injection of PMSG is not justified in non-lactating does that have a high reproduction potential. It must be mentioned that some authors evidenced a positive effect of PMSG only during the first four injections (Canali *et al*., 1989; Lebas *et al*., 1996; Rebollar *et al*., 2006). Several authors have shown that PMSG treatment can increase litter size but Theau-Clément and Lebas (1996) showed that the improvement of prolificacy of treated does is only associated with the increased percentage of receptive does.

The immunogenicity of PMSG was shown for the first time by Canali *et al*. (1991) and confirmed by Boiti *et al*. (1995) following injection of 40 and 20 IU, respectively. According to these authors, the titre of anti-PMSG antibodies depends on the interval between injections (r=~0.51): it increases after the third injection whereas simultaneously, fertility decreases. Theau-Clément *et al* (1998d) studied the kinetics of the antibodies to the wire of the injections, following administration of 8 or 25 IU of PMSG to 124 primiparous does during 11 series of inseminations (interval between injections: 35 days). Anti-PMSG antibodies (measured by binding rate, Figure 3) were not detectable until after the 6th injection, however, their titre depended on the dose administered. At the end of the experiment, only 15 and 39% of the does treated, respectively, with 8 or 25 IU developed immunity against PMSG. In addition, the productivity of lactating does was independent of the immune response (hyperimmunes: 6.9 weaned kits/AI; hypoimmunes: 7.0 weaned kits/AI).

Thus, at the current state of knowledge, the use of PMSG in routine (20-25 IU, 48 hours before insemination) of lactating does at 11 days post partum durably increases the percent of receptive does at insemination and, as a consequence, their productivity (measured on 9 reproductive cycles: +47% of weaned kits/AI) without an important immune risk. However, some authors found a positive PMSG effect on fertility only during the four first injections. Only 8 IU PMSG are necessary to efficiently stimulate does at 4 days post partum (Theau-Clément et al., 1998c;d). However, it must be underlined that few studies have been made on treatment conditions, notably the interval between injection and insemination, as well as the injection volume.

Prostaglandin, PGF2α. The luteolytic effect (regression of *corpora lutea*) of the PGF2α prostaglandins (natural or synthetic) was used to induce and synchronise parturition or induce regression of the *corpora lutea* of pseudopregnant does (McNitt, 1992). An indirect effect of the administration of PGF2α on the 29th day of pregnancy to synchronise birth is the increased sexual receptivity and fertility (+16%) observed when the does were inseminated on 7 days *post partum* (Ubilla and Rodriguez, 1988).

Different authors have studied the efficacy of PGF2α administered 2-3 days before insemination, to synchronise the oestrus of does. The conclusions were diverse. When 200 µg of PGF2α are injected 72 hours before insemination, Mollo *et al.* (2003) did not observed an increase of fertility. In the same conditions, Stradaioli *et al.* (1993) did not improve the ovarian response (ovary weight, number of *corpora lutea* and hemorrhagic follicles) nor the ability of early embryos to develop *in vitro*. On the contrary, Facchin *et al.* (1992), Alvariño *et al.* (1995), and Alaphilippe and Bernard (1998) concluded that PGF2α administration to does inseminated 11 days after parturition improves reproductive performance.

Although the physiological basis of these studies was not indicated by the authors, the improvement of the reproductive performance often observed, suggests that PGF2α may have some relevant physiological role. One of the most likely hypotheses relies on the luteolytic effect of PGF2α acting on pseudopregnant does. Thus, PGF2α leads to the regression of existing *corpora lutea* and consequently, withdraws the inhibition of progesterone notably on oestrogen secretion, therefore allowing a new reproductive cycle. In addition, the simultaneous treatment with PMSG and analogues of PGF2α demonstrated by Facchin *et al* (1998), supports that hypothesis. In comparison with a control group, the combination PMSG+PGF2α increases the fertility (71.4 *vs.* 82.3 %) whereas the percentage of pseudopregant does at the moment of AI decreases (20.0 *vs.* 0 %). Consequently, it is probable that the efficacy of this pharmacological association depends on the number of pseudopregnant does at insemination.

