FOLLICULAR DEVELOPMENT DURING FOUR STAGES OF THE ESTROUS CYCLE OF BEEF CATTLE

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Summary

Estrogen and progestin concentrations in plasma and follicular fluid (FF) of follicles within the small (5 to 100 μl), medium (101 to 400 μl) and large (>400 μl) range, numbers of follicles and volume of FF per follicle within these ranges were determined in beef heifers. There were differences (P<.01) in mean concentrations (±SE) of steroids among and within follicles from the small, medium and large ranges during the estrous cycle. Concentrations of progestins were highest in follicles within the small range (178 ± 12 ng/ml); whereas, concentrations of estrogens were highest in follicles in the large range (55 ± 8 ng/ml). Mean ratio of progestins: estrogens was 12:1 in small follicles, 4:1 in medium follicles and 2:1 in large follicles.

Volumes of FF from follicles within the small, medium and large ranges varied (P<.01) throughout a cycle. Mean volumes of FF from follicles in the medium and large range increased 130% and 180%, respectively, as time of ovulation neared. In contrast, mean volumes of FF from follicles within the small range decreased 170%. Total numbers of follicles per pair of ovaries and heifers with follicles in the large range increased (P<.01) toward the end of the estrous cycle.

(Key Words: Cattle, Estrogen, Progestin, Estrous Cycle, Follicles.)

Introduction

Understanding mechanisms that regulate selection of a species-specific number of follicles to ovulate may require a thorough knowledge of the relationship between morphometric and endocrine changes that occur in populations of follicles during an estrous cycle.

Changes in morphology and numbers of atretic and normal follicles have been thoroughly investigated during the life span (Erickson, 1966) and during the estrous cycle of cattle (Rajakowski, 1960; Marion et al., 1968; Choudary et al., 1968). Although concentrations of steroids in follicular fluid from large follicles of cattle have been determined (Short, 1962, 1964; England et al., 1973; Korenman et al., 1973), changes in concentrations of steroids in developing antral follicles throughout the estrous cycle have not been examined.

This study was designed to determine changes in concentrations of progestins and estrogens in plasma and follicular fluid and changes in volumes and numbers of follicles during the estrous cycle of cattle.

Materials and Methods

Animals and Sampling. In 1974, 180 Hereford heifers (six per pen) of unknown ages and weighing 300 to 400 kg were selected for comparison of growth curves following different diets. Cattle were slaughtered when a pen of heifers averaged 12 mm of backfat. In general, first ovulation in beef heifers occurs between 12 and 14 months or 250 to 350 kg body weight.

Immediately following decapitation, blood samples (jugular) were collected in tubes containing heparin, stored on ice and later centrifuged. Within 30 min after killing, pairs of ovaries from each heifer were obtained, placed on ice and stage of the estrous cycle estimated.
Ireland et al. (1979) established in preliminary experiments that four distinct sequential changes in appearance of the corpus luteum occurred during the bovine estrous cycle (table 1) and that these changes could be used effectively to estimate stages of the estrous cycle (Stage I - days 1 to 4; Stage II - days 5 to 10; Stage III - days 11 to 17; Stage IV - days 18 to 20).

All follicles protruding to the surface of each pair of ovaries were counted and FF was aspirated from most. FF from each pair of ovaries was pooled into three follicle size categories according to volumes of FF recovered from each follicle: small, 5 to 100 μl, medium, 101 to 400 μl and large, >400 microliters. Changes in volumes of FF recovered was used as an index of follicle growth and analyzed within each size category. External diameters were less than 3 mm for follicles in the small range, 3 mm to 9 mm for follicles in the medium range and greater than 10 mm for follicles in the large range.

Statistical Analysis. Differences in mean concentrations of steroids and numbers and volumes of follicles within the small, medium and large range throughout stages of the estrous cycle were determined using Scheffé's simultaneous test (Gill, 1978). Differences in frequencies of heifers with follicles in the medium and (or) large range throughout stages of the estrous cycle were analyzed by chi-square analysis or minimum chi-square analysis (Quade and Salama, 1975) using a Bonferroni chi-square table. Differences between significant (P<.05) correlation coefficients were determined following Z transformations (Gill, 1978).

