UTERINE WEIGHT AND PITUITARY LH CONTENT IN THE PSEUDOPREGNANT HAMSTER

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Summary. Measurements of pituitary LH content, uterine wet and dry weights, and ovarian and pituitary wet weights were obtained for each day throughout pseudopregnancy in the hamster, and were compared with comparable data obtained during the oestrous cycle.

Ovarian weights increase during pseudopregnancy, reflecting activation of corpora lutea; they remain higher than oestrous cycle values even after ovulation recurs, reflecting delayed involution of the corpora lutea. Ovarian weight does not show a regular cycle during pseudopregnancy, in contrast with the regular changes seen during the oestrous cycle.

Uterine wet and dry weights continue to manifest a 4-day periodicity during pseudopregnancy, a finding which parallels oestrous cycle values but at a higher level.

During pseudopregnancy pituitary LH content rises, reaching a peak level on the 7th day; a significant drop occurs at the time of the ovulation at the end of pseudopregnancy. The rise exceeds that seen during the oestrous cycle and correlates with the block to ovulation in pseudopregnancy. Pituitary weights are higher than in cyclic animals, but do not show cyclic changes.

INTRODUCTION

During the oestrous cycle of the hamster, pituitary LH content and uterine weight are high on Day 1 (the day before ovulation) and have dropped precipitously by Day 2, the post-ovulation day (Orsini & Schwartz, 1966), marked by the vaginal post-oestrous discharge and the presence, in the oviducts, of ova 'in cumulus'. In their pre- and post-ovulatory phenomena, these findings resemble similar changes in the rat (Schwartz, 1964). On the 4th and 5th days of pseudopregnancy, the pituitary LH content in the hamster is elevated to typical oestrous cyclic pre-ovulatory levels (Orsini & Schwartz, 1966), and ovulation is blocked at this time during pseudopregnancy, as it is in the rat (Schwartz & Rothchild, 1964). The present paper presents a study of pituitary LH content, and uterine and ovarian changes on successive days throughout
pseudopregnancy in the hamster, in an attempt to determine whether or not there is any evidence of a latent cycle in this species.

MATERIALS AND METHODS

All hamsters (*Mesocricetus auratus* Waterhouse) used were, like those in the previous study (Orsini & Schwartz, 1966), raised and maintained in constant temperature quarters lighted from 07.00 to 19.00 hours. All were virgin, over 80 g in weight, and had displayed at least two normal cycles before the start of the study. Pseudopregnancy was induced by observed matings with vasectomized males; external vaginal phenomena and body weights were recorded daily until autopsy (Orsini, 1961).

Pseudopregnancy in the hamster usually lasts 9 days (Orsini, 1961, 1964; Kent & Atkins, 1959); if the day of post-mating vaginal discharge is considered as the 1st day of pseudopregnancy, the next post-oestrous discharge is usually seen on the 10th day. Less commonly, but often in young animals, pseudopregnancy may last only 8 days with the terminal post-oestrous discharge occurring on the morning of Day 9 (Orsini, unpublished observations). Pseudopregnancy is marked not only by suppression of the cyclic post-oestrous vaginal discharge subsequent to that immediately following mating, but also by development of a slight, sticky, mucous discharge beginning at approximately the 4th day of pseudopregnancy, and a slight increase in body weight. Termination of pseudopregnancy is preceded by a loss of weight, cessation of the mucous discharge, and recurrence of the post-oestrous discharge (Orsini, 1961). Occasionally, the end of pseudopregnancy is marked by a waxy discharge, which may obscure this particular post-oestrous discharge.

Autopsies for this study were carried out between 09.30 and 11.30 hours. Ovaries, adrenals, and the left uterine horn were removed and maintained in a moist chamber until weighed. One, at least, of the oviducts, and one uterine horn were flushed to determine the presence and condition of ova, and thus verify the state of pseudopregnancy (Orsini, 1964). The left uterine horn was dried for 24 to 48 hr at 100°C and re-weighed for determination of tissue water content.