Thus, the prostaglandins may have an indirect action on the induction of receptivity, only on pseudopregnant does, whereas PMSG has a direct action on the ovaries (an increase of follicle growth). These two hormones could thus be complementary on a herd that, for reason not yet well understood, includes pseudopregnant does.

Non-hormonal alternative methods

The foreseeable evolution of the regulations on the use of exogenous hormones has led to research on alternative methods for the improvement of sexual receptivity of rabbits and as a consequence

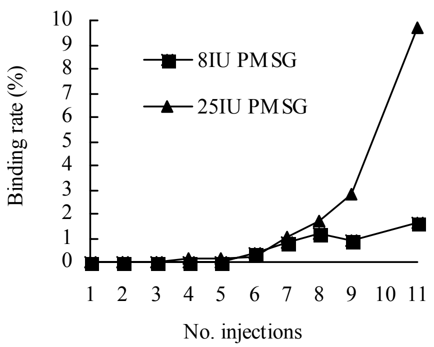

Figure 3: Anti-PMSG antibody rate in relation to the number of injections (in comparison with a control group).

their productivity. For these reasons, an important study was performed recently, in particular by the IRRG (International Rabbit Reproduction Group) to propose non-hormonal alternative methods called “biostimulations” (Boiti, 1998; Theau-Clément *et al*., 1998a; e). These methods applied immediately before insemination should be easy to use, inexpensive, compatible with the animal welfare and well adapted to cyclic production. Until recently, different techniques have been tried such as the handling of animals, a short separation of the mother and her litter, feeding programmes, lighting programmes and male proximity. Indeed, the environmental modifications such as the length of daily lighting, temperature, food, stress, auditive or olfactive stimulations can modify the endocrinal balance of the doe and vary the reproductive performance. Indeed, the environment plays an important role in the regulation of the reproductive function *via* the nervous system and the hypothalamo-pituitary axis.

Handling of the animals. The efficacy of animal handling such as changing the cage (Lefèvre and Moret, 1978; Rebollar *et al*., 1995; Luzi and Crimella, 1998; Rodriguez de Lara *et al*., 2000, 2003) or regrouping the does before insemination (Mirabito *et al*., 1994a; Duperray *et al*., 1999) have not been clearly shown; the conclusions of the different studies have been contradictory. In addition, these methods are difficult to use in breeding where animal management (and their identification) as well as sanitary control is made difficult by frequent changes of the cages.

Short dam-litter separation. In the sow, a daily separation of 6 to 12 hours between 2 and 5 weeks *post partum* induces oestrus in 65% of the mothers (*vs.* 50% in controls; Stevenson and Davis, 1984). In the rabbit doe, a 24 hour dam-litter separation sometimes improves sexual receptivity and fertility of 11 day lactating does (Pavois *et al*, 1994; Maertens, 1998; Theau-Clément and Mercier, 1999, Table 1). However, in some cases, this stimulation is insufficient (Alvariño *et al*., 1998; Maertens *et al*., 2000; Theau-Clément and Mercier, 2003). From 36 hours of separation on, the percent of receptive does and fertility are generally improved (difference of fertility as compared to the control: from +11% to +24%). A dam-litter separation does not generally influence litter size; it neither increases the mastitis frequency of the mothers nor the mortality of kits (Maertens, 1998; Bonanno *et al*., 1999a; b, 2000, 2004). Even if most studies show that a separation is accompanied by a decrease in weaning weight of kits, 36 to 48 hour separations generally improve the overall productivity (as compared to the control : 36h: +14% , Pavois *et al*., 1994; 40h: +9%, Maertens, 1998; 48h: +28%, Bonanno *et al*., 2000; +54%: Bonanno *et al.,* 2002; +35%: Bonanno *et al*., 2004; +25%: Bonanno *et al*., 2005; +20% Virag *et al*., 1999). This stimulation should be performed just before AI (Castellini *et al*., 1998) and insemination should be performed immediately after the first suckling that follows the return of the mother with her kits (Szendrö *et al*., 1999b). However, the positive effect of this stimulation is clear with free suckling before and after the stimulation; it is less so with controlled lactation applied before and after stimulation (Szendrö *et al*., 1999b; Bonanno *et al*., 2000 ; Table 1).

