Control of the oestrous cycle of the mare

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Efficiency of reproduction in horses is low when monitored by man. Foaling percentage in different countries varies from 50 to 70% per year (Osborne, 1975), but when a stallion is left in pasture with mares a conception rate of 85% or more is achieved (Martin-Rosset & Palmer, 1977). This difference shows how important is the requirement for improvement of our management of mares. Because of the high cost of stallions, pasture breeding cannot be used and hand mating or A.I. have to be performed. With both techniques it is necessary to predict when a mare will ovulate.

This review summarizes recent progress in our knowledge of the physiological situations encountered in the mare and of natural and artificial control of the physiological processes that lead to ovulation.

Spontaneous ovarian activity

Methods of study

Oestrus, which in other species is the most usual starting point of reproductive activity, is not a good criterion in the mare. Most workers have extensively used rectal palpation of the ovaries to assess the late development of the follicle and its rupture (Nishikawa, 1959). The method allows a precise determination of the time of ovulation but not its prediction because follicles of various sizes and consistency may ovulate (Hughes, Stabenfeldt & Evans, 1972). Because of the structure of the ovaries, examination by laparoscopy or laparotomy is ineffective: a thick layer of tissue covers all of the surface except for the small zone where the rupture of the follicle occurs, the ovulation fossa (Witherspoon & Talbot, 1970; Stabenfeldt, Hughes, Evans & Geschwind, 1975). The visualization of follicles and corpora lutea needs dissection of the ovaries after surgery or slaughter (Arthur, 1958; Warszawsky, Parker, First & Ginther, 1972).

Assays for plasma progesterone have now been applied to the mare (Smith, Bassett & Williams, 1970) and have become a simple and useful method of assessment of the presence of a functional corpus luteum (Plotka, Witherspoon & Foley, 1972; Stabenfeldt, Hughes & Evans, 1972; Palmer & Jousset, 1975a). The assay of oestrogens in urine (Hillman & Loy, 1975; Palmer & Jousset, 1975a) or in plasma (Noden, Oxender & Hafs, 1975; Palmer & Terqui, 1977) gives a reliable picture of late follicular growth. Plasma LH (Pattison, Chen & King, 1972; Withmore, Wentworth & Ginther, 1973) or FSH (Evans & Irvine, 1975) patterns have been described but not used in the analysis of the annual variations of ovarian activity.

Physiological situations

Cyclic activity. The oestrous cycle of the mare typically lasts about 21 days (15 days of luteal phase and 7 days of follicular phase) and differs from that of other species in several respects, as well as being very variable in length (see below). Oestrus lasts almost the whole time when the progesterone level is < 1 ng/ml plasma (Plotka *et al.*, 1972); it begins 1.2 ± 1.4 (s.d.) days after progesterone has reached this threshold. At this time oestrogens are still much lower than preovulatory values and follicular development is minimal (Palmer & Jousset, 1975a). This situation is different from that in cows, ewes or sows in which oestrus appears at the time of or after the peak of oestrogens. In mares, oestrogen secretion rises progressively from 6 to 10 days before and reaches maximum levels 24–48 h before ovulation is detected. Similarly LH rises progressively but maximum levels are found 24–48 h after ovulation (Geschwind, Dewey, Hughes, Evans & Stabenfeldt, 1975; Noden *et al.*, 1975). Later LH levels decrease gradually during the first half of the luteal phase. Progesterone secretion begins very rapidly and plasma levels become > 1 ng/ml by 1.2 ± 0.5 (s.d.) days after ovulation. Levels remain at

plateau (6–10 ng/ml) values from Day 5 to Day 10 after ovulation, i.e. earlier than in other species. After Day 10 there is a tendency towards lower progesterone levels but an abrupt decrease around Day 14 indicates luteolysis.

Persistent luteal activity. The prolongation of luteal activity (with progesterone > 1 ng/ml plasma) for a long period, generally 2–3 months, is so frequent that it cannot be considered as a pathological situation. During such periods, a high follicular activity was found by rectal palpation (Stabenfeldt, Hughes, Evans & Neely, 1974) or by oestrogen assays (Palmer & Jousset, 1975a). Occasionally ovulations are detected but oestrous behaviour never occurs during prolonged luteal activity.

