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A STUDY ON RELATIONSHIPS BETWEEN RECEPTIVITY AND LACTATION IN THE DOE, AND THEIR INFLUENCE ON REPRODUCTIVE PERFORMANCES

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ABSTRACT

Starting from their own results, authors present a large review of works relating to influence of receptivity and lactation state on reproductive performances of does, using either artificial insemination (AI) or natural mating (NM). All bear out that receptivity is very important factor for ovulating frequency, fertility and litter size. Hormonal stimulation (by GnRH) give best results than forced mating for non receptive does. Likewise, lactation takes a prominent part in reproductive performances by its depressive effect on receptivity, ovulating frequency and embryo viability. This effect seems to be closely related to the stage of lactation, the worst results occuring for 4 - 5 days of lactation stage.

It is suggered that an hormonal antagonism between prolactin and gonadotropin hormons may explain some of these phonomena.

Means to detect receptive does are described : only vulva colour can easily be used in spite of certain inacurracy.

Possibilities to control and (or) induce receptivity are discussed : first results relating to lighting programs show increasing of receptivity without effect on fertility. Attention is also called on use of PMSG and its bounds, involved to antigenic properties of this molecule.

Different reproduction rhythms are compared, emphasizing interest of 10 - 12 days after parturition interval, to combine advantages of good breeding performances and economic requirements.

INTRODUCTION

In opposition to most other domestic species doe does not show estrous cycles with regular heat periods during which ovulation occurs spontaneously. Does have for a long time been thought to be permanently in heat, with ovulation occurring only on mating.

Analyses of vaginal smears carried out during studies on the reproductive tract have been disappointing and no conclusions can be drawn from them relating to the existence of cyclic phenomena.

Studies by HILL & WHITE (1933) and SMELSER and al (1934) on the ovary show that a mature de GRAAF follicle survives for some days before it is replaced by another, so that there is a continuous succession of ripe follicles on the ovary surface. However, other studies come to different conclusions : at the end of their first phase, follicles reach the preovulatory stage with a diameter in excess of 1 mm. These then degenerate in their second phase, while a fresh batch of follicles begins to mature. This means that the number of preovulatory follicles could be variable and depending on the time of overlap between these cycles.

MORET's studies on behaviour (1980) show that in pubescent nulliparous does of oestrus periods during which they will accept a male alternate with periods of dioestrus when mating is refused. The duration of oestrus and dioestrus periods respectively vary widely from one individual to another, and the hormonal and environmental factors determining these are not well understood.

LEFEVRE & CAILLOL (1978) have studied the relationships in virgin pubescent does between the appearance of oestral behaviour, follicle growth and the concentration of sexual steroids in follicular fluid. Females which are on heat (or receptive) have a higher number of large follicles (with a diameter in excess of 1,5 mm). These are oestrogen-secreting follicles, and as a result the concentrations of oestradiol, oestrone and progesterone in follicular fluid are higher. However, this relation was not confirmed by the plasmic tests carried out on does just after parturition by STOUFFLET & CAILLOL (1988), as oestrogen concentrations were too low and too variable to be related to sexual behaviour.

Moreover, YASMINE et al (1967) have shown that in adult does, sexual behaviour decreases with the removal of ovaries but is restored by injections of oestrogen . ELSAESSER (1988) has noted that rutting behaviour disappears in does which have been immunised against 17 ß-oestradiol. This would appear to indicate a probable link between follicle ripening cycles and sexual behaviour.

Finally, the ripening stage in preovulatory follicles present in does is dependent on preovulatory peaks in the concentration of FSH et LH, induced either by mating or by GnRH injections.

The physiological mechanisms operating until parturition, according to the various physiological stages involved up to the time of presentation, are not as yet well understood and will be reviewed here. Female rabbits must first accept covering (in natural mating), produce a large number of ovocytes and be capable of bringing embryo development to a successful term after fertilization.

The influence on these variables of receptivity and of the physiological stage reached by does at the time of mating or artificial insemination (A.I.) will be analyzed below. Various possibilities for detecting and inducing receptivity will then be considered, together with the factors involved in choosing a suitable reproductive rhythm .

RECEPTIVITY

A doe is "receptive" when the behaviour she displays in the presence of a buck shows that she is willing to mate.