Radioimmunoassay of Steroids. Samples of FF (10 μl) from follicles within the small, medium or large ranges of each pair of ovaries and corresponding plasma samples (progestins, 500 μl; estrogens, 2 to 5 ml) were assayed in duplicate for progestins (Morgan and Cooke, 1972) and estrogens (Speroff et al., 1972) by radioimmunoassay using dextran-coated charcoal to separate free from bound hormone. Estrogens and progestins were not determined for all plasma and FF because of limited sample volume. Plasma was extracted (progestins; petroleum ether, 2 x 5 ml; estrogens; benzene, 1 x 7 ml) and assayed directly without chromatography. Plasma and FF were extracted in a similar fashion except where noted in the text.

Mean (±SE) extraction efficiency for 3H-

<table>
<thead>
<tr>
<th>TABLE 1. STAGES OF THE ESTROUS CYCLE</th>
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<tbody>
<tr>
<td>Stages of estrous cycle</td>
</tr>
<tr>
<td>-------------------------</td>
</tr>
<tr>
<td>I</td>
</tr>
<tr>
<td>II</td>
</tr>
<tr>
<td>III</td>
</tr>
<tr>
<td>IV</td>
</tr>
</tbody>
</table>

aSee Ireland et al. (1979) for further descriptions.

bLength of each stage relative to estrous cycle was estimated by multiplying the percentage of heifers within each stage by 20 (average length of estrous cycle).
progesterone from plasma was 89 ± 2% (n = 33) and from FF was 96 ± 3% (n = 26). Corrections were not made for extraction losses or solvent blanks which averaged .07 ± .01 ng (n = 30) for 10 ml of ether in the progestin assay. Pooled standard cow and steer plasma samples averaged .83 ± .03 and .09 ± .01 ng of progesterone per milliliter, respectively, for 25 assays. To 1 ml of steer plasma 500 pg of unlabeled progesterone was added; following extraction, values averaged 562 ± 29 (n = 33) pg per milliliter. Progestin antiserum was generously supplied by Dr. Finney Murray of Ohio State Agriculture Research Center. Significant cross reactivity of other steroids with the progestin antiserum was observed with 20 β-hydroxypregn-4-ene-3-one (100%), 20 α-hydroxypregn-4-ene-3, 20 dione (20%), 6 α-hydroxypregn-4-ene-3, 20 dione (7.9%) and 3 β, 20 β-dihydroxy-pregn-5-ene (2.1%). The minimum amount of detectable progesterone per tube was .2 nanograms. Coefficients of variation among 43 progesterone standard curves (100 to 2,000 pg) ranged from 10.3% at 500 pg to 15% at 2,000 picograms.

Extraction efficiency for 3H-estradiol from cow plasma and follicular fluid averaged 83 ± 1% (n = 15). Solvent blanks averaged 5.2 ± .6 pg (n = 26) for 7 ml of benzene used for extraction of estrogen from plasma and 2.8 ± .5 pg (n = 26) for 3 ml of benzene used to extract estrogen from follicular fluid. Corrections were made for solvent blanks and extraction efficiency. Estrogen antisera kindly donated by Dr. Burton V. Caldwell of Yale University cross reacted with estrone (87%), estriol (7%) and testosterone (2%). No cross reactivity was noted with progesterone or cholesterol at concentrations 1,000- and 5,000-fold, respectively, higher than the estradiol concentration at 50% displacement of labeled estradiol. Addition and extraction of 20, 60 and 100 pg of unlabeled estradiol to and from 1 ml samples of charcoal-extracted pooled cow plasma resulted in values of 37 ± 14, 62 ± 8 and 78 ± 4 pg (n = 5). Data were corrected for extraction losses. Minimum amount of detectable estrogen per tube was 3 picograms. Coefficients of variation among 11 estradiol standard curves (2 to 300 pg) ranged from 10.7% at 200 pg to 17.8% at 60 picograms.

**Results**

Of 180 heifers used in this study, 15 were eliminated for the following reasons: no reproductive tracts (n = 2), cystic corpora lutea (n = 4), cystic follicles (n = 2), died (n = 2) and pregnant (n = 5). Of the remaining 165 heifers, 19 had no identifiable corpora lutea or corpora albicantia. These heifers were considered immature and also eliminated from this study.