The anterior pituitaries were dissected free of the posterior pituitary, weighed and frozen in a Potter-Elvehjem homogenizer standing in a mixture of dry ice and acetone. LH content was measured by a modification (Orsini & Schwartz, 1966, Schwartz, 1964) of the ovarian ascorbic acid depletion method (Parlow, 1961), using a four-point bioassay. Pituitaries were assayed at doses of 1/8 and 1/2 or 1/16 and 1/4 pituitary equivalent per recipient against NIH-LH-s5, corrected to the potency of -s1. The original intention was to perform an autopsy on four animals (constituting a single pituitary pool) on each day of 8- or 9-day pseudopregnancies. Accidental loss, or differences from the standard LH preparations and the unexpected finding with the two Day-9 (ova versus no ova) pools (see below) induced us to collect and assay additional pools. For these reasons, organ weight data were obtained from four to twelve hamsters per stage, not all of the animals being represented by pituitary LH assay data. The number of pituitaries per pool used in the final data for LH
Uterine weight in the pseudopregnant hamster

assay was five for Day 1, two for Day 10 and four for each of the other days.

Pituitary lH content of each pool was calculated as the mean potency with 95% confidence limits; homogeneity of potencies among the pools was also tested (Bliss, 1956). The only lH data reported below were obtained from valid assays.

For body weight and each organ weight separately, an analysis of variance was performed, using all the data, testing the significance of the overall differences among the days of pseudopregnancy. (A second analysis of variance was calculated for each variable using only data from those hamsters represented by pituitary lH information; these analyses revealed the same trends and are therefore not reported.) In addition, two other analyses were done for each organ weight. First, analyses of co-variance (with animal age or body weight the independent variable) were performed to detect possible differences in average levels of organ weights between pseudopregnant and cyclic hamsters (Orsini & Schwartz, 1966). Second, correlation coefficients were calculated, in the case of ovary and uterine weights, between the averages found on each of the 4 days of the cycle and those found on the appropriate days of pseudopregnancy corresponding to the cycle, had pseudopregnancy not occurred. The purpose of this last set of analyses was to detect persistence of cyclic changes (Orsini & Schwartz, 1966).

RESULTS

Fresh ova 'in cumulus' in the oviducts were found only on the 1st morning of pseudopregnancy and on the 9th or 10th mornings, when the hamsters showed vaginal post-oestrous discharges. Two of the animals in the Day-10 group had waxy, as well as post-oestrous, discharges at autopsy: all four showed ova 'in cumulus' indicating fresh ovulation. Thus, all the hamsters missed the ovulation which would have occurred on the 5th day had pseudopregnancy not intervened. For those which ovulated by the 9th day, the original pattern of the cycle was unchanged; the subsequent oestrous cycle was 1 day later than it was before pseudopregnancy in those which ovulated by the 10th day.

Separate analyses of variance of age, body weight and adrenal weight (Table 1), using data from individual hamsters, revealed no significant changes throughout pseudopregnancy. Pituitary, ovarian and uterine weights did show highly significant variations with time (Table 1). The analyses of co-variance indicated that even when organ weights are adjusted for possible differences in age or body weight, uterine, ovarian and pituitary weights are significantly higher in the pseudopregnant animals than in cyclic animals (Orsini & Schwartz, 1966), while adrenal weights do not differ (Table 1).