In the case of artificial insemination, does are inseminated whether they are receptive or not. HULOT (1975) had already suggested that fertility may vary in relation to receptivity, and this was confirmed by THEAU & ROUSTAN (1980).

In the case of natural mating (NM), breeders have always noted that fertility is lower when service is assisted (and therefore when females are not receptive) : ROCA & ALAEE (1989) report 29 per cent fertility and DELAVEAU (1978)10 per cent.

Relation between receptivity and ovulating frequency and fertility.

THEAU-CLEMENT et al (1990a) have studied these effects in relation to different methods of reproduction. It was found that in the case of artificial insemination, ovulating frequency and fertility were very high when the does were receptive (93 and 91 per cent), and significantly lower when they were not (68 and 54 per cent) (Fig. 1a).

The respective results in the case of natural mating were 100 per cent and 88 per cent for receptive females and 13 and 10 per cent for non-receptive females (Fig. 2a).

RODRIGUEZ & UBILLA (1988) had already shown that ovulation in nulliparous does treated with hypothalamic hormones (or analogous) is significantly lower when they are not receptive. The very low rate of fertility in does which have undergone assisted mating, is consistent with DELAVEAU's observations (1978) and shows that the defects in gestation which were noted are essentially the result of defective ovulation.

We may therefore conclude that ovulating frequency and fertility are significantly higher in receptive females, and that in non receptive females hormonal stimulation is more efficient than forced mating.

Relation between receptivity and prolificacy.

Our tests have shown that the total number of youngs born for receptive females is significantly higher than for non receptive females (8.7 *vs* 6.9). The factors determining the size of litters are ovulating intensity on the one hand and embryo survival on the other.

We found that receptivity had no significant influence on the corpus luteum count (12.7 for receptive females, 10.7 for non receptive females). HULOT & MARIANA (1980) found that the corpus luteum count was higher by only 0.5 in receptive females, though ovulation had been induced by HCG. RODRIGUEZ and al (1988) show that the corpus luteum count in receptive lactating females given hypothalamic hormone treatment (10.4) was not significantly higher than in non receptive females (8.9).

The number of live embryos after 14 days of gestation is lower in non receptive females (7.6 *vs* 10.1).

GnRH significantly or analogous hormone treatments used for AI increase ovulation frequency in non receptive females and this advantage is reflected in the level of fertility. However, 21% of ovulating, non receptive females do not give birth. This may be due to defective fertilization or to the death of all embryos.

Mating of non receptive females as opposed to receptive females thus results in :
- less frequent ovulation
- a lower embryo survival rate
and therefore
- lower fertility and litter size.

LACTATION

Relation between lactation and mating acceptance rate

THEAU-CLEMENT et al (1990b) have shown that nursing females at the 3-5 days stage of lactation are significantly less receptive than non lactating females (71 *vs* 39 per cent). The study also shows that at this stage of lactation the number of suckling youngs present at the time of insemination is significantly lower in receptive mothers whether they are naturally or artificially inseminated (6.5 vs 8.8 and 7.6 vs 8.7 respectively). These results are consistent with those noted by DIAZ et al (1988) at the 10 -11 days stage of lactation, and by GARCIA & PEREZ (1989) after 10-11 days of lactation, but are not consistent with results given by BEYER & RIVAUD (1969) and PLA et al (1984).

It is therefore possible that receptivity is depressed to varying degrees in nursing females, depending on the stage reached in lactation. Further studies should be carried out before final conclusions can be drawn.

Relation between lactation and ovulating frequency and fertility

Using artificial insemination, we have noted a 100 per cent ovulation rate in females which are not lactating (because they have not been pregnant for a month or more), as against a 44 per cent and 78 per cent rate in females at the 4 days and 10 days stages of lactation, respectively (Fig 1b).

In the case of natural mating, the respective ovulation rates are 77 per cent for non lactating females, 12 per cent only for nursing females at the 4 days stage, and 60 per cent for those at the 10 days stage (Fig. 2b).

Compared to the natural ovulation process, the exogenous hypothalamic hormones are helpful in does irrespective of the phsyiological stage.