**Plasma Steroids.** As shown in table 2, mean concentrations of plasma progestins increased (P<.05) from days 1 through 17 then declined (P<.05). These changes were similar to values previously reported by many others (Dobson and Dean, 1974; Glencross et al., 1973; Lemon et al., 1975; Snook et al., 1971; Sprague et al., 1971; Wetteman et al., 1972). Since concentrations of estrogens were variable and only a limited number of samples were assayed, no differences (P>.05) in concentrations of estrogens were observed during different stages of the estrous cycle (table 2).

**Follicular Fluid Steroids.** Concentrations of progestins and estrogens were approximately 8- to 190- and 250- to 24,000-fold higher, respectively, in pooled samples of FF than plasma. As shown in table 3, progestins varied (P<.05) throughout stages of the estrous cycle in all

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### TABLE 2. MEAN CONCENTRATIONS OF PLASMA STEROIDS

<table>
<thead>
<tr>
<th>Stages of estrous cycle</th>
<th>Progestins (ng/ml)</th>
<th>Estrogens (pg/ml)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>x</td>
</tr>
<tr>
<td>I (1-4)†</td>
<td>30</td>
<td>1.5</td>
</tr>
<tr>
<td>II (5-10)</td>
<td>42</td>
<td>6.9</td>
</tr>
<tr>
<td>III (11-17)</td>
<td>52</td>
<td>7.8</td>
</tr>
<tr>
<td>IV (18-20)</td>
<td>22</td>
<td>1.2</td>
</tr>
</tbody>
</table>

a,b,c Different letter superscripts represent different means (P<.05).

† Estimated days of estrous cycle.
Concentrations of follicular progestins were highest (P<.05) between days 5 through 10 in follicles within the small range then declined (P<.05) steadily through days 18 to 20. In follicles within the medium range, progestins increased (P<.05) four-fold from days 1 through 10 and remained high during the remainder of the estrous cycle. Progestins were higher (P<.05) in follicles within the large range during days 1 to 10 than days 11 to 20. Overall, pooled values per pair of ovaries for progestins ranged from 4 to 884 ng/ml for follicles within the small range, 17 to 592 ng/ml for follicles in the medium range and 9 to 454 ng/ml for follicles in the large range. The overall mean ± SE concentrations (ng/ml) of progestins were higher (P<.05) in follicles in the small (178 ± 12, n = 137 heifers) and medium range (164 ± 21, n = 54) than follicles in the large range (124 ± 11, n = 84).

Correlations between changes in concentrations of progestins in plasma and FF were determined within stages of the estrous cycle. The changes in concentrations of FF progestins were correlated with changes in plasma progestins in small follicles during days 5 to 10 (r = .33, P<.05, n = 37) of the estrous cycle and in medium follicles during days 11 to 17 (r = .60, P<.01, n = 25). Changes in concentration of progestins in large follicles were not correlated (P>.10) with changes in concentrations of plasma progestins.

As shown in table 3 concentrations of follicular estrogens were greatest (P<.05) during days 1 to 10 in follicles in the medium range and days 1 to 4 and 11 to 20 in follicles within the large range. Overall, values for estrogens ranged from 4 pg/ml to 194 ng/ml in small follicles, 300 pg/ml to 257 ng/ml in medium follicles and 70 pg/ml to 257 ng/ml in large follicles. The overall mean concentrations of estrogens were higher (P<.05) in follicles in the medium (47 ± 14 ng/ml, n = 27) and large range (55 ± 8, n = 62) than small range (15 ± 3, n = 61).

The mean ratio of progestins to estrogens was approximately 12:1 in small follicles, 4:1 in medium follicles and 2:1 in large follicles. Correlations between changes in concentrations of estrogens in plasma and FF were not determined because of limited numbers of comparisons.

**Ovarian Weights:** Total ovarian weights increased (P<.05) from days 1 through 17 then declined (P<.05, table 4). The above results
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TABLE 4. MEAN WEIGHTS OF OVARIIES AND CORPORA LUTEA

