OVARIAN FUNCTION DURING THE ESTROUS CYCLE OF THE COW: OVARIAN BLOOD FLOW AND PROGESTERONE RELEASE RATE

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Summary

To study the function of the corpus luteum (CL) through its major secretory product, progesterone (P₄), catheters were inserted into the carotid artery (via the facial artery) and the ovarian vein (n = 12), and electromagnetic flow transducers were placed around the ovarian artery in cycling Angus and Hereford cows (n = 6). Blood samples were taken four times daily (at 0600, 1200, 1800 and 2400 h) and ovarian blood flow (OBF) was monitored for 60 min immediately after each blood sampling. After chromatography, P₄ was measured by radioimmunoassay. The P₄ concentrations in the ovarian vein (OP₄) were correlated with day of the estrous cycle (r = .25; P<.05) and were higher during the morning hours (P<.05). Arterial progesterone (SP₄) was correlated to OP₄ (r = .24; P<.05) and day of the cycle (r = .35; P<.05). The OBF changed among days (P<.05). The highest rates were noted during luteal maturation (23 ml/min; SE = .09) and the lowest were noted with the demise of the CL (SP₄<1 ng/ml) and approach of estrus (8 ml/min; SE = .07). The OBF was correlated with SP₄ (r = .24; P<.05), although no within-day trends were noted. Exogenous estrone (6 mg) administered via jugular vein decreased OBF within 30 to 45 min, but similar injections of P₄ (up to 100 mg) had no effect. Progesterone release (P₄ R) from the ovary [(OP₄ - SP₄) x OBF] was higher in the morning hours (P<.05). The P₄ concentration (OP₄, SP₄) and release (P₄ R) exhibited wide variations among and within days. The changes in OP₄ and P₄ R were both good indicators of CL development, maturation and regression, as associated with SP₄ changes. Oxygen (O₂) and carbon dioxide (CO₂) concentrations monitored in the carotid artery and ovarian vein indicated that the ovary with the CL was not limited in O₂ availability or CO₂ removal during periods of low blood flow or high secretion of P₄.

(Key Words: Cow, Ovarian Progesterone, Oxygen, Blood Flow.)

Introduction

Fluctuations of systemic progesterone (SP₄) concentrations (Donaldson et al., 1970; Schams et al., 1977) supposedly reflect ovarian release of P₄ and corpus luteum (CL) function in the cow, though this assumption is untested. Few preparations have been available for the study of sequential ovarian secretory measurements in the conscious animal where the effects of stress and anesthesia have been minimized. To monitor the ovarian venous effluent for secretory products may provide insight into ovarian function unavailable from systemic plasma, which constitutes a complex of secretion, metabolism and clearance by other organs and tissues. Until recently, lack of adequate methodologies inhibited the study of the relationships between ovarian physiological activity, hormonal secretion and the response and possible control of the ovarian vascular system.

The specific objectives of this study were to (1) establish a more precise relationship between systemic (SP₄) and ovarian progesterone concentrations (OP₄) as a measure of CL function, (2) analyze the metabolic relationship...
of secreted P₄, ovarian O₂ consumed and CO₂ produced and (3) investigate the relationships of ovarian blood flow with CL function, P₄ secretion and mechanisms of control of ovarian blood flow (OBF) in the cow.

Materials and Methods

Animals (n = 12) were selected randomly from a group of normally cycling Hereford and Angus cows (300 to 500 kg), housed in a 12 × 60 m pen and confined individually to a small room (1.3 × 3.5m) during periods when OBF was monitored.

Before surgery, ovaries were palpated per rectum for determination of the side of the CL, then the facial and flank area were clipped and washed with surgical soap, a cannula was placed into the jugular vein and the flank area was anesthetized with a paravertebral block (lidocaine⁹). Animals were led into the surgical area (5 to 10 d before CL regression), injected with sodium thiamylal⁹ (1 g/100 kg body weight) via the jugular catheter, intubated and maintained on a mixture of halothane¹⁰ (1.5%) and O₂ using a large animal anesthetic unit¹¹. The reproductive tract was exposed via a vertical flank incision just anterior to the paralumbar fossa. The tract was exteriorized and the ovarian vasculature observed for the location of the uterine branch anastomosis so that the cannula was not inserted into or beyond this point, but was instead maintained in the main anastomosed vein draining the ovary (Figure 1). A branch of the ovarian vein near the hilus was dissected from the adventitia and a small incision was made allowing a polyvinyl catheter¹² (.86 mm id × 1.52 mm od) to be introduced 2 to 5 cm into the vein. The cannula was exteriorized through the original flank incision and placed in a canvas pouch sutured to the side of the animal.