Controlled lactation, which consists in closing the nest box and only opening it for few minutes per day, is a common practice in farms (Le Normand *et al*., 1994). In order to limit the effect of separation on the growth of kits, the effect of 2 or 3 days of controlled lactation before AI was studied (Table 2). This practice corresponds respectively to 2×24 h or 3×24 h of dam-litter separation, thus allowing the young rabbits to suckle as soon as the nest box is opened (from 15 to 30 minutes in the morning). Sometimes, controlled lactation is prolonged 3 to 7 days after insemination. With the exception of the study by Matics *et al.* (2005), who obtained a high fertility in a control herd (78%), controlled lactation 2 days before insemination increases fertility (from 15 to 17%: Eiben *et al*, 2004b; Bonanno *et al*., 2004, 2005). Thus, when the kits are nursed every day, their growth is no longer depressed and overall productivity is systematically improved (as compared to the control: Eiben *et al*., 2004b : +51%; Bonanno *et al*., 2004: +44% ; Bonanno *et al*., 2005: +21%).

Table 1: Reproductive performance of lactating does (11 days post partum) shortly separated from their litter, in comparison with a control group (without separation)

Nursing system before and after DLS[1]	Separation length	Authors	Receptivity (%)	Fertility (%)	Born alive/litter	Individual weaning weight (age in days)	Weight of weaned kits/AI
Free nursing	24 h	Pavois *et al.* (1994)	+ 26%	+ 13%	NS	-	+ 16% (at birth.)
		Alvariño *et al.* (1998)	-	NS	NS	~ 36 g (32)	-
		Theau-Clément and Mercier (1999)	+ 8%	+ 13%	NS	~ 34 g (28)	+ 1%
		Maertens *et al.* (2000)	-	NS	-	NS (28)	NS
		Theau-Clément *et al.* (2003)	NS	NS	NS	NS (35)	
	36 h	Pavois *et al.* (1994)	+ 23%	+ 11%	NS	NS	+ 14%
		Alvariño *et al.* (1998)	-	+ 11%	NS	~73 g (32)	-
	40 h	Maertens (1998)	+ 38%	+ 11%	+ 1.1	~ 47 g (28)	+ 9%
	48 h	Alvariño *et al.* (1998)	-	NS	NS	~ 68 g	-
		Bonanno *et al.* (2000)	+ 21%	+ 23%	NS	NS (35)	+ 28% (at 70d)
		Bonanno *et al.* (2002)	NS	+ 24%	NS	~ 38 g (35)	+ 54%
		Bonanno *et al.* (2004)	NS	+ 17%	NS	~ 48 g (35)	+ 35%
		Bonanno *et al.* (2005)	+ 27%	+ 18%	NS	NS (35)	+ 25%
	48 h	Virag *et al.* (1999)	-	+ 20%	NS	~ 27 g (35)	+ 20%
Controlled nursing	48 h	Szendrö *et al.* (1999)	NS	NS	NS	~ 34 g	-
		Bonanno *et al.* (2000)	NS	NS	NS	NS (35)	+ 7% (at 70d)

[1] DLS: Dam-Litter Separation, NS: Non Significant ($P < 0.05$)

Table 2: Reproductive performance of lactating does (11 days post partum) when nursing method is changed from free to controlled nursing 2 or 3 days before AI in comparison with a control group (free access to the nest box, from kindling to weaning)

Controlled nursing[(1)] length		Authors	Receptivity (%)	Fertility (%)	Born alive/portée	Individual weaning weight (35 days)	Weight of weaned rabbits /AI (%)
before AI	after AI						
2 days	0 day	Matics *et al.* (2004b)	NS	NS	NS	NS	-
		Eiben *et al.* (2004b) [(2)]	-	+ 17%	NS	+ 29 g	+51%
		Bonanno *et al.* (2004)	NS	+ 15%	NS	NS	+44.%
		Bonanno *et al.* (2005)	+ 18%	+15%	NS	NS	21%
2 days	3 days	Eiben *et al.* (2004b)[(2)]	-	+ 27%	+ 1.6	+ 34 g	86%
		Eiben *et al.* (2004b)[(3)]	-	+ 26%	NS	+ 37 g	76%
2 days	7 days	Eiben *et al.* (2004a)[(3)]	NS	NS	NS	- 67 g	26%
3 days	0 day	Matics *et al.* (2004b)	21%	NS	+ 1.2	NS	?
		Szendrö *et al.* (2005c)	-	9%	NS	-20g	5%