In addition, the negative influence of lactation on ovulating frequency in primiparous females - though not multiparous females - has been demonstrated by HARNED & CASIDA (1969). LAMB et al (1991) have shown that while 100 per cent of lactating females ovulate within 24 hours of parturition, this rate drops to 64 per cent 14 days later. This study shows that in females which do not ovulate, the preovulatory LH peak is not reached, and that plasmic concentrations of 17 ß-oestradiol and prolactin (the lactation hormon) are significantly lower than in females which have ovulated. This could mean that pituitary sensitivity is reduced at certain stages of lactation, and would bear out the relevance of the observations made by RODRIGUEZ and UBILLA (1988) on increased hypothalamic hormon doses for artificially inseminated lactating females.

The differences in ovulating frequency we have noted, are linked to fertility.

When artificial insemination is used, 99 per cent of non lactating females give birth, as opposed to 22 per cent and 70 per cent of lactating females inseminated after 4 and 12 days of lactation respectively (Fig. 1b).

When they are naturally inseminated, 73 per cent of non lactating females give birth as opposed to 0 per cent and 53 per cent of lactating females inseminated after 4 and 12 days respectively (Fig. 1b).

These different observations all point to the existence of a partial antagonism between lactation and ovulating frequency, which in turn affects fertility and varies in relation to the stage of lactation. This antagonism can be very pronounced, particularly at the 4 days stage of lactation.

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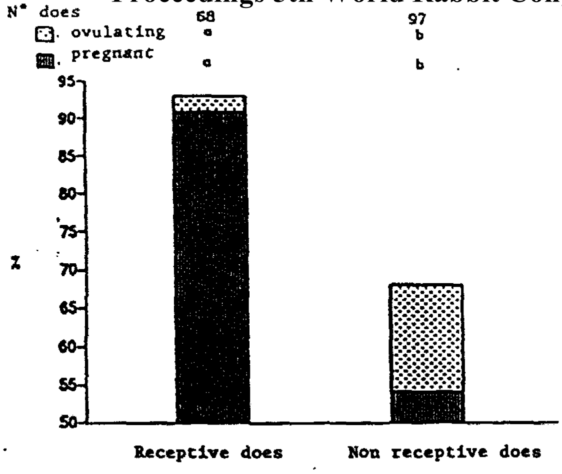