Ovarian inactivity. After luteolysis, follicular growth may not occur and the animal remains in an anovulatory state for a long period (20–180 days). During ovarian inactivity, the ovaries are small and rarely have large follicles, and progesterone and oestrogens remain at low levels. In spite of these low oestrogen levels some animals show oestrous behaviour at irregular intervals or almost continuously (Ginther, 1974; Palmer & Jousset, 1975a).

Post-partum ovarian activity. In spite of the very high frequency of the suckling stimulus (more than 40 suckling periods per day), ovarian activity is not inhibited during the post-partum period. A foal heat occurs in 86 % of mares and begins between the 6th and 13th day *post partum* (Matthews, Ropiha & Butterfield, 1967). After the foal heat the mare has regular cycles. However, some mares may not continue to cycle because of a persistent corpus luteum (Allen & Cooper, 1975).

The variability of parameters of ovarian activity of the mare

If the physiological status of a mare is easy to define, this does not mean that one can predict precisely what will happen: the major problem of mare physiology resides in the variability of the indicators (duration, probability of occurrence, endocrine levels) of ovarian activity. Table 1 shows the mean and standard deviation of several characteristics of ovarian activity in a group of 8 mares studied during a period of more than 1 year (Palmer & Jousset, 1975a). Especially when using an endocrinological criterion such as progesterone level, the follicular phase appears more variable (s.d. = 2·7 days) than the luteal phase (s.d. = 1·8 days) of the cycle. The criterion best related to ovulation is progesterone increase. Its small variability (s.d. = 0·5 days) may be due to the fact that only a single teasing and blood sampling were carried out each day. A larger variability of the follicular phase of the cycle was found by Ginther (1974) but not by Stabenfeldt *et al.* (1972).

Similarly, the length of persistent luteal activity (83 ± 23 (s.d.) days, N = 8) appears more predictable than that of ovarian inactivity (84 ± 53 days, N = 7). In a high percentage of mares the persistent luteal phase lasts 2–3 months. However, a better prediction of the end of ovarian inactivity is probably given by the interval from 1 January than by the duration of this ovarian condition.

Table 1. Various characteristics (mean ± s.d.) of cyclic ovarian activity in the mare (70 cycles of 8 mares)

Characteristics	Duration (days)
Judged by behaviour	
Dioestrus	15·4 ± 2·2
Oestrus—total	6·2 ± 2·7
—onset to ovulation	5·1 ± 2·1
—ovulation to end	1·0 ± 1·1
Judged by progesterone pattern	
High progesterone	14·3 ± 1·8
Low progesterone—total	7·5 ± 2·7
—onset to ovulation	6·3 ± 2·7
—ovulation to progesterone increase	1·2 ± 0·5
Relationship between oestrus and progesterone	
Luteolysis to oestrus	1·1 ± 1·3
Progesterone increase to end of oestrus	−0·1 ± 1·4

Onset of oestrus = 1st day of standing oestrus; ovulation = day of detection by rectal palpation; end of oestrus = 1st day when mare refuses mounting; high progesterone = >1 ng/ml plasma; low progesterone = <1 ng/ml plasma.

In a group of mares all combinations of presence and absence of persistent CL and ovarian inactivity may occur and the number of cycles in a 12-month period may vary from 3 to 16 (Palmer & Jousset, 1975a).

Sources of variations

Seasonal influence. A seasonal influence on the mare's ovarian activity, in the form of ovarian inactivity, cyclicity or persistent CL, has been known for a long time.

Ovarian inactivity occurs in winter, the highest incidence being in January–February. Persistent luteal activity tends to occur in summer and autumn, although some cases have been reported in winter and spring (Hughes *et al.*, 1972). Depending on the breed, cyclic activity may exist at any time of the year or only during a limited period.