Facial Artery Cannulation. The facial artery (Figure 2) was selected for arterial blood samples because of its size and accessibility. The distal end of the catheter was exteriorized on the neck by running the catheter subcutaneously with a probe. This simplified sampling and eliminated annoyance to the animal.

Ovarian venous and carotid arterial blood samples (10 ml each) were collected four times

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⁹Mogal Corp., Chagrin Falls, OH.
¹⁰Surital, Parke-Davis, Detroit, MI.
¹²Fraser Sweatman Inc., Lancaster, NY.
¹³V6, Bolab Inc., Derry, NH.

Figure 1. Anatomy of the bovine ovarian vasculature and location of the venous catheter in the anastomosing ovarian vein and ovarian artery blood flow transducer.

Figure 2. Cannulation of the carotid artery via the facial artery located under the masseter muscle for collection of systemic blood samples.
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daily (0600, 1200, 1800 and 2400 h) in lightly
greased, heparinized glass syringes. Duplicate
.5-ml samples of blood were analyzed for O₂
and CO₂ by the volumetric method of Van
Slyke and Sadie (1921). Plasma was obtained
by centrifugation and stored at -20 C for
later analysis of P₄ in the ovarian vein (OP₄)
and the carotid artery (SP₄).

Blood Flow Measurements. In six of the 12
animals, a blood flow transducer was placed
around the ovarian branch of the uteroovarian
artery. A 2-cm section of the artery just above
the uterine anastomosis was dissected free of
peritoneum and a transducer of a size ensuring
a snug fit (1.5 to 2.0 mm) was placed around
the artery (figure 1) supplying the ovary that
contained the CL. The transducer cable was
sutured in place and the peritoneum closed
around the cable and transducer. The cable
connections were exteriorized via the flank
cision and placed in the canvas pouch sutured
to the animal's side. Since one of the objectives
was to correlate CL function with OBF and P₄,
only animals that ovulated on the ovary with a
blood flow transducer are reported here.

Flow transducers were calibrated in vitro
before use by the perfusion of fresh heparinized
ewe blood through a segment of a carotid
artery from a fetal lamb. The transducer was
placed around the artery in physiological saline
(.9% NaCl) and the rate of blood flow was
altered by air pressure changes (Wise, 1979).
Flow was calibrated by the collection of blood
in a graduated cylinder over a period of time,
monitored with a stop watch and compared
with the readings on an electromagnetic flow
meter . A calibration factor was established to
provide a linear flow response from .6 to 60
ml/min (y = .34 + .99x) as described by Roman-
Ponce et al. (1978). A physiograph was used
to monitor continuous changes in blood flow.
After removal from the animal, flow transducers
were rechecked for operation and accuracy and
were found to be capable of chronically operat-
ing for more than 60 d.

Blood flow was monitored for 60 min
starting at 0600, 1200, 1800 and 2400 h. To
attain a representative rate, the value assigned
for each period of blood flow (ml/min) was
determined by discarding the first 10 min of
recordings and averaging the next 24 min (one
observation/min).

Due to the potential damage to the catheter
and probe, behavioral estrus was not tested.
However, surgical manipulation did not alter
estrous cycle length as determined by (1)
palpation per rectum of the ovary and exhibition
of behavioral estrus following removal of the
OBF transducer, (2) decline in OBF and SP₄ to
less than 1 ng/ml and (3) the subsequent
increase in OBF and P₄. At the time of removal
of OBF transducer (generally 10 to 15 d into
the next cycle), cannula and transducer position
was confirmed and the uterus and ovary ap-
peared normal with a CL that was located on
the ovary associated with the transducer.

The immediate and short term effects of
exogenous P₄ and estrone on OBF were tested
before removal of the flow probes from animals
that had ovulated. Aqueous estrone suspension
(6 mg) was administered via the jugular vein
to three animals (two mid-luteal, SP₄ 5.6 and
8.1 ng/ml; cow no. 15 and 7, respectively, and
one late luteal SP₄ 2.4 ng/ml; cow no. 8). A
suspension of aqueous P₄ was administered
twice daily for 3 d to two animals (25 mg, cow
no. 7, and 100 mg, cow no. 11).

