

Plasma Levels of Estradiol and Progesterone in the Cat During Polyestrus, Pregnancy and Pseudopregnancy

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ABSTRACT

The levels of estradiol and progesterone in the systemic plasma of four domestic cats during pregnancy, pseudopregnancy and polyestrus were determined by radioimmunoassay. During polyestrus, estradiol values fluctuated between peaks (59.5 ± 13.4 (SD) pg/ml; $n = 13$) and troughs (8.1 ± 3.8 (SD) pg/ml; $n=12$) with an interpeak period of 15.8 ± 3.8 days ($n=9$). After the animals had been mated to either intact or vasectomized males, their estradiol levels declined sharply from peak values and remained low (6-12 pg/ml) during pseudopregnancy and pregnancy except for a slight rise just before parturition. Essentially no progesterone could be detected during polyestrus and for 2 to 3 days after copulation with either intact or vasectomized males, but by Day 21 of pregnancy or pseudopregnancy progesterone rose to a peak of either ~ 35 or ~ 24 ng/ml respectively. After Day 21 of pregnancy, progesterone gradually declined to ~ 10 ng/ml by Day 60, ~ 5 ng/ml just before parturition, and <1 ng/ml just after parturition. After Day 21 of pseudopregnancy, progesterone levels declined rapidly to ~ 4 ng/ml by Day 40, ~ 2 ng/ml by Day 50 and <1 ng/ml by Day 63-65. Estrone was measured throughout pregnancy, pseudopregnancy and polyestrus in one animal; no major elevations were detected.

INTRODUCTION

Many of the behavioral and morphological events that occur during the reproductive cycle of the cat have been described (Scott, 1970; Dawson, 1950; Marshall, 1956; Young, 1941; Whalen, 1963; Michael, 1961; Rosenblatt and Schneirla, 1962). Cats are seasonal breeders with two peak seasons of activity, January through March, and May through June. During estrus, ovulation must be induced by copulation or some other comparable stimulus. If copulation does not occur, cats undergo estrus every 2 to 3 weeks. The gestation period is 65 ± 4 days (SD). Follicular development coincides with estrous behavior, and ovulation occurs between 25 and 26 h after mating. Even though the granulosa cells show some evidence of luteinization before ovulation, progestational changes in the uterus are not apparent until 3 or 4 days after mating.

Most authors generally agree with these data on the reproductive cycle of the cat, but certain reproductive events have engendered some controversy. For example, the period of pseudo-

pregnancy has been reported to last from as little as 30 days to as long as 73 days (Gros, 1935; Liche, 1939; LeRoux, 1971; Paape, 1975). According to Windle (1939) spontaneous ovulation can not be ruled out and pregnant cats sometimes experience behavioral estrus and accept the male (Scott and Lloyd-Jacob, 1955). More recently, Stabenfeldt (1974) pointed out that cats sometimes remain in estrus for 3 or 4 days after mating whereas other animals (sow, ewe, mare) are usually out of estrus a few hours after ovulation. Dawson (1950), who had observed these discrepancies some years ago suggested that they are due to environmental (geographic) and/or genetic (use of heterogeneous stock) differences. However, the systemic patterns of estradiol and progesterone in the cat during polyestrus and pregnancy and estradiol during pseudopregnancy are not known, and have not been correlated with either behavioral changes or reproductive events in the female reproductive tract. Here we report the results of a longitudinal study of the systemic levels of estradiol and progesterone in four domestic cats during pregnancy, pseudopregnancy and polyestrus and discuss the relation between the hormone levels and the behavioral and histological changes which occur during the reproductive cycle.

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MATERIALS AND METHODS

Animals

Four mature multiparous domestic cats (of mixed phenotype) were maintained under controlled illumination (14 h light, 10 h dark) and temperature (22°C). A commercially prepared ration (Purina) and water were provided ad lib. At their first heat, the four queens were mated to an intact male, allowed to deliver, and nursed their litter for six weeks. At their first heat after their first litters had been weaned, they were mated to a sterile male. The tom was then removed from the room and the queens were studied for another 120 days. Three times a week during pregnancy, pseudopregnancy, and polyestrus, three ml blood samples were collected between 0900 and 1100 h by femoral venipuncture in heparinized syringes and centrifuged. The plasma was stored frozen until assayed. The complete series of samples for each animal was assayed at one time.