Fig. 1a. Effect of receptivity

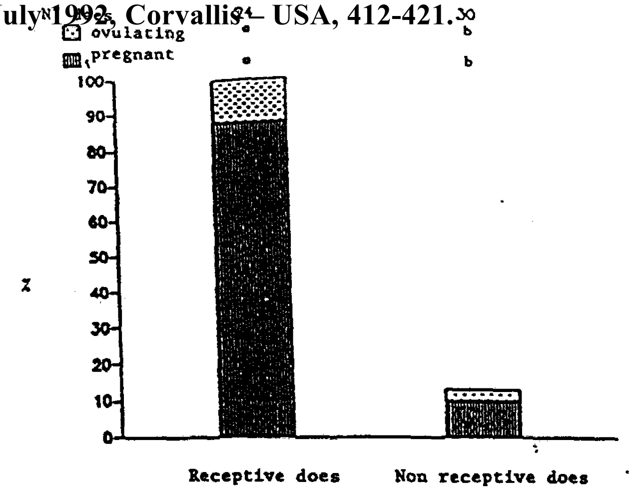

Fig. 2a. Effect of receptivity

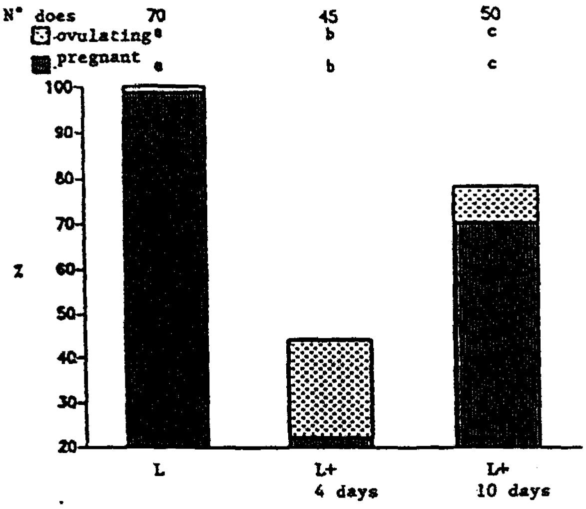

Fig. 1b. Effect of lactation

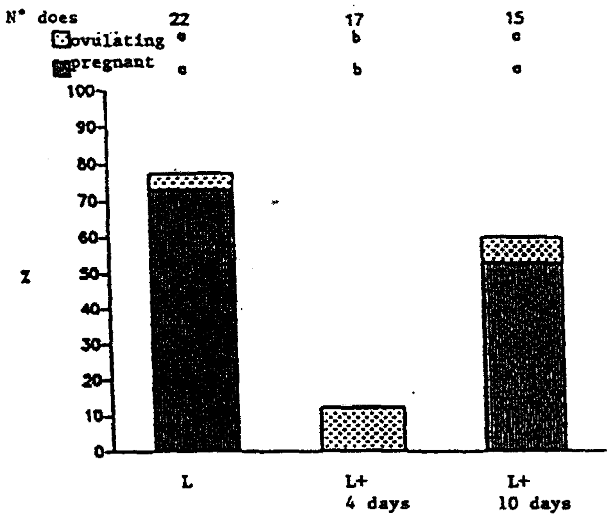

Fig. 2b. Effect of lactation

Natural Mating

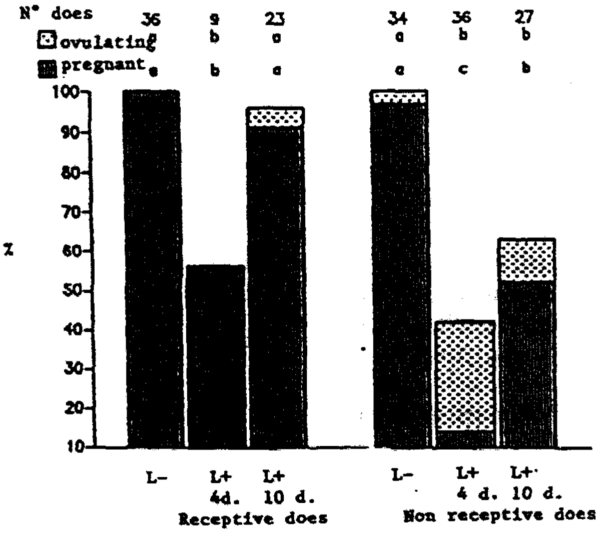

Fig. 1c. Interaction Receptivity-Lactation

Artificial Insemination

Relation between lactation and litter size

In our experiment, the total number of youngs born was significantly higher in non lactating females (6.5 *vs* 9.0).

There is no significant variation in the corpus luteum count in lactating and non lactating females (11.1 and 12.0 respectively). This is consistent with the studies carried out by HARNED & CASIDA (1969) on multiparous females. However, these authors as well as LAMB et al (1991) show that ovulation varies in relation to the different stages in lactation.

Embryo deaths between 0 and 14 days of gestation are significantly higher in lactating females (44 *vs* 15 per cent) although the rate of implantation is the same in both. Post implantation mortality thus appears to be higher in lactating females, and this is borne out by observations made by HARNED & CASIDA (1969) over the period extending from 6 days after the start of gestation to parturition.

To conclude, the negative effects of lactation on the mating acceptance rate, at least at certain stages of lactation, on ovulating frequency and on embryo mortality can be very pronounced.
This in turn affects fertility and prolificacy.

INTERACTION BETWEEN RECEPTIVITY AND LACTATION

The combination of receptivity and lactation factors in non receptive nursing females produces low ovulation frequencies and additional defects in gestation which are not accounted for by defective ovulation. As a result, the fertility rate for lactating females at the 4 days stage is only 14 per cent, and 52 per cent at the 10 days stage (Fig. 1c). This problem is aggravated by the fact that receptivity in females at the 4 days stage in lactation is very low (20 per cent as opposed to 46 per cent for nursing females at the 11 day stage and 51 per cent for non lactating females).

If these results are born out a larger sample, this would mean that the antagonistic effect of lactation ont the reproductive function concerns only **lactating and non receptive** females. This is a major problem since the intensive methods of production generally applied require does to be inseminated at the start of the nursing period. **It should also be emphasized that in the case of natural mating, the negative effect has escaped notice until now, since this antagonism is hidden when non receptive lactating females refuse to mate.**

Hormone tests conducted by RODRIGUEZ et al (1989) conclude that prolactin secretion may be responsible for lower responses to GnRH (lower pituitary discharge of LH and FSH) in lactating females with low receptivity.