In addition to these differences in the occurrence of the type of ovarian activity the season has an influence on the follicular phase of the cycle (Table 2), which is longest in the early months of the year and shortest in July and August. The influence of the season on the length of the luteal phase of the cycle is absent (Palmer & Jousset, 1975a) or of little importance (Ginther, 1974). When assessed by measurement of plasma total conjugated oestrogens (Palmer & Terqui, 1977), follicular activity at the mid-luteal period of the cycle also seems to be affected by season (Table 2). The seasonal variation of preovulatory oestrogen levels which was found in urine (Palmer & Jousset, 1975a) may be an artefact due to variations of urine production, as we did not find it again in plasma.

Table 2. Seasonal effects on various characteristics (mean $\pm$ s.e.m.) of the mare's oestrous cycle ($n = 70$)

Characteristic	Significance	Months*					
		1–2	3–4	5–6	7–8	9–10	11–12
Length of low† progesterone phase of the cycle (days)	$P < 0.01$	10.0[a] ±0.7	8.3[ab] ±0.7	6.3[c] ±0.8	6.1[c] ±0.7	6.8[bc] ±0.8	7.4[bc] ±0.9
Interval from onset of oestrus to ovulation (days)	$P < 0.01$	7.8[a] ±0.6	6.0[b] ±0.6	4.1[c] ±0.6	3.9[c] ±0.5	5.0[bc] ±0.7	4.7[c] ±0.5
Total oestrogen levels during luteal phase‡ (ng/ml plasma)	$P < 0.01$	0.33[a] ±0.05	0.44[ab] ±0.05	0.67[c] ±0.05	0.60[cd] ±0.05	0.47[bd] ±0.05	0.47[bd] ±0.04

Means with different superscripts are significantly different in linear contrast test.
* 1 = January; 2 = February, etc...
† <1 ng/ml plasma.
‡ Mean of Day 5–10 of luteal phase measured by the technique described by Palmer & Terqui (1977).

Breed and individual influences. In dissimilar breeds, differences in fertility have been shown (Sullivan, Turner, Self, Gutteridge & Bartlett, 1975) but they may be due to differences in management techniques. Genetic influences on the parameters of ovarian activity have not been described in such detail as seasonal influence. Differences between breeds are obvious. For example, in our laboratory the incidence of ovarian inactivity in winter was 100 % in 57 Welsh ponies, but only 66 % in 24 saddle-type mares within the same year and with similar feeding ($P < 0.01$). Differences between individuals of the same breed were found in a large number of parameters of ovarian activity in our study of 8 French Trotter mares during the course of 14 months, i.e. the length of the luteal phase ($P < 0.01$), length of the follicular phase corrected for seasonal influence ($P < 0.01$) and interval from ovulation to end of oestrus ($P < 0.01$); each mare seemed to have its own characteristics of long or short luteal and follicular phases. Some endocrine levels, e.g. mid-luteal progesterone level ($P < 0.05$) and preovulatory oestrogen ($P < 0.01$), were also influenced by individuals.

In breeds in which ovarian inactivity occurs only in some of the animals the individual tendency can be shown by the recurrence of winter anoestrus: in a group of 30 mares studied during two successive winters, of 18 mares with ovarian inactivity in Year 1, 14 (78 %) were again inactive in Year 2, whereas of 12 with active ovaries in Year 1 only 4 (33 %) had ovarian inactivity in the second year ($P < 0.05$) (unpublished data).

Nutritional influences. Van Niekerk & Van Heerden (1972) have stressed the effect of nutrition on the onset of ovarian activity at the end of winter. After 43 days of high nutritional supplement, all 8 treated mares had ovulated, compared to 1 out of 7 control animals kept on veld grazing. However, one must keep in mind how extreme was the nutritional condition of these two groups of mares (one group losing weight, the other gaining 1 kg/day).