A visual comparison of ovarian weights from cyclic and pseudopregnant hamsters (Table 1) is seen in Text-fig. 1. The significantly increased weight of the pseudopregnant compared with the cyclic ovaries is undoubtedly due to the weight of the functional corpora lutea of pseudopregnancy; the increase in weight at the end of pseudopregnancy reflects the delayed involution of these corpora lutea which may be compared with the swift involution which occurs during the cycle. There was no periodicity in this variable.
TABLE 1
ORGAN WEIGHTS IN THE PSEUDOPREGNANT HAMSTER

| Day of pseudopregnancy | N | Ovaries (mg) | Adrenals (mg) | Pituitary (mg) | Wet Uterus (mg) | Dry Uterus (mg) | Dry/wet (%)
<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
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<td>1 (Ova)—P.O.</td>
<td>9</td>
<td>22.1b</td>
<td>12.2b</td>
<td>3.45b</td>
<td>141.7b</td>
<td>23.4b</td>
<td>16.1b</td>
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<tr>
<td>2</td>
<td>8</td>
<td>25.9</td>
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<td>3.76</td>
<td>119.5</td>
<td>20.7</td>
<td>17.2</td>
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<td>3</td>
<td>8</td>
<td>23.8</td>
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<td>3.74</td>
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<td>15.6</td>
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<tr>
<td>4</td>
<td>12</td>
<td>28.1</td>
<td>14.7</td>
<td>4.33</td>
<td>217.5</td>
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<td>14.7</td>
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<tr>
<td>5</td>
<td>4</td>
<td>27.8</td>
<td>16.4</td>
<td>3.92</td>
<td>178.9</td>
<td>29.1</td>
<td>16.3</td>
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<td>4</td>
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<td>14.6</td>
<td>4.04</td>
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<td>23.0</td>
<td>17.2</td>
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<td>25.9</td>
<td>13.9</td>
<td>3.45</td>
<td>178.1</td>
<td>25.8</td>
<td>14.8</td>
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<tr>
<td>8</td>
<td>4</td>
<td>23.8</td>
<td>14.3</td>
<td>3.64</td>
<td>271.6</td>
<td>37.3</td>
<td>13.9</td>
</tr>
<tr>
<td>9 (Ova)—P.O.</td>
<td>8</td>
<td>27.3</td>
<td>13.1</td>
<td>4.30</td>
<td>210.2</td>
<td>31.7</td>
<td>15.1</td>
</tr>
<tr>
<td>9 (No ova)</td>
<td>11</td>
<td>25.8</td>
<td>13.4</td>
<td>4.34</td>
<td>311.2</td>
<td>44.2</td>
<td>14.3</td>
</tr>
<tr>
<td>10 (Ova)—P.O.</td>
<td>10</td>
<td>33.6</td>
<td>15.1</td>
<td>5.13</td>
<td>195.7</td>
<td>31.7</td>
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Analysis of variance:

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<th>P&lt;0.01</th>
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<th>P&lt;0.01</th>
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</thead>
<tbody>
<tr>
<td>Ovaries</td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Adrenals</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pituitary</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wet Uterus</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Dry Uterus</td>
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<tr>
<td>Dry/wet (%)</td>
<td></td>
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</tbody>
</table>

* Data are based only on the left uterine horn.

b Mean value for organ weight for each day for all hamsters.

c Analysis of variance for all data of a given variable; overall probability of difference among days is given.

P.O. = post-oestrous vaginal discharge. (Ova) = fresh ova 'in cumulus' in oviducts.

Text-fig. 1. Ovarian weights during pseudopregnancy (Table 1) displayed against ovarian weight in cyclic hamsters (1). Confidence limits are 2 x S.E.M. On Day 9 of pseudopregnancy, data from animals displaying the post-oestrous discharge and ova are separated from data from negative animals (see Table 1). Beneath the figure are shown the days of the hypothetical recurrent oestrous cycle, and the corresponding day of pseudopregnancy.
Uterine weight in the pseudopregnant hamster

As can be seen on a comparable plot of uterine wet weights (Text-fig. 2), there is a definite parallel with the 4-day cycle during the first part of pseudopregnancy. Both cyclic and pseudopregnant curves show a peak at Day 4 of pseudopregnancy (equivalent to Day 1 of the cycle), and a trough 2 days later. Parallelism between the cycles and pseudopregnancy is only apparent in those animals with 8 days of pseudopregnancy (Day 9, post-oestrous discharge and