PECLARIS (1988) has shown that fertility in ewes is increased with the suppression of prolactin during lactation. HAMADA et al (1980) have shown that ovulating frequency in female rabbits is reduced when prolactin is added to the perfusion solution where HCG (LH effect) is administered into the ovarian vein. This effect does not appear to vary with dosage.

A number of hypotheses follow from these different observations :
Antagonism between receptivity and lactation may be a reflection of hormonal antagonism between prolactine and the gonadotropic hormones. Prolactine secretion may :

- **decrease pituitary sensitivity (lower LH and FSH discharge rate)**
- **in the ovary, inhibit the later stages in follicle ripening and possibly ovulation also, and/or affect the number of LH receptors in follicular cells.**

DETECTION OF RECEPTIVITY

These different observations show that there would be obvious advantages for animal producers using artificial insemination if receptivity in does could be readily detected.

Receptivity test in the presence of a buck rabbit

This test involves placing each doe in a male's cage prior to insemination, in order to find out whether she displays mating acceptance behaviour (lordosis posture). This test has been of major importance in

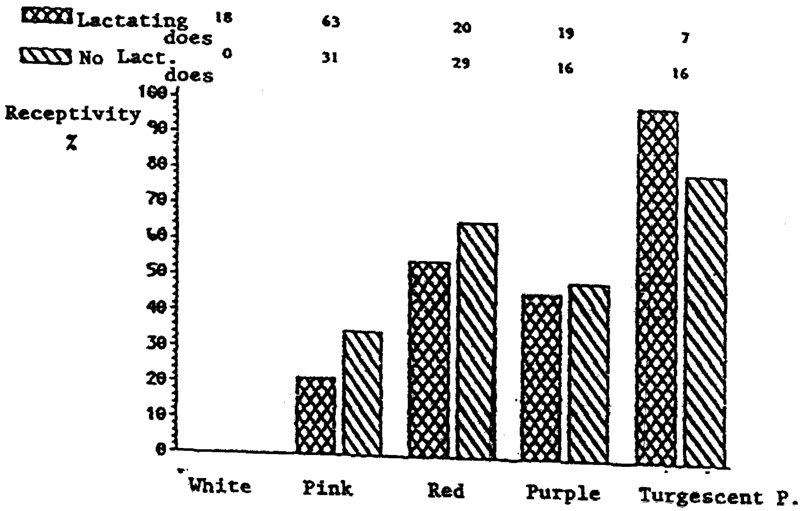

Fig. 3a. Relation between vulva colour and level of receptivity

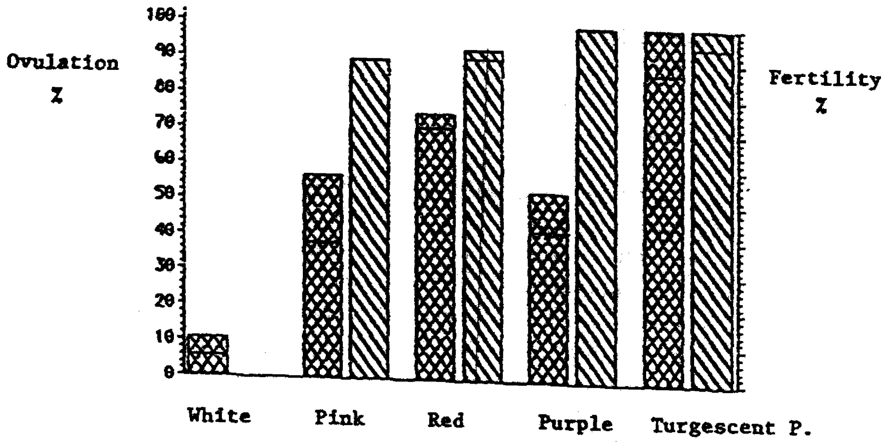

Fig. 3b. Relation between vulva colour and ovulation frequency and fertility

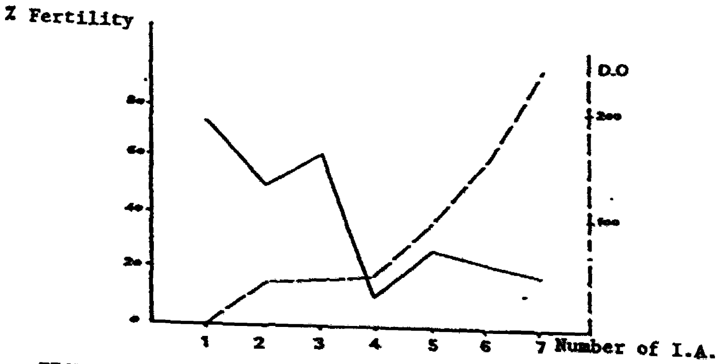

FIGURE 4 : Evolution of fertility according to antibody anti-PMSG rate and number of treatments

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identifying those females which are unlikely to gestate successfully. Moreover, the behavioural test is well related to ovulating frequency and fertility (Fig. 1a and 2a). Unfortunately the test is too time-consuming to be applied as a matter of routine in intensive production units.

Vulva colour

When females are inseminated by natural means, there is no justification for observations of vulva colour as females accepting a male are receptive in any case. A few authors have studied the relationship between vulva colour and ovulating frequency (sometimes), fertility and litter size, with the aim of predicting receptivity for A.I. purposes. In nulliparous females, which are generally highly receptive, fertility rates are fairly similar regardless of vulva colour. In multiparous females, however, fertility is higher when the vulva is pink, red and - sometimes - purple (according to different observers). Whatever the case, it may be concluded that less than 35 per cent of females with a white vulva are fertile, as opposed to 70 per cent with a red vulva.

Simultaneous observations of vulva colour and turgescence have been made by ROCA et al (1986). There was a 10 per cent improvement in fertility when only females presenting a red, turgescent pink or turgescent purple vulva were inseminated.

In the experiment described by THEAU-CLEMENT et al (1990a), vulva colour was systematically noted in the case of both artificial and natural mating, and the following remarks may be made (Figs. 3a and 3b) :

In non lactating females :
- none of the 92 individuals had a white vulva