Natural and artificial regulation of the mare's ovarian activity

Control of winter ovarian inactivity

Photoperiodic control. The increase of daylength is the major signal that monitors the end of winter anoestrus. Following Burkhardt (1947) all authors have used a photoperiod of 16 h/24 h after a progressive (Loy, 1968; Oxender, Noden & Hafs, 1977) or an abrupt (Kooistra & Ginther, 1975) increase. In spite of the absence of comparative studies, both seem to give similar results. Treatments are begun at different periods of autumn between 15 October and 15 December, and first ovulation occurs in February, i.e. 1–3 months earlier than in control animals (Text-fig. 1). The minimum light intensity and daylength that can stimulate mares are unknown. Light treatments begun in summer, so that the natural decrease of daylength is suppressed, have delayed but not suppressed winter anoestrus (Kooistra & Ginther, 1975).
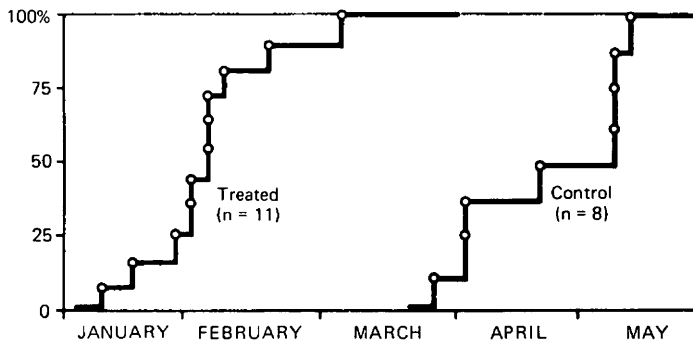
Text-fig. 1. The effect of light treatment (16 h/day) from 25 November on the percentage of Welsh Pony mares starting to show oestrous cycles. The first ovulation was detected from estimations of plasma progesterone twice a week.

Little is known about the mode of action of light on the mare. Are epiphyseal secretions and/or prolactin involved? LH secretion is low, as in the late luteal phase of cyclic mares, during the whole winter period in intact (Oxender *et al.*, 1977) and ovariectomized (Garcia & Ginther, 1976) mares. The first increase of LH occurs a few days before the first ovulation of the year (Oxender *et al.*, 1977); this is much later than the beginning of follicular growth which is continuous during 2 months of light stimulation before ovulation (Sharp, Kooistra & Ginther, 1975).

Pharmacological stimulation. Follicular growth and ovulation can be induced by high doses of pituitary extracts injected daily for 2–3 weeks during the winter period (Douglas, Nuti & Ginther, 1974). However, such treatment has no practical value because the doses are too high for economic use and it induces multiple ovulations, which are undesirable in the mare, in some animals.

Gn-RH induces gonadotrophin secretion during this period and thus may induce ovulation in the mare. Encouraging results have been obtained when Gn-RH is associated with a progesterone treatment (Evans & Irvine, 1977). However, confirmation of the results in larger numbers of animals and simplification of the treatment are needed before there can be a practical application. Although not published, many authors have tried, without success, to stimulate the mare's inactive ovaries with PMSG. We have tested either a high dose (one injection of 20 000 i.u.) or a long treatment (15 daily injections of 4000 i.u.) without effect on follicular development or ovulation.

Control of onset of follicular phase of the cycle

Progesterone inhibitory effect. As in other species endogenous progesterone suppresses oestrus and ovulation during the period of active secretion of the corpus luteum. Exogenous progesterone injections, 50 mg daily for pony mares (Holtan, Douglas & Ginther, 1977) and 100 mg or more daily for large mares (Loy & Swan, 1966), suppress oestrus for the duration of treatment. However, the dose needed for suppression of oestrus is lower than that needed for the suppression of ovulation. For example with a 100 mg/day regimen for 20 days in large mares (Palmer, 1976a) all animals refused mounting by the stallion but a high percentage (27 %; N = 30) ovulated during treatment and did not come in heat after withdrawal. Studies on endogenous production rate and half-life of progesterone (Ganjam, Kenny & Flickinger, 1975; Evans, Faria, Hughes, Stabenfeldt & Cupps, 1975) have shown that the dose of 200–300 mg progesterone/day is close to the normal production level and induces concentrations normally circulating in mares in the luteal phase of the cycle.

Some synthetic compounds, such as progestagens, 17α-allyl-oestratriene-4,9,11-17β-ol-3-one, (Webel, 1975; Palmer, 1976a), or non-steroidal inhibitors like methallibure (First, 1973), have been used with success.