Radioimmunoassays

Tritiated steroids (approx. 100 Ci/mM) were obtained from New England Nuclear; unlabeled steroids from Steraloids, Inc.; and antibodies from Holly Hills Biological, Inc. The antibody for estradiol was produced in rabbits by injecting them with estradiol-6-oxime bovine serum albumin; progesterone-11 α -succinyl bovine serum albumin was injected to produce the progesterone antibody. We tested these antibodies for cross reactivity with 30 steroids and found them to be highly specific for estradiol and progesterone, respectively. Plasma (0.5 cc portions) was extracted, purified by chromatography, and assayed for estradiol and progesterone by the methods of Resko (1971) and Resko et al. (1974).

Blank values for plasma from ovariectomized cats were $3.0 \text{ pg} \pm 0.5 \text{ (SE)}$, $n = 5$, for estradiol and $22.6 \text{ pg} \pm 5.0 \text{ (SE)}$, $n = 6$, for progesterone. The accuracy and precision of the estradiol assay when 10, 30, or 50 pg ($n = 5$ at each dose level) of estradiol was added to 0.5 cc of ovariectomized cat plasma were $13.0 \pm 0.4 \text{ (SE)}$, 31.9 ± 1.0 , and 52.3 ± 0.7 , respectively. Similarly, the accuracy and precision of the progesterone assay when 250, 500, or 1500 pg ($n = 4$ at each dose level) of progesterone were added to ovariectomized cat plasma were $249 \pm 25 \text{ (SE)}$, 591 ± 32 , and 1455 ± 54 , respectively.

Silastic implants of estradiol ranging from 0.5 to 4.0 cm were prepared (Verhage and Brenner, 1975). The implants were placed in ovariectomized cats, and blood was drawn to measure plasma estradiol. We found a nearly linear dose response relation between the size of the silastic implant and the amount of RIA-measurable plasma estradiol (0.5 cm = 17 pg/ml; 1 cm = 28 pg/ml; 2 cm = 34 pg/ml; 4 cm = 75 pg/ml).

We determined the estrone levels in one cat using an antibody produced by injecting rabbits with estrone-17-oxime bovine serum albumin (Holly Hills Biological, Inc.). Although this antibody binds estradiol as well as estrone, these compounds were well separated by our thin-layer chromatography step (Resko et al., 1974).

Data Analysis

The significance of differences among mean progesterone

values during pregnancy and pseudopregnancy were determined using Student's *t* test.

RESULTS

The concentrations of estradiol and progesterone in the systemic plasma of four cats during pregnancy, pseudopregnancy, and polyestrus are shown in Fig. 1 and their mean (\pm SEM) plasma levels during pregnancy and pseudopregnancy are compared in Fig. 2.

Estradiol

Pregnancy. On the day of mating, systemic levels of estradiol peaked at $\sim 60 \text{ pg/ml}$ (Fig. 1, and 2), then dropped precipitously to 8 to 12 pg/ml during the first 5 days after copulation. They remained low until Days 58–62, then rose slightly in three animals just before parturition. In animal No. 34 (Fig. 1B), a sharp peak of estradiol (44 pg/ml) on Day 60 was followed by a slight decline at the time of parturition (Days 63–65).

Pseudopregnancy. For the first 40 days, estradiol concentrations were similar to but somewhat lower than those observed during pregnancy (Fig. 2). After 40 days, these patterns varied considerably from individual to individual (Fig. 1). In animal No. 34 a small surge (27 pg/ml) occurred on Day 44 and was accompanied by an increase in progesterone concentration from 3 to 7 ng/ml (Fig. 1B). In animal No. 35, the first small surge of estradiol (34 pg/ml on Day 56) (Fig. 1C) was not accompanied by an increase in progesterone which remained at 2 ng/ml. The first surge of estradiol to exceed 40 pg/ml in each animal occurred on Days 62, 64, 65 and 69 respectively. Each of these "normal" surges was correlated with an immediate decline of progesterone to $< 1 \text{ ng/ml}$.