- the mating acceptance rate varies in relation to vulva colour does (18 representing 14 % of total lactating)
- ovulating frequency and fertility were always either in excess of or equal to 90 per cent.

In lactating females :
- mating was refused by all females with a white vulva
- the mating acceptance rate, ovulating frequency and fertility are related to vulva colour, the highest results being related to red and turgescent purple vulvae.

The size of our sample was too small for definite conclusions to be drawn but results indicate that vulva colour may be a valid predictive criterion of fertility in lactating females.

Vaginal electro-conductivity measurements

In an attempt to discover an objective and effective criterion of sexual behaviour, GOSALVEZ et al (1988) carried out measurements of vaginal electro-conductivity. There was a significant correlation with vulva colour but not with the behaviour of the female rabbits. Further studies should be carried out to conclude as to the validity of this criterion.

INDUCED RECEPTIVITY

Breeders wishing to apply synchronized breeding methods to improve on organizational efficiency need to be able to detect receptivity, but must also be able to control it. Reliable techniques are therefore needed to induce and synchronize oestrus in rabbits on a large scale. Studies have been made on two different techniques : hormone treatment and artificial light regulation.

Hormone Treatment

TORRES & COTTON (1978) were able to synchronize oestrus with 5 consecutive daily injections of progesterone. Unfortunately this is too time-consuming to be applied as a routine technique.

We have made induced receptivity trials with oestradiol benzoate injections every three days prior to insemination, but the percentage of receptivity in comparison to the control group was not improved (results not published).

BONNANO et al (1990) have shown that PMSG (Pregnant Mare Serum Gonadotropin) produces an increase in the number of preovulatory follicles. MAERTENS et al (1983) have demonstrated the effects of

PMSG treatment on sexual behaviour and reproductive performances in naturally inseminated females. Mating acceptance rates and litter size were high in comparison to the control group, but fertility was lower and mortality in the period from birth to weaning was higher. CANALI et al (1991) have shown that in female rabbits given repeated doses of PMSG (40 ui Ciclogonina, PROCHENA, 2 days before insemination) there is a significant correlation between fertility and the concentration of anti PMSG antibodies (r = - 0.41), fertility and the number of inseminations (r = - 0.45), antibody concentration and the time-lapse between treatments (r = - 0.51). Figure 4 shows the progressive drop in fertility which occurred while the treatment was repeated, as well as the increase in the anti PMSG antibody count (expressed in optical density). This result is not surprising in that PMSG is an exogenous hormone for the rabbit and is also a large protein molecule. Immune responses varied from one individual to another : 15 per cent of females having received at least 6 PMSG treatments showed no significant immune response (average fertility = 78 per cent), whereas in 55 per cent of the females in the group, immune response increased with the number of inseminations and was proportional to fertility (average fertility = 38 per cent).