[(1)] During 2 or 3 days before AI, the nest box is closed from 24 h from 9 or 10:00 h of day X to 9 or 10:00 h of day X+1, the nest box is closed again after a controlled nursing lasting maximum 15 minutes. [(2)]The nest box is removed and not only closed. [(3)]A wire mesh is inserted during the separation. NS: Non Significant (P<0.05).

When lactation was pursued 3 days after insemination, Eiben *et al* (2004b) observed an increase of fertility and prolificacy leading to an appreciable improvement of productivity (+25% - +35% of weaned kits weight/AI, as compared to only 2 days of controlled lactation before insemination).

Controlled lactation, continued for 7 days after insemination, depressed the growth of the kits, but, when compared with controls with low fertility (33%), the productivity increased by 26% (Eiben *et al.*, 2004a).

The application of controlled lactation 3 days before insemination gave variable results (Szendrö *et al.*, 2005a; b; c: improvement of fertility but reduction of the young growth; Matics *et al.*, 2005 : improvement of litter size at birth and weaning).

Eiben *et al* (2004b, 2005) showed that the separation method could also influence productivity. A separation with a fence (visual, olfactive and auditive stimulation) was less efficient than a separation made with a metallic plate (no visual stimulation) or withdrawal of the young rabbits (no stimulation).

The efficacy of a dam-litter separation could depend on parity. Thus, Maertens (1998) and Virag *et al.* (1999) mainly improved the fertility of primiparous does (+30% and +43%, respectively). Bonanno *et al.* (2000, 2002, and 2005) observed an improvement of fertility (from 19 to 35%) following 48 hours of separation with the first 3 litters whereas the stimulation was inefficient on does of higher parity. In addition, Bonanno *et al.* (2002) showed that when separation was used consecutively on does having produced more than 3 litters, the fertility is no longer improved as compared to the control. This result suggests that the effect of the separation on the mother and the kits, depends on the number of successive treatments.

It is noteworthy that in these studies there is a large variability of fertility of the controls (from 33 to 82%) despite similar experimental conditions (reproduction rhythm: 42 days, single batch and artificial insemination). This observation illustrates the limit of our current knowledge of rabbit doe physiology. In addition, the positive relationship that associates receptivity and fertility is not systematically found. This is probably due to the method of evaluation of receptivity that is often subjective being based on visual observation and thus, on colour and turgescence of the vulva.

On the physiological level, 48 hours of separation are generally accompanied by a decrease in prolactin secretion 24 hours after the start of the stimulation, whereas on the AI day the oestradiol-17β plasmatic concentration increased (confirmed by Rebollar *et al*., 2005, 2006 on 4 days lactating does); in addition, the LH response to GnRH treatment is higher (Ubilla *et al*., 2000, 2001). This result suggests that a decrease in prolactin secretion due to the absence of suckling stimulates follicle growth and steroidogenesis, thus improving the receptivity and fertility of does momentarily separated from their litter. In addition, the separation could act as a positive stress and influence the hormonal equilibrium of the does. Indeed, early maternal privation influences the development of young rabbits, reduces mortality before weaning and improves later fertility (Boiti *et al*., 2001; Brecchia *et al.*, 2001).