Polyestrus. When maintained under constant periods of illumination and temperature and without male contact, each of the four cats varied considerably, both in the number of estradiol surges and the peak level of estradiol attained during each surge. Only No. 34 and 35 (Fig. 1B, and 1C) experienced more than two surges of estradiol during the last 60 days of the study. The interval between estradiol surges in No. 34 was $17.7 \pm 2.9 \text{ (SD) days}$ ($n = 3$), in No. 35, $13.8 \pm 3.7 \text{ (SD) days}$ ($n = 4$). Cats No. 31 and No. 39 had only two estradiol surges with an interval of 18 and 16 days, respectively. The mean (\pm SD) for the 9 intervals experienced by

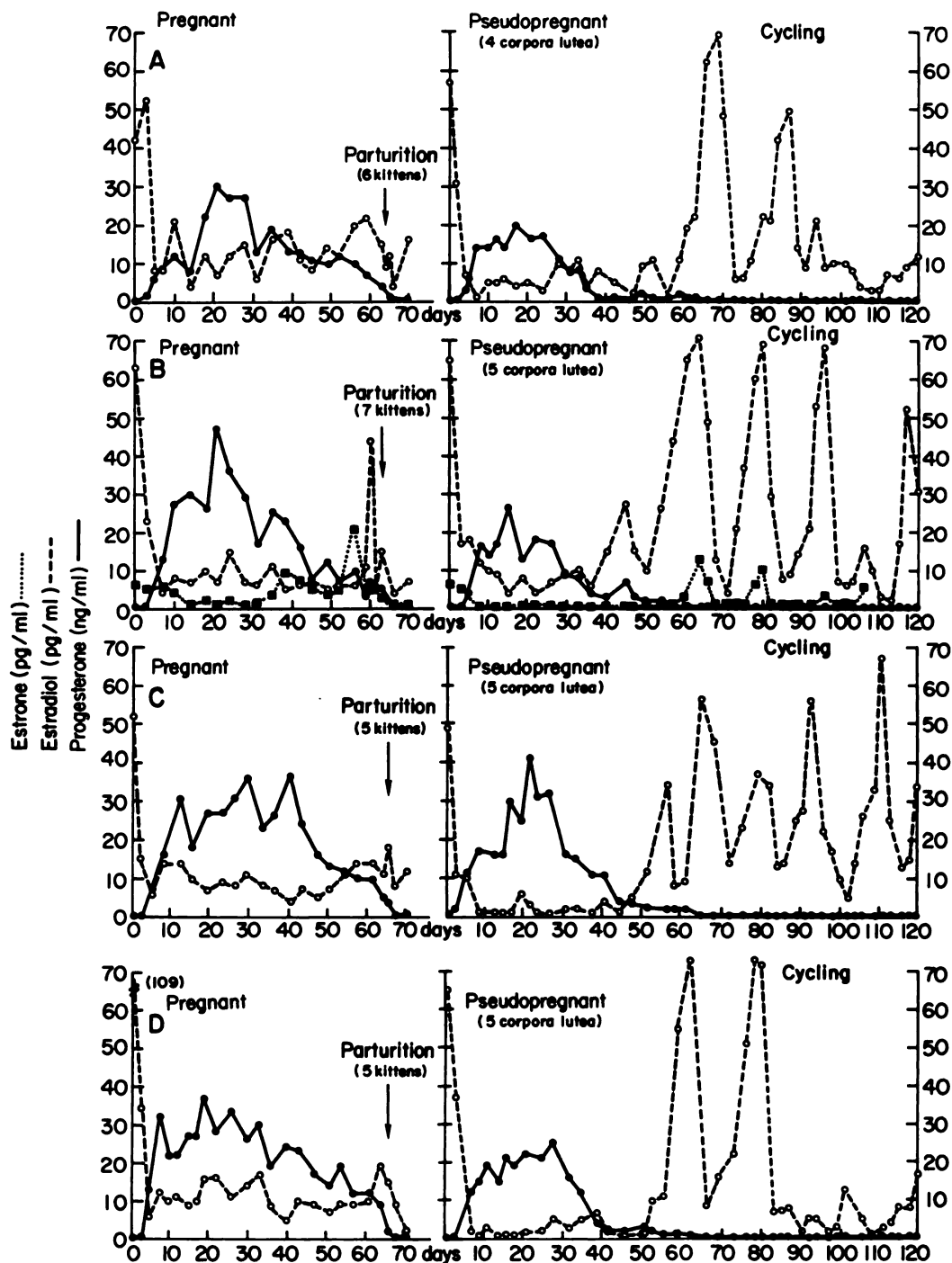


FIG. 1. Profiles of plasma estradiol and progesterone in four individual cats and estrone in one cat (B) during pregnancy, pseudopregnancy and polyestrus.

the 4 cats was 15.8 ± 3.8 days. For all surges which rose to peaks greater than 30 pg/ml, the mean (\pm SD) estradiol peak was 59.5 ± 13.4

pg/ml ($n = 13$) and the trough was 8.1 ± 3.8 pg/ml ($n = 12$). After this study was completed, each female came into estrus and mated with a

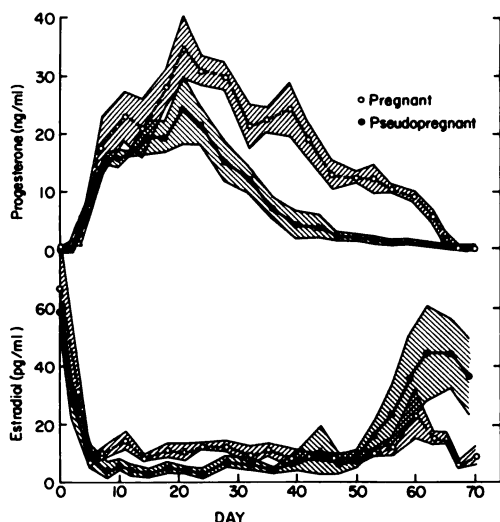


FIG. 2. Mean (\pm SE) levels of estradiol and progesterone in pregnant and pseudopregnant cats ($n = 4$ except for Δ where $n = 3$).

male placed in the room. Ovulation was confirmed in each animal by laparotomy.

Progesterone