Progesterone Quantitation. The SP₄ was
extracted from 4 ml of carotid arterial plasma
twice with 15 ml of ether, after the addition of
1,000 dpm of [1,2,6,7-3H]--P₄ for recovery
purposes. Because only P₄ was measured in
systemic plasma, the extract was chromato-
graphed on a .5 x 7 cm LH-20 column with a
cyclohexane-benzene-methanol (90:5:5) sol-
vent system (figure 3a).

The OP₄ was extracted from 1 ml of ovarian
vein plasma twice with 10 ml of freshly glass-
distilled diethyl ether. Approximately 3,500
dpm of [1,2,6,7-3H]--P₄(SA 90 Ci/mmol)
were added to correct for procedural losses.
The aqueous phase was frozen in liquid N₂ and
decanted ether was evaporated to dryness under
N₂ at 40 C. The OP₄, androstenedione,
dehydroepiandrosterone and testosterone were
separated on a 1 x 25 cm Sephadex LH-20 column with cyclohexane-benzene-methanol
(90:25:5; figure 3b). Eluates were collected in
2-ml aliquots.

The P₄ was measured by radioimmunoassay
procedures similar to those described by

13 C & C Instruments, Culver City, CA.
14Narcomatic, Model RT-500, Narco Biosystems
Inc., Houston, TX.
15Model DMP-4B, Narco Biosystems Inc., Hous-
ton, TX.
16Ampoule, Eli Lilly Co., Indianapolis, IN.
17ESI Pharmaceuticals, Cherry Hill, NJ.
Figure 3. Sephadex LH-20 chromatography of (a) systemic progesterone (.5 × 7 cm; cyclohexane: benzene:methanol; 90:5:5) and (b) ovarian venous progesterone (1 × 25 cm; cyclohexane:benzene:methanol; 90:25:5).

Abraham et al. 1971; Antisera, S-49 #6). Modification in dilution of OP4 and SP4 for the radioimmunoassay were due to 100-fold differences in levels of OP4 and SP4 monitored from the ovarian vein and carotid artery. The chromatographed OP4 was diluted with 5 ml of phosphate buffer and analyzed in triplicate (100-, 50- and 25-μl aliquots removed from the original dilution and adjusted to 500 μl for assay). The SP4 was diluted in 4 ml of buffer and duplicate 500-μl aliquots assayed. In both cases, 500 μl were removed for the determination of procedural losses. After overnight incubation and removal of unbound steroid with dextran charcoal and centrifugation, a 600-μl aliquot was pipetted into minivials for scintillation counting.

Duplicate samples of ovariectomized cow plasma with standard amounts of P4 added (mass added, recovered ± SE, number, respectively: 200, 221 ± 14, 20; 600, 685 ± 17, 15; 1,000, 1,137 ± 31, 25; 2,000, 1,951 ± 11, 13; 5,000, 5,550 ± 137, 6; 8,000, 8,460 ± 222, 9) were extracted, chromatographed and quantified like SP4 and OP4, with each group of samples assayed. The pooled intra- and inter-assay coefficients of variation (Steel and Torrie, 1960) were 4.0 and 10.4%.

Statistical Analysis. Data were analyzed by least-squares multiple regression analysis (Barr and Goodnight, 1976) to obtain: (1) variation due to treatment (animals with or without flow transducers), day, time of day, treatment × day and treatment × time interaction; (2) least-squares polynomial regression equations for hormonal and physiological responses over days, and to (3) test the heterogeneity of regression between treatments for differences in changes over days in the physiological responses measured. Coefficients of correlation (gross, among and within animals) were determined for characteristics for general relationships. Chi-square analysis was utilized to detect large variations in hormonal changes (spikes) during the estrous cycle.

**Results**

We partitioned the analyses of OP4 concentrations into two groups (animals with and without blood flow transducers.) To determine if blood flow transducers affected hormones secreted, we compared OP4 concentrations of animals with and without blood flow transducers. Least-squares regression analysis revealed no differences in ovarian steroid concentrations between animals with or without blood flow transducers. Least-squares regression analysis revealed no differences in ovarian steroid concentrations between animals with or without blood flow transducers within day (0600, 1200, 1800 and 2400 h) or between days of the cycle. To reduce the influence of differences in estrous cycle length upon ovarian secretion, these data were adjusted to the day of luteal regression (d 0), when SP4 concentrations decreased below 1 ng/ml in two successive samples.