<table>
<thead>
<tr>
<th>Stages of estrous cycle</th>
<th>Total ovarian weights</th>
<th>Weights of corpora lutea</th>
<th>Total ovarian weight minus corpora lutea weight</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n x ± SE</td>
<td>n x ± SE</td>
<td>n x ± SE</td>
</tr>
<tr>
<td>I (1-4)</td>
<td>30 9.8 ±.4a</td>
<td>22 1.00 ±.26a</td>
<td>22c 8.8 ±.5a</td>
</tr>
<tr>
<td>II (5-10)</td>
<td>42 11.8 ±.4b</td>
<td>42 3.35 ±.13b</td>
<td>42b 8.4 ±.4a</td>
</tr>
<tr>
<td>III (11-17)</td>
<td>52 13.2 ±.4c</td>
<td>50 3.61 ±.11c</td>
<td>50f 9.6 ±.4b</td>
</tr>
<tr>
<td>IV (18-20)</td>
<td>22 11.3 ±.6b</td>
<td>22 1.34 ±.14d</td>
<td>22e 9.9 ±.5b</td>
</tr>
</tbody>
</table>

a,b,c,d Different letter superscripts represent different means (P<.05).

e Eight newly formed corpora lutea could not be accurately removed and weighed and were not included in the analysis.

f Two corpora lutea were not weighed.

Most likely reflect cyclic changes in weights of corpora lutea and numbers and sizes of follicles. Therefore, changes in weights of luteal and nonluteal components of the ovary during the estrous cycle were examined.

Changes in weights of corpora lutea were highly correlated with changes in concentrations of plasma progesterins during days 1 to 4 (r = .77, n = 22, P<.01), but the correlation decreased markedly (P<.01) thereafter (days 5 to 10, r = .34, n = 42, P<.05; days 11 to 17, r = .30, n = 50, P<.05; days 18 to 20, r = .39, n = 22, P>.05). Fifty-one percent of the total number of heifers (n = 146) had corpora lutea on the left ovary. Weights of corpora lutea from right or left ovaries were not different (P>.10) but increased three-fold (P<.01) during days 1 to 10 and decreased (P<.01) 3-fold from days 11 to 20. When mean nonluteal weights of pairs of ovaries (ovarian minus CL weight) were compared during stages of the cycle, no change (P>.10) occurred from days 1 through 10. Thereafter, mean nonluteal weights increased (P<.05). In summary, these data suggested that cyclic changes in weights of corpora lutea influenced gross changes in total ovarian weights and that fluctuations in weights of nonluteal tissue (i.e., follicle numbers, size) occurred during the estrous cycle.

Volume of Follicular Fluid. Mean volumes (total volume collected divided by numbers of follicles) of follicles in the medium and large categories increased (P<.05) 130% and 180% from days 1 to 20 after ovulation. Over the same period follicles in the small category decreased (P<.05) in volume 170% (table 5). The overall mean volume (±SE) of FF per follicle was 19 ± .9 µl (n = 100) for follicles in the small range, 248 ± 9 µl (n = 57) for follicles in the medium range and 714 ± 40 µl (n = 91) for follicles in the large range. The overall mean total volumes of FF (±SE) aspirated from each pair of ovaries was 777 ± 50 µl (n = 100) for follicles in the small range, 338 ± 34 µl (n = 57) for follicles in the medium range and 752 ± 42 (n = 91) for follicles in the large range.

TABLE 5. MEAN VOLUMES (µl) OF FOLLICULAR FLUID PER FOLLICLE

<table>
<thead>
<tr>
<th>Stages of estrous cycle</th>
<th>Size of follicles</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small</td>
<td>Medium</td>
<td>Large</td>
</tr>
<tr>
<td></td>
<td>n x ± SE</td>
<td>n x ± SE</td>
<td>n x ± SE</td>
</tr>
<tr>
<td>I (1-4)d</td>
<td>20 25 ±2a</td>
<td>10 212 ±23a</td>
<td>9 611 ±59a</td>
</tr>
<tr>
<td>II (5-10)</td>
<td>31 16 ±2b</td>
<td>13 220 ±24a</td>
<td>37 615 ±32a</td>
</tr>
<tr>
<td>III (11-17)</td>
<td>31 21 ±2c</td>
<td>27 267 ±10b</td>
<td>31 673 ±44b</td>
</tr>
<tr>
<td>IV (18-20)</td>
<td>18 15 ±1b</td>
<td>7 279 ±15b</td>
<td>14 1121 ±195c</td>
</tr>
</tbody>
</table>

a,b,c Different letter superscripts represent different means (P<.05).

d Estimated days of estrous cycle.
Changes in volumes of follicles within the small, medium and large categories during the estrous cycle were not correlated with changes in concentration of plasma or follicular progestins or estrogens, except follicular progestins in small follicles between days 1 to 4 (r = .59, n = 19, P<.01) and days 5 to 10 (r = .36, n = 28, P<.05).