For practical purposes, progesterone or progestagen treatments are limited until implants or vaginal pessaries will allow avoidance of daily treatments. In addition, their use is limited to cyclic animals, because in spite of some responses during the transitory period from anoestrus to cyclicity (Van Niekerk, Combrough & Doms, 1973), most mares in deep ovarian inactivity and mares in persistent luteal activity will still remain in their initial condition after a progestagen treatment. In cyclic mares, a progestagen treatment should last 3 or 4 days longer than the luteal phase of the cycle, as ovulation is not suppressed at the beginning of treatment.

Prostaglandins and luteolysis. In cyclic animals, the signal for onset of oestrus and late follicular growth is the end of progesterone secretion by the corpus luteum, i.e. luteolysis. The natural luteolytic factor, of uterine origin (Ginther & First, 1971), is most probably prostaglandin (PG) F-2α. This hypothesis is supported by the presence of a surge of PGF in uterine venous blood (Douglas & Ginther, 1976) and of 15 keto-13,14-dihydro PGF-2α in peripheral plasma (Kindahl *et al.*, 1976) and by the presence of PGF-2α receptors in the mare corpus luteum (Kimball & Wyngarden, 1977). The absence of a local effect from the uterine horn to the adjacent ovary explains why systemic administration does not need a higher dose than intrauterine administration. The young corpus luteum is refractory to PG and luteolysis cannot be induced earlier than Day 5 after ovulation (Allen & Rowson, 1973). Whether persistence of the corpus luteum in non-pregnant mares is due to a lack of PG discharge at the normal time or to an increased secretion of luteotrophic factors is unknown. However, the persistent corpus luteum remains sensitive to exogenous PG treatments (Allen & Cooper, 1975). In recent years, PG injections have become widely used for the treatment of mares with a persistent CL (Allen & Cooper, 1975) or for stud management (Palmer, 1976b). Prostaglandin F-2α, in spite of mild side effects (Miller, Lauderdale & Geng, 1976), can be used for this purpose. Synthetic analogues (Allen *et al.*, 1974; Witherspoon, Lamond, Thompson & Stevenson, 1975) allow the same luteolytic effect without side effects. In almost all animals treated at an appropriate time of the luteal phase, oestrus will begin 2–5 days later. During induced oestrus, hormonal levels (Oxender *et al.*, 1975) and

Table 3. The length (days) of the follicular phase (spontaneous or induced) in mares

	No. of mares	Mean ± s.d.	Reference
Spontaneous			
(from luteolysis to ovulation)	70	6·3 ± 2·7	Palmer, 1975
Prostaglandin-induced			
(from PG to ovulation)	71	7·9 ± 2·4	P. A. Noden, pers. comm.
After progesterone			
(100 mg daily) injections (from last injection to ovulation*)	13	7·9 ± 2·9	E. Palmer, unpublished

* Mares which ovulated during treatment and non-cyclic mares have been discarded.

fertility (Allen & Cooper, 1975; Nelson, 1976) are normal. The limits of the practical use of PGs for induction of oestrus in mares are the absence of response in mares with ovarian inactivity, and in those in the follicular phase of the cycle or early after ovulation.

Control of timing of ovulation

Variability of timing of ovulation is similar after natural luteolysis, PG-induced luteolysis or withdrawal of exogenous progesterone (Table 3). What are the reasons for such variability?

The LH concentrations during natural and PG-induced oestrus do not show a peak as is found for other species. In consequence, there is no well defined signal that triggers ovulation. This does not mean that the preovulatory follicle cannot respond to a short surge of gonadotrophin: i.v. or i.m. injection of 1500–3000 i.u. hCG will induce ovulation about 24–48 h later (Loy & Hughes, 1966; Sullivan, Parker & Larson, 1973) when mares are treated on the 2nd day of oestrus. One Gn-RH injection might also induce ovulation (Irvine, Downey, Parker & Sullivan, 1975; Kreider, Cornwell & Godke, 1976), but this result has to be confirmed as other authors have found no effect on the time of ovulation (Garcia & Ginther, 1975; Noden & Oxender, 1976). In untreated animals, the theoretical model of control of ovulation should take into account a progressive increase of sensitivity of the follicle and a gradual LH stimulation, rather than a short signal that triggers ovulation. Ovulation would occur when an equilibrium between hormone level and follicle sensitivity is reached.