Pregnancy. The first 2 or 3 days after mating, progesterone remained virtually undetectable then increased dramatically to 22.9 ± 4.1 ng/ml by Day 11 (Fig. 2). A slight decline preceded the peak levels (34.9 ± 6.2 ng/ml) on Day 21. It then declined gradually, reaching 12.6 ± 0.9 ng/ml by Day 50 and $4-5$ ng/ml just before parturition (Days 63-65). Immediately after parturition, progesterone values dropped to <1 ng/ml.

Pseudopregnancy. For the first 21 days the progesterone rise paralleled that observed during pregnancy except that the peak values on Day 21 were 24.6 ± 6 ng/ml; the difference was not, however, statistically significant ($t = 1.30$, 6 df, $P > 0.05$) (Fig. 2). The drop in the systemic concentrations was more dramatic than during pregnancy; the differences became significant ($t = 3.39$, 6 df, $P < 0.02$) on Day 28 (29.8 ± 2.3 ng/ml vs. 15.3 ± 3.6 ng/ml) and continued through Day 62 (5.8 ± 1.2 ng/ml vs. 1.0 ± 0.4 ng/ml; $t = 3.79$, 6 df, $P < 0.01$). By Day 40 the concentrations had decreased to 4.2 ± 2.5 ng/ml, remained above 2 ng/ml through Day 50, and did not drop below 1 ng/ml until after Day 62.

Polyestrus. The mean (\pm SD) progesterone levels in the peripheral plasma during polyestrus

were 0.56 ± 0.19 ng/ml ($n = 22$) for No. 31 (Fig. 1A), 0.19 ± 0.11 ng/ml ($n = 22$) for No. 34 (Fig. 1B), 0.11 ± 0.06 ng/ml ($n = 22$) for No. 35 (Fig. 1C), and 0.47 ± 0.15 ng/ml ($n = 22$) for No. 39 (Fig. 1D).