**Numbers of Follicles.** An increase (P<.05) in total numbers of follicles on the surface of the ovary occurred from days 1 to 20 (table 6) possibly explaining the increase in nonluteal ovarian weight also occurring during this period (table 4).

All heifers had follicles in the small range (<100 μl) during each stage of the cycle. The overall mean (±SE) number of follicles in this range per pair of ovaries was 40 ± 2, (n = 146). The percentage of heifers with follicles in the medium range (101 to 400 μl) was similar throughout the estrous cycle averaging 38% overall. However, the percentage of heifers with follicles in the large range (table 6) was lowest (30%, P<.05) between days 1 to 4 and highest between days 5 and 10 (88%) and 18 to 20 (73%). Overall, 64% of the heifers had follicles within the large range. Surprisingly, only 8% and 3% of the heifers (n = 146) had multiple follicles in the medium or large range, respectively, per pair of ovaries (data not shown).

Changes in the percentage of heifers with follicles in the medium and (or) large range (table 6) on either ovary or the same ovary varied during the estrous cycle. Overall, 13% of the cycling heifers had ovaries with follicles in the medium and large category per pair of ovaries, 6% had follicles in the medium and large category present on the same ovary and 89% had a follicle in the medium or large range present per pair of ovaries. No heifer had follicles in the medium and large range per pair of ovaries during days 1 to 4, which differed (P<.05) from the remainder of the cycle. Changes in total numbers of follicles per pair of ovaries were not correlated with changes in concentrations of plasma progestins but were negatively correlated with changes in concentrations of progestins in FF of follicles in the small range during days 1 to 4 (r = -.41, n = 29, P<.05), 5 to 10 (r = -.34, n = 38, P<.05) and 11 to 17 (r = -.31, n = 49, P<.05).

The possible effects of the corpus luteum on follicle development were examined by determining the numbers of heifers with and without follicles on the ovary with a corpus luteum

<table>
<thead>
<tr>
<th>Stages of estrous cycle</th>
<th>Total number of follicles per pair ovaries (mean ± SE)</th>
<th>Percentage heifers with at least one medium or large follicle</th>
<th>Percentage heifers with at least one medium and large follicle</th>
</tr>
</thead>
<tbody>
<tr>
<td>I (1-4)</td>
<td>30 ± 38</td>
<td>30a</td>
<td>30a</td>
</tr>
<tr>
<td>II (5-10)</td>
<td>42 ± 42</td>
<td>31a</td>
<td>31a</td>
</tr>
<tr>
<td>III (11-17)</td>
<td>52 ± 43</td>
<td>32a</td>
<td>32a</td>
</tr>
<tr>
<td>IV (18-20)</td>
<td>22 ± 46</td>
<td>30b</td>
<td>30b</td>
</tr>
</tbody>
</table>

a,b: Different letter superscripts represent different means (P < .05).
No relationship between corpora lutea and antral follicles occurred during the estrous cycle. Overall, 58% (n = 146) of the heifers had greater numbers of follicles within the small range on the ovary without a corpus luteum, 61% had follicles in the medium range and corpora lutea on the same ovary, 48% had follicles in the large range and corpora lutea on the same ovary, and 55% had follicles in the medium or large range and corpora lutea on the same ovary.

Discussion

Cyclic changes in weights of ovaries primarily resulted from independent changes in weights of corpora lutea and numbers and volumes of follicles. Weights of corpora lutea increased from days 1 to 17 then declined. In contrast, nonluteal ovarian weights increased from days 11 to 20. The tendency for decline in nonluteal ovarian weight during days 1 through 10 appeared to be the result of a marked decrease in size rather than numbers of follicles in the small range. The concentrations of follicular progestins and ratio of progestins to estrogens in follicles within the small range were also highest during this time. Perhaps, these follicles were undergoing atresia and regressing.

From days 1 through 10, follicles within the small range decreased in size but not numbers, while size of follicles and numbers of heifers with follicles in the medium range remained unchanged. In follicles within the large range, size remained unchanged yet numbers of heifers with follicles in this range increased. This may suggest that different size follicles respond differently to similar stimuli and that control of turnover of follicles differs among follicles within the small, medium and large categories.