**Systemic Progesterone.** Presented in table 1 are the means of SP4 in all animals by day before and after luteolysis of the CL (r = .35; P<.05). The SP4 was correlated positively with OP4 (r = .24; P<.05) and differed between cows with and without blood flow probes. However, further analysis revealed these SP4 differences could be attributed to low SP4 from 9 to 13 d before CL regression in a single animal in the group without flow transducers. The fifth-order regression curve fitting the SP4 concentrations for both groups is depicted in figure 4b. Arithmetic means for each period have been included to show the trends and variability in SP4 levels. No differences were detected in SP4 within day.

**Ovarian Vein Progesterone.** Concentrations of P4 in the ovarian vein (ovarian branch) were highest during the luteal phase, but noted in all
<table>
<thead>
<tr>
<th>Day before and after luteal regression</th>
<th>SP&lt;sub&gt;4&lt;/sub&gt; (μg/ml)</th>
<th>OBF (ml/min)</th>
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<tbody>
<tr>
<td>No. b</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
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</tr>
<tr>
<td>-13</td>
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<td>9</td>
<td>687 to 1,490</td>
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<td>7</td>
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<td>6</td>
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<td>1</td>
<td>5</td>
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</tr>
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<td>2</td>
<td>4</td>
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</tr>
<tr>
<td>3</td>
<td>3</td>
<td>1,150 to 2,177</td>
</tr>
<tr>
<td>4</td>
<td>2</td>
<td>1,200 to 2,177</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>1,210 to 941</td>
</tr>
</tbody>
</table>

Note: OBF values are presented for the following range: 23 to 26.

4 Day of luteal regression was the day when two successive samples of SP<sub>4</sub> fell below 1 ng/ml.

Number of observations: Data from 12 cows with parent camels.

*Data from six cows with parent camels and ovarian blood flow transducers.
Figure 4. Least-squares regression and arithmetic means by day for all cows (n=12) (a) ovarian progesterone and (b) peripheral progesterone.

stages of the estrous cycle. Depicted in figure 4a are the regression curve and arithmetic means, while table 1 lists the mean levels of $P_4$ detected in the ovarian vein on each day ($r = .25; P<.05$) in all animals. The OP$_4$ was highest during the morning hours (724.5 ng/ml, SE = 53.2) and decreased towards the evening hours (649.0 ng/ml, SE = 47.6; P<.05).

Ovarian Blood Flow. Representative physiographic recordings of mean OBF and the arterial pulse wave are shown in figure 5. Blood flow to the ovary with the CL is presented over day in table 1. Blood flow to the ovary was highest when $P_4$ concentrations were high and decreased during luteal regression (table 1, figure 6). Blood flow remained low throughout the period of functional luteolysis, but increased with the development of the CL for the next cycle. Depicted in figure 6a are changes in OBF in individual animals. Some animals exhibited dramatic OBF changes at luteal regression, while others showed a more gradual decrease. Blood flow did not change significantly within day, but did change significantly between days

Figure 5. Representative physiographic recordings of mean ovarian blood flow accompanying arterial pulse wave from three different cows.

Figure 6. Ovarian blood flow (a) arithmetic means for three representative animals by day and (b) least-squares regression and arithmetic means by day of all cows (n=6).
Ovarian Blood Flow and Progesterone Release Rate

The administration of estrone resulted in a sharp decrease in OBF within 30 to 45 min (figure 7a). This was the only time that a decline in blood flow was observed during a single observation period. Progesterone administered twice daily for 3 d in two cows with low OBF (figure 7b) produced no measurable responses.

**Oxygen and Carbon Dioxide in the Carotid Artery and Ovarian Vein.** Differences in O$_2$ and CO$_2$ content in the carotid artery and ovarian vein (table 2) were small. Arterial venous blood gas differences on d -13 to -9 were tested against d - 7 to 0 and no differences were noted.

**Progesterone Release.** Rate of release of P$_4$ from the ovary was calculated by multiplying OBF and OP$_4$-SP$_4$ (table 3). Shown in figure 8 are the regression (P<.05) curve and arithmetic means for P$_4$ release. A diurnal pattern was also noted for P$_4$R (am>pm, P<.05).

**Discussion**

**Progesterone Changes during the Period of Luteal Function.** Changes in SP$_4$ generally reflect changes in OP$_4$ (r = .24; P<.05) and P$_4$R (r = .34; P<.05). Trends in SP$_4$ concentrations were similar to those described in the literature (Donaldson et al., 1970; Schams et al., 1977).