For a reproduction rhythm of 42 days in a free lactating situation, a separation of 36 hours between the mother and her litter is an alternative to the use of hormones in inducing the receptivity of does and in improving their productivity (Maertens, 1998; Alvariño et al., 1998; Bonanno et al., 2005). This stimulation should be applied just before insemination, which is practiced immediately after the first suckling following the separation. However, this short maternal privation depresses the kits growth. Thus, the studies have been orientated more towards the optimisation of controlled lactation applied just before insemination. In the current state of our knowledge, when free lactation is applied before and after insemination, 2 days of controlled lactation by closing the nest box improves the productivity (at least by 20%) without affecting the growth of the young. This method produces the same level of productivity as 48 hours of separation or the prior injection of 20 IU PMSG (Bonanno et al., 2005). The interest of pursuing controlled lactation after insemination should be confirmed since when used over longer periods it may depress the performances.

On 4-day lactating does (reproduction rhythm: 35 days), in comparison with a control group, only 24h dam-litter separation improves fertility (Alvariño et al., 1998: + 17%) at least during three reproduction cycles (Rebollar et al., 2006: from +19 to +33%).

However, other questions remain, notably the lasting of the effect of this stimulation in relation with the number of successive treatments and doe parity.

Feeding Programmes. In ewes, the weight before mating reflects the nutritional status and has a determining influence on the ovulation rate, fertility and prolificacy (Theriez, 1984). Thus, the increase in weight before mating has a positive effect on reproduction performances. On the contrary, a nutritional deficiency before mating depresses ovulation rate and embryo survival. Thus, the "flushing" which consists in increasing the food ration (energy) just before mating is currently practiced.

In the rabbit doe without any prior food restriction, Fortun-Lamothe (1998) suggests that "flushing" may improve fertility. Conversely, she shows that food restriction depresses the receptivity and litter weight of kits. Maertens (1998) did not improve the reproduction performances of lactating does receiving food flushing 4 days before insemination. On the contrary, Luzi *et al.* (2001) improved fertility and productivity of does by administrating an energetic flushing (2% of propylene glycol in drinking water) 4 days before insemination.

Following feed restriction for two weeks, Gosalvez *et al.* (1995) improved the percentage of ovulating does (at the age of 17 weeks) after flushing, 4 days before LHRH injection. Brecchia *et al.* (2005) studied the effects of 24 and 48 hours of fasting followed by a stimulation that consisted in feeding the does again 2 hours before insemination. When comparing with controls fed *ad libitum*, the food flushing was not sufficient to improve the reproduction performances of the does. On the physiological level, these authors showed that this food programme reduced the expression of the oestradiol-17β receptors in the hypothalamus-pituitary complex, the frequency and amplitude of oestrogen secretion, LH peak and leptin concentration in the plasma.

Feed flushing after a period of restriction could improve the reproduction performance, at least at the beginning of the reproductive carrier. Even though it is clearly shown that food programmes can depress reproduction performance, no study has, however, identified a programme that could improve the reproduction performance without depressing the growth of kits.

Lighting programmes. At our latitudes, Hammond and Marshall (1925) and Boyd (1986) showed that the wild rabbit (*Oryctolagus cuniculus*) has a well-defined seasonal reproduction cycle: most pregnancies occurred between February and August, with a peak in May. Fertility is thus maximal in increasing day-light. Walter *et al.* (1968) showed that in the domestic rabbit, 16 hours of daily continuous artificial lighting throughout the whole year reduces the reproduction problems normally associated with decreasing daylight periods. On the contrary, Schüddemage *et al.* (1999) showed that during a 1-year experiment, does receiving 8 hours of daily artificial lighting produce +5% more born alive per litter than those receiving 16 hours of lighting. In a recent study, Theau-Clément and Mercier (2005) showed that under constant lighting, the choice of 8 or 16 hours of light only slightly influences productivity. However, under 16 hours of lighting, meat rabbits (INRA 0067) are more receptive and kits have better growth.

Compared with a control group (continuous lighting 16 hours/day), the sudden passage from 8 to 16 hours of lighting per day, 8 days before insemination, improved the sexual receptivity (Theau-Clément *et al.,* 1990b) and fertility (Mirabito *et al.*, 1994b, Gerencsér *et al.*, 2006). However, the litters are lighter at weaning. The light stimulation should be sufficient. Indeed, the sudden passage from 10 to 16 hours of light does not improve the reproduction performance when applied only 5 days before insemination (Maertens and Luzi, 1995).