![Text-fig. 2. Uterine wet weights during pseudopregnancy, displayed against uterine wet weight in cyclic hamsters (1). Weights of the left horn from Table 1 have been doubled to facilitate comparison with the cyclic data. Confidence limits are 2 x S.E.M. On Day 9 of pseudopregnancy, data from animals displaying the post-oestrous discharge and ova are separated from negative animals (see Table 1). Beneath the figure are shown the days of the hypothetical recurrent oestrous cycle, and the corresponding day of pseudopregnancy.

ova ‘in cumulus’), but not in those animals which ovulated by Day 10. Expanded confidence limits on Day 8 reflect the probably mixed nature of this group of hamsters. Attempts to fit these data on uterine weights during pseudopregnancy to a 4-day mathematical sine wave were almost as satisfactory as the fit obtained with the 4-day oestrous cycle data (Orsini & Schwartz, 1966).
Regression curves of these weights during pseudopregnancy on the cyclic data confirm the parallelism between the two sets of wet weights. Uterine dry weight and percentage dry weight also show the same relationship (Table 1).

Pituitary LH contents are presented in Table 2 and Text-fig. 3. Pituitary LH appears to rise during pseudopregnancy and exceeds normal cyclic values on Days 5, 6 and 7. On Day 9, in the first two pools analysed (Table 2), there was a significant fall in LH content to ‘oestrous’ levels not only in those hamsters which had ovulated (2.7 µg) but also in those which had not (2.8 µg). Two more Day-9 pools were assayed (Table 2); these showed a significantly higher LH content for the pituitaries from the non-ovulating hamsters (15.2 µg) than for those which had just ovulated (5.4 µg), although this latter value was also significantly higher than that obtained for the previous pool of Day-9 ovulating hamsters (2.7 µg). On Day 10, LH content resembled cyclic values (Orsini & Schwartz, 1966). Pituitary weight changes (Tables 1 and 2) did not parallel changes in LH content.

A simple correlation was calculated between pituitary LH content and day of pseudopregnancy, using only the first 8 days. The correlation was 0.8765, which is significant in the one-tailed test at the 1% level. The calculated regression equation is: Estimated LH content = 2.493 + 0.7571 (day of pseudopregnancy).

### Table 2

<table>
<thead>
<tr>
<th>Day of pseudopregnancy</th>
<th>LH content (µg/pit.) (mean and 95% confidence limits)</th>
<th>N</th>
<th>Pituitary wt* (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (Ova)—P.O.</td>
<td>2.4 (1.1 to 5.3)</td>
<td>5</td>
<td>3.55</td>
</tr>
<tr>
<td>2</td>
<td>3.9 (1.7 to 9.5)</td>
<td>4</td>
<td>4.21</td>
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<tr>
<td>3</td>
<td>5.1 (1.9 to 28.4)</td>
<td>4</td>
<td>3.62</td>
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<tr>
<td>4</td>
<td>6.7 (4.5 to 10.0)</td>
<td>4</td>
<td>3.97</td>
</tr>
<tr>
<td>5</td>
<td>5.3 (3.4 to 9.2)</td>
<td>4</td>
<td>4.92</td>
</tr>
<tr>
<td>6</td>
<td>8.3 (5.0 to 17.7)</td>
<td>4</td>
<td>4.04</td>
</tr>
<tr>
<td>7</td>
<td>8.4 (4.1 to 33.2)</td>
<td>4</td>
<td>4.45</td>
</tr>
<tr>
<td>8</td>
<td>7.1 (4.3 to 14.9)</td>
<td>4</td>
<td>3.64</td>
</tr>
<tr>
<td>9 (Ova)—P.O.</td>
<td>2.7 (1.7 to 4.3)</td>
<td>4</td>
<td>3.88</td>
</tr>
<tr>
<td>9 (Ova)—P.O.</td>
<td>5.4 (3.7 to 8.8)</td>
<td>4</td>
<td>4.74</td>
</tr>
</tbody>
</table>

Chi-square test for homogeneity*  
* Average weight of pituitaries contributing to these valid assays.  
** Two separate pools of four pituitaries apiece were assayed (slopes significantly different from standard LH) before this valid assay was obtained.  
* First assay on pool from this stage of pseudopregnancy.  
** Second assay with another pool from same stage. Chi-square test for homogeneity (8) reveals a significant difference between the potencies of the two pools of the same stage.  
* Includes all pools above line (8).  
** One pool of four pituitaries was assayed (slope significantly different from standard LH) before this valid assay was obtained.