Estrone

Estrone was determined in No. 34 during pregnancy, pseudopregnancy, and polyestrus (Fig. 1B). No estrone could be detected except for a slight elevation during the last trimester of pregnancy and for minor increases ($4-12$ pg/ml) which coincided with the estradiol peaks.

DISCUSSION

The results of this study confirm earlier reports that polyestrus can be induced in cats by exposing them to controlled light cycles and constant temperature (Scott and Lloyd-Jacob, 1959; Hamner et al., 1970). The interval between estradiol peaks (15.8 ± 3.8 (SD) days) compares favorably with the interestrus periods during anovulatory cycles reported by others (Marshall, 1956; Foster and Hisaw, 1935; Scott and Lloyd-Jacob, 1955; Paape et al., 1975). If a male was present, coitus occurred during estrus, and ovulation and the formation of corpora lutea occurred. These observations support the hypothesis that the cat is an induced ovulator (Hamner et al., 1970), and that corpora lutea are formed only after mating or some other appropriate stimulus (Colby, 1970).

Estrus periods usually last for 3 or 4 days after mating (Vanderstricht, 1911; Stabenfeldt, 1974) but from 6 to 10 days when coitus does not occur (Hamilton, 1896; Liche, 1939). Our data show that 3 or 4 days after coitus estradiol drops precipitously to between 20 to 30 pg/ml. During each estradiol surge in the polyestrus phase, estradiol remains at 25 pg/ml or more for a mean (\pm SD) period of 8 ± 2.7 days. Although we did not make systematic observations of sexual behavior, we noted that lordosis and estrous behavior (Michael, 1961) usually coincided with the estradiol surges.

The formation of corpora lutea during pregnancy and pseudopregnancy follows a similar sequence (Foster and Hisaw, 1935; Liche, 1939; Dawson and Friedgood, 1940; Dawson, 1941, 1950). During pregnancy and pseudopregnancy, progesterone levels rise at equivalent rates for the first 10 to 12 days after coitus,

after which, the pregnant animals have higher progesterone levels than the pseudopregnant ones. This divergence coincides with the time of implantation (12 or 13 days) in the cat (Manwell and Wickens, 1928; Courrier and Gros, 1933). The differences in the systemic levels of progesterone in pregnant and pseudopregnant animals become significant on Day 28, when regressive luteal changes during pregnancy and pseudopregnancy are first detected (Foster and Hisaw, 1935; Dawson, 1950). The differences between the progesterone levels during pregnancy and pseudopregnancy observed in this study must remain unexplained. They could be due to placental synthesis of progesterone, heightened function of the corpora lutea of pregnancy or other factors.

Uterine changes during estrus, which include dilation of the endometrial glands along with hypertrophy and hyperplasia of the glandular surface epithelium (Foster and Hisaw, 1935; Dawson and Kosters, 1944), correlate well with the surge of estradiol during estrus and the absence of progesterone. The preimplantation changes in the endometrium after ovulation are the same whether they follow a successful mating, a sterile mating, or mechanical stimulation of the cervix (Foster and Hisaw, 1935; Dawson and Kosters, 1944). The typical 'pregnastational response' is not detected in the endometrium of the cat until 2 to 4 days after mating (Gros, 1933; Dawson and Kosters, 1944); the vaginal smear does not change until about 3 days after coitus (Foster and Hisaw, 1935). In this study, we did not detect any progesterone in the systemic blood for the first 3 or 4 days after coitus. Corpora lutea development may be slower in the cat, an induced ovulator, than in other animals which ovulate spontaneously, or the interval from coitus to ovulation may be longer than 25 to 26 h (Paape et al., 1975).