The antigenic properties of PMSG are thus made clear in this study, which advises against the routine use of this molecule.

UBILLA & RODRIGUEZ (1988) have shown that the systematic induction of parturition through intramuscular injections of 50μg of a Prostaglandine F2α analogue (Etiproston) on the 29th day of pregnancy does not alter production parameters but does concentrate female receptivity around the 6th to the 9th day after parturition, and also produces a significant increase in the fertility rate in the case of natural matings occurring 6-7 days after parturition.

Lighting program

Studies by LEFEVRE & MORET (1978) on nulliparous females and by THEAU-CLEMENT et al (1990b) on multiparous females have shown that artificial light regulation can increase the percentage of females accepting a male. However, the latter were not able to show any significant repercussion on fertility and litter size. MAERTENS & OKERMAN (1987a) have shown that stress produced by a move to a different cage or by a change in daylight rhythm gives positive results only when the change is towards a more favourable environment.

These studies suggest that further work should be carried out on photoperiodism in the rabbit.

Though a high level of receptivity is a necessary condition, results obtained up to now show that it is not sufficient to ensure high reproductive performance. The various techniques applied to obtain the required level can produce more or less negative effects on the factors determining numerical productivity, i.e. ovulating frequency and intensity, fertilization, embryo development, viability of young rabbits after birth. These effects must be identified and taken into account before these techniques are made available, so that their economic and technical advantages can be assessed.

CHOICE OF REPRODUCTIVE RHYTHMS

We have noted the effects of the lactation stage on reproductive performance and it follows that the choice of reproductive rhythms is of major importance. Various authors have carried out studies on different reproductive rhythms, and although we cannot make an exhaustive list of these here, some of their characteristics need to be mentioned.

Postpartum breeding systems

Does are inseminated within 48 hours of parturition (lactating females within 1-2 days). During this time practically all does are on heat and therefore accept a male (BEYER & RIVAUD, 1969 ; HARNED & CASIDA, 1969 ; DELAVEAU, 1978 ; MAERTENS & OKERMAN, 1987b). However, LAMB et al (1991) have shown that ovulating intensity is much lower at this stage, while TORRES et al (1977) have shown that a larger number of unfertilized ovocytes are present. These observations probably account for the fact that prolificacy is often lower at this stage.

Insemination 3 - 4 days after parturition

We have shown that few females are receptive at this stage, and production levels obtained appear to confirm that this reproductive rhythm should be proscribed.

Insemination 10-12 days after parturition

This is a less intensive reproductive rhythm and seems to produce better breeding results despite the fact that females are often less receptive 12 days after parturition.

Insemination after weaning

Reproduction after weaning appears to improve fertility. Females in this situation are appreciably more receptive and there is no longer any competition between gestation and lactation. But in view of production conditions today, an extensive post-weaning reproductive rhythm is unlikely to be cost-effective.

Recent studies have shown that there are major obstacles to reproduction in non receptive lactating does. The required studies are now being carried out at INRA to analyse the effects of the lactation stage on :

- mating acceptance percentages in lactating females, which should make up the major part of rabbit stock. This is a fundamental requirement when artificial insemination is practised.
- reproductive performance in non receptive lactating females.

This paper has given conclusions from different authors which are sometimes at variance with each other, but this demonstrates the complexity of the mechanisms involved. However, the factors involved are not only physiological as they include season, feed, genetic characteristics and breeding conditions. The reproductive physiology of the doe is not yet well understood, and a considerable amount of research is still required in order to bring all its subtleties to light. Although interest on the part of breeders and researchers in this field is on the increase in several countries, the means which are currently available to meet the needs of modern rabbit breeding are still far from adequate.

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