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Uterine weight in the pseudopregnant hamster

DISCUSSION

Comparisons of the data from pseudopregnant and cyclic hamsters (Orsini & Schwartz, 1966) present interesting similarities and dissimilarities (Text-figs. 1 to 3). The rise in pituitary LH content during pseudopregnancy (Table 2, Text-fig. 3) occurs despite the block to ovulation until the night of the 8th or 9th day after mating, the LH content rising to a level exceeding that of the pro-oestrous hamster, just as in the rat (Schwartz & Rothchild, 1964). High progesterone secretion rates are probably the cause of the block to ovulation, the absence of mating behaviour (Kent & Atkins, 1959) and the increased storage of LH during pseudopregnancy (Rothchild, 1965).

No discrepancy could be found within the data for the individual hamsters constituting the terminal pools to explain the abrupt drop in LH content in one pool which had not ovulated by Day 9 (Table 2), and the high LH content in the other pool which also had not ovulated. The acute drop might be due to release of the LH ovulatory surge too late in the 'ovulation clock' sequence for ovulation to occur, to decreased LH synthesis in face of steady release, to a block interposed, or to a chance finding. Little is known about ovulation immediately following pseudopregnancy, but all ova recovered on Day 10, during the time-span used here for autopsy, were 'in cumulus', suggesting a regularity like that of the cycle. Uterine weight continued high in both non-ovulating pools, resembling the continued uterine distension found by Schwartz.
cycle) in rats blocked from ovulating by pentobarbital injection, this having been interpreted as failure of the ovulatory surge of LH to act on the follicle to terminate oestradiol secretion. The uterine weight data (Table 1) suggest that release of LH had not occurred.

The high level of LH in the other non-ovulating pool suggests an acute build up of LH here, though the confidence limits are extremely wide. It is obvious from the present data that no valid conclusions are possible on changes in LH content at termination of pseudopregnancy, but the regression curve definitely supports a positive relationship between day of pseudopregnancy and LH content during the first 8 days.

Significant uterine weight cycles of 4 days do appear to persist in the pseudopregnant hamster (Table 1, Text-fig. 2). In those animals with an 8-day pseudopregnant cycle, the parallelism is exact; in those with a 9-day cycle, the second peak is deferred 1 day. These uterine changes do suggest a latent cycle, which would be due to ovarian hormonal changes, the nature of which cannot be determined from these data. The higher level of the pseudopregnant weights may well be due to the high progesterone level produced from the active corpora lutea.

A parallel situation is seen in the pseudopregnant rat, where uterine growth begins at ovulation and peaks at the sensitive period (Saldarini & Yochim, 1967; De Feo, 1963), i.e. the 5th day in the rat, which also corresponds to the time of optimal decidual cell induction in pseudopregnancy and parallels implantation in pregnancy (Psychoyos, 1960, 1961). This peak in the rat has been ascribed to an ovarian oestrogen contribution occurring on the afternoon of the 4th day, without which optimal decidual cell induction cannot be obtained or implantation occur (Shelesnyak, Kraicer & Zeilmaker, 1963; Zeilmaker, 1963), although decidual cell induction can occur with progesterone alone (Rothchild & Meyer, 1942; Alloiteau & Vignal, 1961). Moreover, anti-oestrogens prevent decidual cell induction or implantation (Shelesnyak et al., 1963).