The length of the interestrual period in pseudopregnant cycles, determined by morphological and behavioral parameters, has been reported to last from 30 to 44 days (Gros, 1935; Foster and Hisaw, 1935; Liche, 1939; Paape, 1975) and for 73 days in one cat (Paape, 1975). The main surge of progesterone observed in this study is also complete around Day 40, but detectable quantities were observed for an additional 20 days. Gros (1935) reported that the female is in estrus 40 days after mating with a sterile male whereas LeRoux (1971) did not observe the next estrus

until 63 days after coitus. In our animals the first surge of estradiol to levels above 25 pg/ml occurred about 60 days postcoitum. We did not make systematic observations of behavioral estrus during this period. We noted, however, that the estradiol surge did not begin until progesterone had declined to levels below 1–2 ng/ml. This inverse relationship between the blood levels of these two steroids might well be fortuitous, but there are reports that progesterone can act at ovarian sites to suppress estrogen synthesis (Hess and Resko, 1973; Kalra and Kalra, 1974). Some of the reported variation in the time of onset of behavioral estrus, as well as the variation we observed in the time of onset of the first estradiol surge, might well be related to differences between animals in the rate of luteal regression and the consequent decline of progesterone secretion.

The rabbit, a lagomorph, and the cat, a carnivore, are both induced ovulators, but their steroid hormone patterns are quite different. In estrous rabbits, the secretion rate of estradiol, ~ 18 ng/ovary/h, surges to a peak of ~ 63 ng/ov/h 2 h after copulation, becomes nondetectable by ovulation (8 h later), and increases modestly to 20 ng/ovary/h by Days 8–10 of pregnancy (Hilliard and Eaton, 1971). In the cat, as we have shown, the surges of estradiol during polyestrus do not depend on mating and the estradiol levels fall dramatically immediately after coitus.

In the rabbit, a preovulatory surge of progestins (progesterone and 20 α -OH progesterone) follows coitus (Hilliard and Eaton, 1971), but, as we have shown, progesterone is detectable in the cat only when corpora lutea have formed in the ovary.

The cat, mink (Møller, 1973a), and ferret (Heap and Hammond, 1974), all carnivores and induced ovulators, have similar profiles of plasma progesterone during pregnancy. The lag period immediately after mating is followed by a dramatic rise which peaks (30–40 ng/ml) at the time of, or shortly after, implantation and then gradually declines for the rest of gestation. In the mink and ferret, ovariectomy at any time during pregnancy results in abortion or resorption of the conceptus (Møller, 1974; McPhail, 1935). Scott (1970) states that the ovaries of the cat can be removed after Day 45 without interrupting pregnancy. This suggests that in the mink and ferret, but not the cat, the placenta either does not secrete progesterone or does not do so in sufficient amounts to

maintain pregnancy. This is also suggested by the results of Heap and Hammond (1974) who showed that progesterone concentrations in the plasma of ferrets are similar during pregnancy and pseudopregnancy.

The bitch, a spontaneous ovulator, is the only other carnivore in which both plasma estrogens and progesterone have been reported throughout the entire reproductive cycle (Concannon et al., 1975; Nett et al., 1975; Edqvist et al., 1975; Smith and McDonald, 1974; Jones et al., 1973a, b). Cats and dogs are remarkably similar in the peak levels of estradiol during estrus (~50–80 pg/ml), the peak levels of progesterone during pregnancy (~30 ng/ml), and the general profile of both estradiol and progesterone during pregnancy. In the dog, but not the cat, progesterone levels are similar during pregnancy, pseudopregnancy, and non-mated cycles. Presumably progesterone synthesis by the placenta is minimal in the dog as in the ferret (Heap and Hammond, 1974) and blue fox (Møller, 1973b). Whether the placenta, the corpora lutea or extragonadal sources are responsible for the elevated levels of progesterone in the pregnant (compared to pseudopregnant) cat is an endocrinological problem of considerable interest, worthy of additional study.