The relationship between LH pattern and the length of follicular phase has not been studied in detail, but oestrogen levels, used as a criterion of follicular development (Palmer & Terqui, 1977), have permitted an interpretation of the variability of the length of the follicular phase. (1) The ovulation of follicles at different stages of maturation can explain part of the variability: ovulations at an early stage, i.e. when the follicle is secreting little oestrogen, give rise to short follicular phases. This is supported by the correlation ($r = +0.40$; $P < 0.01$) between preovulatory total conjugated and unconjugated plasma oestrogen levels and the duration of the follicular phase (Palmer & Terqui, 1977). (2) On the other hand, the interval from luteolysis to ovulation is dependent on the degree of follicular development at the time of luteolysis: again a correlation ($r = -0.47$; $P < 0.01$) was found between oestrogen levels at the time of luteolysis and the length of the follicular phase. These two phenomena act independently as we found no correlation between total oestrogen levels at the time of luteolysis and preovulatory oestrogen levels. A multiple regression, $Z = A + BX + CY$ where Z is the length of the follicular phase, X is the oestrogen level at the time of luteolysis (log scale), and $Y =$ the preovulatory oestrogen level, gave a correlation $r = 0.76$ ($P < 0.01$) when applied to 73 cycles of 8 mares, and thus gave an explanation for 58% of the variance (Text-fig. 2).

A similar effect of follicular development was found by rectal palpation in PG-treated mares (Loy & Sharma, 1976): in mares with small follicles at treatment the interval to ovulation was 7 days compared to an interval of 5–6 days in mares in which the follicle due to ovulate was already large at treat-
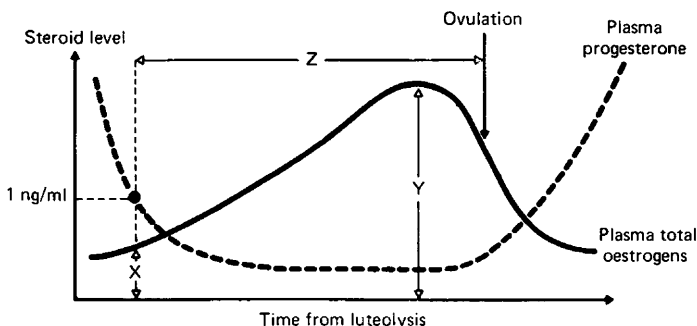
Text-fig. 2. A multiple regression diagram to explain the variability of length of the follicular phase of the cycle in 71 cycles of 8 mares. The regression equation is $Z = A + BX + CY$. On a linear scale for oestrogen, $A = 6.21$, $B = -3.72$, $C = +1.53$ and $r = 0.69$. On a log scale for oestrogen, $A = 3.14$, $B = -9.27$, $C = +7.28$ and $r = 0.76$.

ment. These authors described a third type of mares in which a large follicle was present but regressed and ovulation occurred after growth of another follicle 9 days later. These three types of response were also found by oestrogen assay after PG treatment; Text-fig. 3 shows three examples of the oestrogen pattern after PG injection. In Mare 1 oestrogen levels were high at the time of injection but decreased for 2·5 days before increasing towards ovulation. In Mare 2 a high oestrogen level was already present at the time of treatment and a further increase occurred immediately after PG and ovulation took place early. In Mare 3 the oestrogen levels were very low at injection and the increase was progressive until ovulation, which occurred much later.
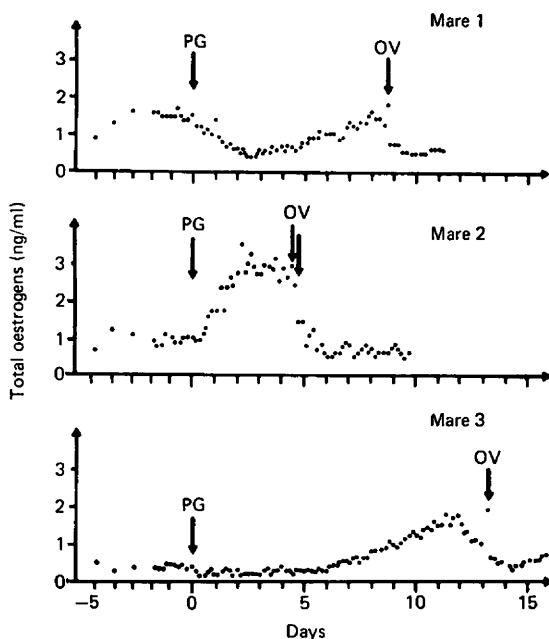
Text-fig. 3. Examples of three patterns of total oestrogen (conjugated and unconjugated) secretion in the mare after treatment with prostaglandins (PG). OV = ovulation.