In the hamster, Duncan & Lyster (1962) have demonstrated that implantation is not prevented by anti-oestrogens. Implantation can occur with progesterone alone (Prasad, Orsini & Meyer, 1960; Orsini & Psychoyos, 1965), but success is increased by addition of oestrogen (Harper, Prostkoff & Reeve, 1966). Deciduoma can be elicited in ovariectomized hamsters given progesterone alone (Czyba, Chiris & Dubois, 1962). Moreover, evidence recently obtained utilizing ovariectomy during the hamster oestrous cycle (Brom & Schwartz, 1968) indicates that the uterine growth seen on Day I of the oestrous cycle (Text-fig. 2) is the result of an ovarian secretion during the preceding 24 hr. From this, we feel that the increased uterine weights reported here suggest that oestrogen is produced, before the 'sensitive period' which occurs on the 4th day and parallels the time of implantation in pregnancy, and also before the oestrus concluding pseudopregnancy.

The corpora lutea of pseudopregnancy are larger than those of the oestrous cycle, 820 to 860 µ as opposed to 700 µ (Deanesly, 1938). They are functional, allowing decidual cell formation after trauma (De Feo, 1967; Orsini, 1963, 1964), suppressing ovulation and eliciting vaginal epithelial changes (Klein,
1938), they last for 8 to 9 or 10 days (Kent & Atkins, 1959) and, in older animals, 10 to 11 days (Orsini, unpublished observations) while those of the cycle are unresponsive by the 3rd day post-ovulation (Choudary & Greenwald, 1967). Prolactin and FSH have been shown by Choudary & Greenwald (1967) to be the luteotrophic factors in pseudopregnancy; the true mechanism of luteolysis is still unclear although Duby, McDaniel & Black (1965) have shown that uterine removal prolongs their life to approximately 18 days, and unilateral hysterectomy, causing dyssymmetry of the ovaries, has been reported by Orsini (1968). Mazer & Wright (1968) have published evidence for a hamster luteolytic factor, appearing on the 6th and 7th days of pseudopregnancy.

Corpora lutea of the oestrous cycle have approximately a 4-day life-span, starting degeneration on the 3rd day post-ovulation and becoming grossly obscure by the next post-oestrous discharge. Corpora of pseudopregnancy persist longer and are clearly visible as ischaemic bodies at the time of the post-oestrous discharge terminating pseudopregnancy. This delay in degeneration is mirrored in the ovarian weight data (Table 1, Text-fig. 1). Kirby & Kent (1962), studying corpora lutea transferred to the anterior chamber of the eye, observed maximal vascularity at 36 hr, persisting until 108 hr (Day 5) after sterile mating, and stasis at 144 hr. They reported maximal size at 24 hr, followed by a decline in size until 108 hr (Day 5), and a rapid decline to 156 hr (Day 7). Choudary & Greenwald (1967) reported that the corpora lutea of pseudopregnancy were large from Days 3 to 6, but became ischaemic and were regressing on Day 7.

Turnbull & Kent (1963) found that deciduomata in the hamster attained peak differentiation at 144 hr (Day 6), showed necrosis at 186 hr (Day 8), and lost all connection with the uterus, lying free in reconstituted lumina by Day 9, suggesting a sequential effect of the ovarian changes mentioned above.

Thus, two critical stages exist in pseudopregnancy. The first is the sensitive period during the 4th day after ovulation, when relatively non-traumatic stimuli can elicit decidual cell formation (Orsini, 1964, 1965) and when ‘pseudo-implantation’ occurs. (‘Pseudo-implantation’ is the term used to imply loss of the zona from the ovum, and development of a definite transient ovo-uterine relationship, as revealed by a specific localized reaction of the uterus to pontamine blue. The coloured regions are confined to the discrete areas where the ova lie in positions exactly paralleling early implantation.) This first sensitive period parallels, in post-ovulation age, the time of implantation in the pregnant hamster.

The second critical period of pseudopregnancy lies between the 6th and 7th days, characterized by ischaemia and decline of the corpora lutea.

ACKNOWLEDGMENTS

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