Concentrations and fluctuations of OP$_4$ were similar to those described by Gomes et al. (1963) and Dobrowolski et al. (1968). Fluctuations in OP$_4$ noted between 6-h periods were much more abrupt than those of OBF within individual animals. The wide fluctuations seen with OP$_4$ in individual cows may be indicative of an episodic release of steroids. Such an episodic type of release has been observed for estradiol and P$_4$ in cows bled from the ovarian vein every 15 min (M. J. Fields and D. Caton, unpublished data); an episodic release of P$_4$ by the ovary was noted also in the ewe (Baird et al., 1976).

While OP$_4$ and P$_4$R in individual animals changed within day (am>pm), there were no diurnal patterns detected for SP$_4$ or OBF. The absence of a diurnal pattern may be related to the wide fluctuations within animals, which may be influenced not only by changes in secretion, but also by clearance rates. A proestrus (d -4 to 0) increase in progesterone metabolic clearance rate (Wise, 1979) may have aided in clearing the P$_4$ from the systemic circulation in conjunction with the decline in P$_4$R with the demise of the CL.

Relationships during the cycle of SP$_4$, OP$_4$ and P$_4$R are not unknown, but these data present a unique analysis, establishing the common interrelationships of ovarian vein P$_4$ concentration, P$_4$ release and systemic P$_4$ concentrations over the period of luteal function. This analysis did establish that SP$_4$, OP$_4$ and P$_4$R all followed CL development, maturation and regression in an expected manner and, more importantly, that SP$_4$, OP$_4$ and P$_4$R changed temporally. The only discernible difference between SP$_4$ and OP$_4$ was a diurnal pattern for OP$_4$ (am>pm) that was not detected for SP$_4$.

Ovarian Blood Flow during the Bovine Estrous Cycle. Blood flow to the bovine ovary was highest during the luteal phase, decreased with luteal regression and reached a nadir just before the time of expected ovulation. The OBF then increased with the establishment of the newly developing CL. The decline in blood
### TABLE 2. OXYGEN (O₂) AND CARBON DIOXIDE (CO₂) CONTENT IN THE CAROTID ARTERY AND OVARIAN VEIN BEFORE FUNCTIONAL LUTEOLYSIS

<table>
<thead>
<tr>
<th>Days before luteal regression</th>
<th>Arterial O₂&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Venous O₂&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Arterial CO₂&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Venous CO₂&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No.</td>
<td>Mean</td>
<td>Range</td>
<td>Mean</td>
</tr>
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<td>−13</td>
<td>4</td>
<td>17.1</td>
<td>16.6 to 17.5</td>
<td>15.1</td>
</tr>
<tr>
<td>−12</td>
<td>8</td>
<td>16.6</td>
<td>15.5 to 17.6</td>
<td>14.4</td>
</tr>
<tr>
<td>−11</td>
<td>8</td>
<td>15.1</td>
<td>13.0 to 16.4</td>
<td>13.6</td>
</tr>
<tr>
<td>−10</td>
<td>5</td>
<td>14.9</td>
<td>12.8 to 16.3</td>
<td>14.2</td>
</tr>
<tr>
<td>−9</td>
<td>4</td>
<td>13.8</td>
<td>13.1 to 15.1</td>
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<td>−7</td>
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<tr>
<td>0</td>
<td>6</td>
<td>14.0</td>
<td>12.7 to 15.0</td>
<td>12.7</td>
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</table>

<sup>a</sup>Volume percentage of gases.

<sup>b</sup>Number of observations.
flow appeared to follow the abrupt decline in SP₄ \( (r = .24; P < .05) \) noted at the time of CL regression. It is not known which of these variables decreased initially. Changes in OBF during the follicular and luteal phases were variable and, in this manner, were similar to the 80 to 300% fluctuations reported for the ewe by Niswender et al. (1975) and Nett et al. (1976).

The control of OBF may be explained by changes in concentrations of \( \text{O}_2 \) or \( \text{CO}_2 \) diffusing or shunting across the venous membranes into the ovarian artery, which is located on the surface of the ovarian vein. This could result in a local control of OBF as determined by the metabolic needs of the ovary. The high rate of blood flow to the ovary noted in this study, however, suggested little deficiency in \( \text{O}_2 \) availability or \( \text{CO}_2 \) removal. Analysis revealed a limited role for \( \text{O}_2 \) and \( \text{CO}_2 \) (less than 10% arterial-venous difference in \( \text{O}_2 \) or \( \text{CO}_2 \)) in the regulation of OBF (table 2).