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REFERENCES

- Colby, E. D. (1970). Induced estrus and timed pregnancies in cats. *Lab. Anim. Care* 20, 1075-1080.
- Concannon, P. W., Hansel, W. and Visek, W. J. (1975). The ovarian cycle of the bitch: plasma estrogen, LH, and progesterone. *Biol. Reprod.* 13, 112-121.
- Courrier, R. and Gros, G. (1933). Donnees complementaires sur le cycle genital de la chatte. *C.R. Soc. Biol.* 114, 275-277.
- Dawson, A. B. (1941). Early estrus in the cat following increased illumination. *Endocrinology* 28, 907-910.
- Dawson, A. B. (1950). The Domestic Cat. *In: "Care and Breeding of Laboratory Animals."* (E. J. Farris, ed.), John Wiley & Sons, New York, pp. 202-233.
- Dawson, A. B. and Friedgood, H. G. (1940). The time and sequence of preovulatory changes in the cat ovary after mating or mechanical stimulation of the cervix uteri. *Anat. Rec.* 76, 411-429.
- Dawson, A. B. and Kosters, B. A. (1944). Preimplantation changes in the uterine mucosa of the cat. *Am. J. Anat.* 75, 1-27.
- Edqvist, L.-E., Johansson, E. D. B., Kasstrom, H., Olsson, S.-E. and Richkind, M. (1975). Blood plasma levels of progesterone and oestradiol in the dog during the oestrous cycle and pregnancy. *Acta Endocrinol.* 78, 554-564.
- Foster, M. A. and Hisaw, F. L. (1935). Experimental ovulation and resulting pseudopregnancy in anestrus cats. *Anat. Rec.* 62, 75-93.
- Gros, G. (1933). Recherches preliminaires sur le cycle genital chez la chatte. *Bull. Hist. Appl.* 10, 5-11.
- Gros, G. (1935). Evolution de la muqueuse uterine chez la chatte. *C.R. Soc. Biol.* 118, 1575-1578.
- Hamilton, E. (1896). The wild cat of Europe. *Quart. J. Microscop. Sci.* 44, 1900-1.
- Hamner, C. E., Jennings, L. L. and Sojka, N. J. (1970). Cat (*Felis catus* L) spermatozoa require capacitation. *J. Reprod. Fert.* 23, 477-480.
- Heap, R. B. and Hammond, J., Jr. (1974). Plasma progesterone levels in pregnant and pseudopregnant ferrets. *J. Reprod. Fert.* 39, 149-152.
- Hess, D. L. and Resko, J. A. (1973). The effects of progesterone on the patterns of testosterone and estradiol concentrations in the systemic plasma of the female rhesus monkey during the intermenstrual period. *Endocrinology* 92, 446-453.
- Hilliard, J. and Eaton, L. M., Jr. (1971). Estradiol-17 β , progesterone, and 20 α -hydroxypregn-4-en-3-one in rabbit ovarian venous plasma. II. From mating through implantation. *Endocrinology* 89, 522-527.
- Jones, G. E., Boyns, A. R., Cameron, E. H. D., Bell, E. T., Christie, D. W. and Parkes, M. F. (1973a). Plasma oestradiol, luteinizing hormone, and progesterone during the oestrous cycle in the beagle bitch. *J. Endocrinol.* 57, 331-332.
- Jones, G. E., Boyns, A. R., Cameron, E. H. D., Bell, E. T., Christie, D. W. and Parkes, M. F. (1973b). Plasma oestradiol, luteinizing hormone, and progesterone during pregnancy in the beagle bitch. *J. Reprod. Fert.* 35, 187-189.
- Kalra, S. P. and Kalra, P. S. (1974). Temporal interrelationships among circulating levels of estradiol, progesterone, and LH during the rat estrous cycle: effects of exogenous progesterone. *Endocrinology* 95, 1711-1718.
- LeRoux, P. H. (1971). The use of a teaser tom to terminate oestrus in female cats. *J.S. Afr. Vet. Med. Assoc.* 42, 95.
- Liche, H. (1939). Oestrous cycle in the cat. *Nature* 143, 100.
- Manwell, E.-J. and Wickens, P. G. (1928). The mechanism of ovulation and implantation in the domestic cat. *Anat. Rec.* 38, 54 (Abstr.)
- Marshall, F. H. A. (1956). The Oestrous Cycle in the Mammalia. *In: "Marshall's Physiology of Reproduction."* (A. S. Parkes, ed.), Longmans, London, 3rd Ed., pp. 288-305.