Little is known about the control of follicular development at the time of natural or artificial luteolysis. In spite of a cyclic pattern of two surges of FSH per cycle (Evans & Irvine, 1975) follicular growth seems to occur continually during the oestrous cycle. Further work on FSH secretion and follicular growth is necessary.

For practical purposes, the only possibility for the artificial control of ovulation is to induce ovulation with hCG when follicular development is adequate. The time for injection can be decided by rectal palpation, by detection of oestrus (injection on Day 2 of oestrus) or by a set interval from PG treatment or from progestagen withdrawal. Such treatments are limited by (1) the possible production of antibodies to hCG after multiple hCG injections (Sullivan *et al.*, 1973), although a decreasing efficacy is not certain (Loy & Hughes, 1966), and (2) the absence of response if follicular development is inadequate, as when using an hCG injection on Day 2 or 3 of oestrus early in the season (S. K. Webel unpublished data; E. Palmer, unpublished data).

The conditions for use of Gn-RH or its analogues need further study before they can be used for ovulation induction.

Synchronization of oestrus and ovulation

The purpose of synchronization of oestrus and ovulation may be for naturally or artificially in-seminating batches of animals at the same time, but it may also furnish a simple technique to decide

the right time for mating individual animals without detection of oestrus. A treatment for synchronization should work in all animals of a group treated at the same time, regardless of their individual ovarian condition, but can be modified for different breeds and for different periods of the year. Unlike cattle in which the control of the onset of the follicular phase is generally sufficient, the mare needs additional control of ovulation timing, and, when working in winter, stimulation of follicular growth is also required. All authors have used hCG for the control of ovulation, but different techniques have been chosen for controlling the onset of the follicular phase. (1) Prolongation of the luteal phase of the cycle with a long treatment of progesterone injections (Holtan *et al.*, 1977), progestagens (Webel, 1975) or non-steroidal inhibitors (First, 1973). (2) A sequence combining a short progesterone or progestagen treatment that delays ovulation of some mares and a PG injection at the end of treatment that hastens it in other animals (see Text-fig. 4a) (Palmer, 1976a; Holtan *et al.*, 1977). (3) Successive PG injections combined with successive hCG injections (Palmer & Jousset, 1975b) at precise intervals (see Text-fig. 4b). All three possibilities, when applied to cyclic animals with adequate doses and with suitable times between the hCG injections, give similar results: between 70 and 80% of the mares ovulate within 4 days (Palmer, 1976b). The 20–30% of unsynchronized mares is caused by the large variability of length of the follicular phase of the cycle and this cannot be overcome by hCG injection.
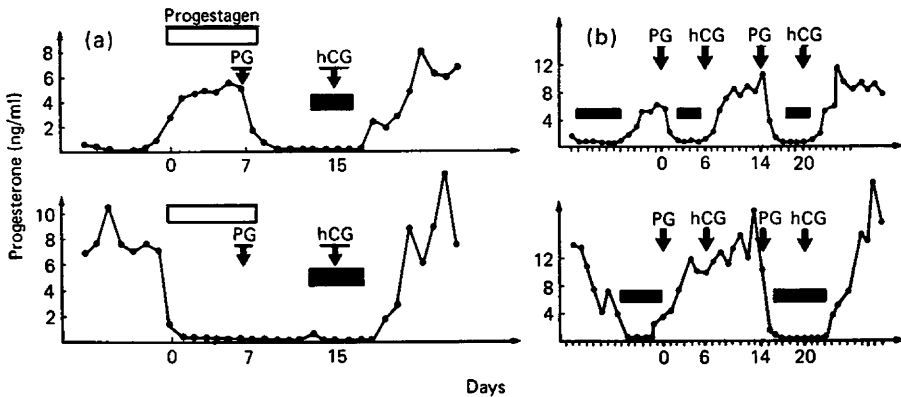
Text-fig. 4. Illustration of effects of two methods for synchronization of oestrus and ovulation in the mare. (a) A sequence combining a short progestagen treatment (Days 0–7) and prostaglandin (PG: Day 7) and hCG (Day 15) injections. (b) A sequence of prostaglandin (PG: Days 0 and 14) and hCG (Days 6 and 20) injections. Oestrus is shown by the solid horizontal bar.