High blood flow at a time of relatively high concentrations of \( \text{P}_4 \) in the systemic plasma and low blood flow during the assumed follicular stage, when the animal is under the expected influence of estrogens, may be more than coincidental. Examination of data for individual animals revealed that blood flow and \( \text{P}_4 \) declined and increased concurrently at a similar percentage rate. Consequently, one may speculate that the relationship of CL function and its control over OBF may occur through its secretion of \( \text{P}_4 \). However, in cows with low OBF, exogenous administration of \( \text{P}_4 \) did not affect ovarian blood flow. Although these are only preliminary data, they do suggest that \( \text{P}_4 \) is not the dominant modulator of OBF; alternatively, the influence of \( \text{P}_4 \) on blood flow could depend on the stage of the estrous cycle.

The OBF could be regulated by estrogen from developing ovarian follicles (Wettemann et

<table>
<thead>
<tr>
<th>Days before luteal regression</th>
<th>No.ᵃ</th>
<th>SP₄ (ng/ml)</th>
<th>P₄ R (ng/min)ᵇ</th>
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<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>Range</td>
</tr>
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<td>-1</td>
<td>4</td>
<td>2.4</td>
<td>.7 to 3.3</td>
</tr>
<tr>
<td>0</td>
<td>4</td>
<td>.5</td>
<td>.4 to .6</td>
</tr>
</tbody>
</table>

ᵃNumber of observations in animals with ovarian blood flow transducers.
ᵇ\( P₄ \) R = (ovarian progesterone-systemic progesterone) \( \times \) blood flow.
al., 1972), which may cause a decrease in OBF at the time of a simultaneous decline in P4 and presumably a regression of the CL from the preceding estrus. In support of estrogen control of OBF, exogenous estrogen decreased OBF within 30 to 45 min of administration. A lack of sustained estrogen production from growing follicles undergoing atresia during the luteal phase, concurrent with high P4, may allow for passive maximum blood flow to the ovary, during CL development and maturation.

However, the vascular responses noted in the ovary from steroid modulation in this study and others (Abdul-Karim and Bruce, 1973; Niswender et al., 1975; Nett et al., 1976; Wehrenberg et al., 1977) are opposite to those reported for blood flow to the uterus. Blood flow to the uterus of a number of species is highest during the follicular phase and lowest during the luteal phase (Dickson et al., 1969; Greiss and Anderson, 1969; Moor and Bruce, 1976; Eley, 1980; Ford and Chenault, 1981). Exogenously administered estrogen and P4 mimicked vascular changes found in the uterus during the estrous cycle (Greiss and Anderson, 1970; Huckabee et al., 1970; Killam et al., 1973; Caton et al., 1974; Resnik et al., 1974; Roman-Ponce et al., 1978). Changes in OBF may be closely related to uterine blood flow and each may complement the other, depending on the endocrine status.

It has been suggested that the large uterine branch of the ovarian artery (figure 1) provides some portion of the ovarian arterial blood supply (Del Campo and Ginther, 1972, 1973; Lamond et al., 1973; Ginther et al., 1974; Lamond and Drost, 1974; Ford and Chenault, 1981). Analysis of the direction of flow through the uterine branch of the ovarian artery (Ginther et al., 1974; Ford and Chenault, 1981) indicates that blood may flow in both directions, depending on the stage of the estrous cycle or hormonal status. Vasocostriction of the ovarian artery (ovarian branch) from the effects of estrogen may increase shunting of blood flow to the uterus, which would produce an increase in blood flow to the uterus and a decrease in blood flow to the ovary. The vasocostrictive properties of P4 on the uterine arteries could have the opposite effect upon the ovarian vasculature and shift blood flow to the ovary during the luteal phase. If in fact, arterial blood from the uterus is flowing to the ovary (under P4 influence), this could provide another model for the potential influence of uterine secreted products on OBF (Ford et al., 1977). Shunting of OBF to the uterus (under the influence of estrogen from the latest estrus) may also provide the answer why prostaglandin P2 alpha is not luteolytic to the developing CL during the first 5 d of the bovine estrous cycle (Hafs et al., 1974).

**Literature Cited**