- McPhail, M. K. (1935). Hypophysectomy of the cat. Proc. Roy. Soc. ser. B 117, 45-63.
- Michael, R. P. (1961). Observations upon the sexual behavior of the domestic cat (*Felis catus l.*) under laboratory conditions. Behavior 18, 1-24.
- Møller, O. M. (1973a). The progesterone concentrations in the peripheral plasma of the mink (*Mustela vison*) during pregnancy. J. Endocrinol. 56, 121-132.
- Møller, O. M. (1973b). Progesterone concentrations in the peripheral plasma of the blue fox (*Alopex lagopus*) during pregnancy and the oestrous cycle. J. Endocrinol. 59, 429-438.
- Møller, O. M. (1974). Plasma progesterone before and after ovariectomy in unmated and pregnant mink, *Mustela vison*. J. Reprod. Fert. 37, 367-372.
- Nett, T. M., Akbar, A. M., Plemister, R. D., Holst, P. A., Reichert, L. E., Jr. and Niswender, G. D. (1975). Levels of luteinizing hormone, estradiol, and progesterone in serum during the estrous cycle and pregnancy in the beagle bitch. Proc. Soc. Exptl. Biol. Med. 148, 134-139.
- Paape, S. R., Shille, V. M., Seto, Helen and Stabenfeldt, G. H. (1975). Luteal activity in the pseudopregnant cat. Biol. Reprod. 13, 470-474.
- Resko, J. A. (1971). Sex steroids in adrenal effluent plasma of the ovariectomized rhesus monkey. J. Clin. Endocrinol. Metab. 33, 940-948.
- Resko, J. A., Norman, R. L., Niswender, G. D. and Spies, H. G. (1974). The relationship between progestins and gonadotropins during the late luteal phase of the menstrual cycle in rhesus monkeys. Endocrinology 94, 128-135.
- Rosenblatt, J. S. and Schneirla, T. C. (1962). The Behavior of Cats. In: "Behavior of Domestic Animals." (E. S. E. Hafez, ed.), Williams & Wilkins Co., Baltimore, 1st Ed., pp. 453-488.
- Scott, P. P. (1970). Cats. In: "Reproduction and Breeding Techniques for Laboratory Animals." (E. S. E. Hafez, ed.), Lea & Febiger, Philadelphia, pp. 192-208.
- Scott, P. P. and Lloyd-Jacob, M. A. (1955). Some interesting features in the reproductive cycle of the cat. Stud. Fertil. 7, 123-129.
- Scott, P. P. and Lloyd-Jacob, M. A. (1959). Reduction in the anoestrous period of laboratory cats by increased illumination. Nature 184, 2022.
- Smith, M. S. and McDonald, L. E. (1974). Serum levels of luteinizing hormone and progesterone during the estrous cycle, pseudopregnancy, and pregnancy in the dog. Endocrinology 94, 404-412.
- Stabenfeldt, G. H. (1974). Physiologic, pathologic and therapeutic roles of progestins in domestic animals. J. Am. Vet. Med. Assoc. 164, 311-317.
- Vandertricht, R. (1911). Vitellogenese dans l'ovule de chatte. Arch. Biol. 26, 365-481.
- Verhage, H. G. and Brenner, R. M. (1975). Estradiol-induced differentiation of the oviductal epithelium in ovariectomized cats. Biol. Reprod. 13, 104-111.
- Whalen, R. E. (1963). Sexual behavior of cats. Behavior 20, 321-342.
- Windle, W. F. (1939). Induction of mating and ovulation in the cat with pregnancy urine and serum extracts. Endocrinology 25, 365-371.
- Young, W. C. (1941). Observations and experiments on mating behavior in female mammals. Quart. Rev. Biol. 16, 135-156, 311-335.

RECOMMENDED REVIEWS

- Brenner, R. M. and West, N. B. (1975). Hormonal regulation of the reproductive tract in female mammals. Ann. Rev. Phys. 37, 273-302.
- Dawson, A. B. (1950). The Domestic Cat. In: "Care and Breeding of Laboratory Animals." (E. J. Farris, ed.), John Wiley & Sons, New York, pp. 202-233.