Treatments have to be adapted to the breed and season. When working with a breed in which persistent luteal activity is frequent, the scheme should include PG injection (Palmer, 1976a): when working in winter, a photoperiodic stimulation of ovarian activity is necessary before the synchronization treatment. Such a combination (2 months stimulation by light + synchronization treatment) has resulted in synchronization of ovulation in 80% of mares in February (Palmer, 1977a). Even during the breeding season the interval between the PG and hCG injections may need to be modified. An interval of 6 days which was effective in May was too long in July and resulted in ovulations before the hCG injection in a large number of mares (Palmer, 1976a).

Fertility after control of the oestrous cycle

In farm practice the mare is considered to have a low fertility (40% or less pregnant per oestrus). However, many authors have reported conception rates of 70% when mares are mated every 48 h of oestrus after the beginning of May, or earlier if cyclicity is assessed for each animal before mating. After control of oestrus the same wide range of fertility is found: authors working with experimental animals have compared fertility after mating treated and control animals every 48 h and obtained a

high fertility in both groups. Others have studied the effect of treatment on fertility obtained in farm practice where low conception rates are usually observed. In all cases PGs alone (Allen & Cooper, 1975; Nelson, 1976), progesterone (Loy & Swann, 1966), hCG (Loy & Hughes, 1966) or combined treatments (Holtan *et al.*, 1977; Palmer, Saint-Quentin & Thimonier, 1976) have never been shown to decrease fertility significantly in experimental or in farm animals. However, comparison between inseminating once after synchronization and multiple insemination of treated or control animals (Holtan *et al.*, 1977) revealed a decrease, although this was not significant. If confirmed this would mean that synchronization of ovulation is still insufficient to allow mating at a predetermined time after treatment and achievement of maximum fertility.

With traditional breeding techniques several successive cycles are used to achieve a high fertility rate at the end of the breeding season. The control of oestrus and ovulation can be spread to successive cycles. For this purpose, encouraging results were obtained by a progestagen treatment begun 7 days after mating for 15 days, obviously without knowing whether conception had taken place. After this post-coital treatment, fertility seems not to be affected while returns of non-pregnant mares to oestrus are synchronized and ovulation may be induced by hCG at a predetermined time. This scheme was tested in 22 mares: fertility was identical at each successive cycle (1st cycle, 41 %, N = 22; 2nd cycle, 38 %, N = 13; 3rd cycle, 38 %, N = 8) and resulted in 77 % of the mares being pregnant after three cycles when mating had been performed only at predetermined times (Palmer, 1977b).

Conclusions

Recent investigations have advanced our knowledge and understanding of the ovarian activity and its control of the mare. They have highlighted some specific problems relative to the mare, e.g. persistency of the corpus luteum, refractoriness of follicles to pharmacological stimulation, variability of the length of the natural or induced follicular phase and abnormal LH patterns. However, a large area remains open for further investigations on the physiological mechanisms of regulation of seasonal phenomena, follicular growth and control of ovulation. Our results on artificial control of the different steps which precede ovulation have allowed a total control of the time of ovulation of 70–80 % of mares. The remaining 20–30 % is the challenge for new investigations.

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