However, in the rabbit, the way of action of the photoperiod is poorly known. In mammals, the knowledge of photoperiod effects on the neuroendocrine system and on reproduction function has allowed the application of light treatments to control seasonal reproduction activity (Chemineau *et al.*, 1992).

The results of these few experiments are encouraging and illustrate the necessity to study the effects of photoperiod on rabbit reproduction. Szendrö et al. (2005a, b) showed that lighting programmes interact with lactation. It is likely that light influences the milk production of mothers, feeding and growth of the kits. Lighting programmes, which are easy to apply and are low cost, will be all the more efficient if the rabbits are in the same physiological state. They are therefore perfectly adapted to cycled production.

Male proximity. In different physiological situations, the presence of the male could influence the hormonal secretions and the behaviour of the females in many ungulate species. In the ewe (Mauléon and Dauzier, 1965), cow (Signoret, 1980), and sow (Rowlinson and Bryant, 1974), the introduction of males in the herd reduces the length of lactation anoestrus and advances ovulation following the beginning of oestrus (Lindsay *et al*., 1975; Poindron and Le Neindre, 1980), by advancing the preovulatory LH peak (Martin and Scaramuzzi, 1983). In ewes of different breeds in seasonal anoestrus, the introduction of males (after a period of isolation) induces and synchronises oestrus (Oldham *et al*., 1978). Similarly, the introduction of bucks among anovulatory goats after a period of complete segregation (odor, sight, sound and touch), induces synchronous ovulations in the following days (Chemineau, 1987).

For some farm species, the "male effect" has been used to control reproduction and appears as a biological alternative to hormonal treatments, at least during certain periods of the year. We do not know if similar mechanisms can be transposed to species such as the rabbit whose ovulation is induced by mating. Some authors hypothesise that the doe emits specific signals that attract males and contain information on her sexual state (Vodemeyer, 1989; Hudson and Distel, 1990; McNitt, 1992). On the contrary, the nature of olfactive exchanges between the male and female are poorly known. The pheromones secreted by the sebaceous glands of males could induce the sexual receptivity of the does (Franck, 1966). In nulliparous does, the presence of males contributes to increase the rate of acceptation of mating (Lefèvre *et al*., 1976) and improves fertility (Berepudo *et al*., 1993). However, neither the presence of males nor their proximity during a period of 4 or 48 hours (Bonanno *et al*., 2003), 3 or 4 days (Kustos *et al*., 2000 ; Eiben *et al*., 2001) before insemination improves the receptivity and the fertility of lactating does.

The proximity of males does not seem to influence the reproduction performances of inseminated rabbits. In addition, these practices are too laborious to be practiced in rabbit farming.

CONCLUSION

In farming, at any given moment, the productivity of any healthy herd will be more elevated and homogenous if it includes many receptive does and few lactating, non-receptive, and/or pseudopregnant does as well. Thus, it is pertinent to look for methods of induction of receptivity susceptible to improve not only fertility, but also global productivity of does, without depressing the growth of kits before weaning.

The routine use of PMSG (eCG) on lactating does increases the proportion of receptive does at AI and, as a consequence, their productivity, without an important immunological side effects. Applied just before AI, the non-hormonal alternative methods were studied. Handling of animals (change of cage or does gathering before insemination) or the proximity of males does not clearly improve the reproduction performances of does. In addition, these methods are costly in terms of time and are difficult to manage on farms. A 36 hours dam-litter separation could be an alternative to hormonal treatments, if applied just before insemination, on does previously freely lactating. However, the application of controlled lactation 2 to 3 days before insemination allows the preservation of kit growth with an identical efficacy on fertility. Feed programmes (flushing) or light stimulation hold interesting research perspectives, but need further studies.

Even though some of these methods improve fertility, they can sometimes decrease the growth of kits (lighting programmes, a short dam-litter separation,…). As a consequence, for a reasoned application on farms, it is important to consider overall productivity criteria and to study the durability of the effects. In addition, the study and use of genetic variability of sexual receptivity of does at insemination could also be a way to improve insemination results. However, a better knowledge of the underlying physiological mechanisms would greatly help the improvement of the control of reproduction on farms.

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