Interestingly, Rajakowski (1960) reported that two growth waves of follicles occur in bovine ovaries. First, a large ovulatory-size follicle develops between days 1 to 12 and then undergoes atresia. Second, the ovulatory follicle begins development between days 12 to 13 and ends at ovulation. Our study suggests that few heifers (30%) have follicles in the large range between days 1 to 4 but most (80%) have follicles in this range after this time, also suggesting a growth wave. However, only one follicle in the medium or large range but not both are generally observed per pair of ovaries on any day of the cycle. Perhaps, large viable follicles secrete products (i.e. estrogens) that inhibit growth of new follicles until a large dominating follicle becomes atretic and disappears. Goodman et al. (1977) have proposed similar mechanisms in the monkey. Atresia and disappearance of follicles in the large range must be rapid in heifers since two follicles greater than 5 mm in diameter on the same ovary or on a pair of ovaries were rarely observed. Clearly, turnover of large antral follicles after day 10 of the estrous cycle in cattle is rapid. Dufour et al. (1972) marked largest and second largest follicles on ovaries of cattle during various days of the cycle. Only after day 18, did the largest follicle ovulate. Adelakoun (1977) also marked follicles during various days of the estrous cycle and concluded that turnover was much slower early in the estrous cycle than during the preovulatory time period. Two peaks of estradiol-17β occur in cattle, one during days 3 through 7 and another during days 18 through 21 (Glencross et al., 1973). The relationship of secretion of estradiol to growth and atresia (turnover) of follicles is not clearly understood.

During the estrous cycle changes in hormone concentrations in FF of follicles in the small, medium or large range were for the most part not correlated with changes noted in plasma concentrations of progestins. Perhaps maturing follicles synthesize steroids at different rates and control of steroid release in FF or plasma may be different from that in corpora lutea. Progestin concentrations were greater in follicles in the small than large range and estrogens were greater in follicles within the large range. As previously reported by Moor (1973) for sheep, large follicles apparently have the capacity (i.e., necessary enzymes) for estrogen synthesis, whereas, small follicles have limited ability to convert progestins to estrogens. Perhaps, follicular progestins are rapidly converted to estrogens by large mature follicles; whereas, small follicles which had the highest concentrations of progestin lack necessary enzymes for aromatization. Alternatively, capacity of follicles to synthesize estrogens regardless of size or maturity may be a function of whether that follicle is atretic (Moor et al., 1978).

Atresia is an acknowledged problem in interpretation of studies involving follicular development and steroid synthesis. The extreme variation in steroid concentrations from FF samples was similar to that reported by
others (Korenman et al., 1973; Sanyal et al., 1974) and may result from combining samples of FF from each pair of ovaries into only three categories (small, medium, and large). In addition, each follicle was not examined histologically for signs of atresia. Rajakowski (1960) has reported that the majority of bovine ovarian follicles are in various states of atresia and that atresia was most rampant during mid-cycle. In sheep, Moor et al. (1978) reported that FF from small (2 to 3 mm) and large (3.1 to 6 mm) normal follicles had approximately 8- and 25-fold higher concentrations of estrogens than atretic small and large follicles suggesting that atresia diminished the ability of follicles to produce estrogens.

Increasing concentrations of estrogens in the corpus luteum occurs in primates (Butler et al., 1975) and is involved in luteal regression (Karsch and Sutton, 1976). Although changes in luteal estrogens during an estrous cycle have not been clearly defined in cattle, estrogen binding proteins have been observed in bovine luteal tissue (Kimball and Hansel, 1974). It is tempting to speculate that follicular estrogens may have a direct effect on luteal function. Depending upon time during the cycle and dose, injections of estradiol can result in maintenance (Piper and Foote, 1968) or regression (Cook et al., 1974; Stormshak et al., 1973) of the corpus luteum in sheep.

Follicular fluid is not just a simple transudate of blood (Edwards, 1974). Although it could not be determined from this study whether fluctuations in concentrations of FF steroids reflected changes in plasma fluctuations of steroids, the extremely high concentrations of FF in luteal estrogens during an estrous cycle have likely that follicular progestins and estrogens may potentially be used as physiological indicators of follicular function in cattle.


Morgan, C. A. and I. D. Cooke. 1972. A comparison of the competitive protein binding assay and radioimmunoassay for plasma progesterone dur-

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