

Effect of Expected Peripheral Concentrations of Progesterone on Ovulation Rate and Litter Size in Barbados Blackbelly Ewes¹

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¹ Published with the approval of the Director of the West Virginia Agricultural and Forestry Experiment Station as Scientific Paper No. 3029. Supported by Hatch Project 427 (NE-1007). This work was done in partial fulfillment of requirements for the M.S. degree (EHD) in reproductive physiology at West Virginia University.

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Acknowledgements

The sheep and reagents were provided by the Ministry of Agriculture and Rural Development, Graeme Hall, Christ Church, Barbados. The authors thank the Ministry, the staff of the Greenland Livestock Research Station, Greenland, St. Andrew, Barbados (where Ezra Devonish is the Agricultural Officer) for animal care and assistance in treatment, and the late Dr. George Seidel of the West Virginia Agricultural and Forestry Experiment Station for advice and assistance in statistical analyses.

Summary

To determine whether luteal phase concentrations of progesterone (P_4) altered ovulation rate and litter size in ewes, mature Barbados Blackbelly ewes were assigned to groups treated so that they would be expected to have low, medium or high P_4 ($n = 23$ or 33 per group in two seasons). Each ewe on low and high P_4 received a P_4 -containing intravaginal insert from d 4 through d 14 after estrus. Ewes in low group were given $PGF2\alpha$ on d 6 to regress corpora lutea (CL). Ewes with medium P_4 were untreated. Ovaries in 10 or 8 ewes per group (in seasons 1 and 2, respectively) were observed by transrectal ultrasonography from d 6 of the pre-breeding cycle until ovulation, and in all ewes on d 7 after breeding (one ram to 10 to 16 ewes). Numbers of follicles that disappeared at estrus ($P < 0.02$) and of CL

formed ($P < 0.001$) increased linearly with decreasing P_4 . As P_4 decreased, more follicles disappeared from the penultimate than the final wave of development. Disappearance of follicles was correlated with CL formed (0.53 ; $P < 0.0001$). Conception rates did not differ with expected concentration of P_4 . Lambs born per CL decreased linearly ($P < 0.001$) with decreasing concentrations of P_4 . Prolificacy did not differ ($P > 0.32$) among ewes treated to have low, medium or high concentrations of P_4 (2.0, 1.9, and 1.9 ± 0.1 lambs, respectively), despite greater ovulation rates. On a practical basis, altering progesterone before breeding did not change productivity of the ewe in terms of number of lambs born.

Key Words: Barbados Blackbelly, Ovulation Rate, Progesterone, Prolificacy, Ewe, Sheep

Introduction

Patterns of follicular development and ovulation rates in ewes have varied with dosages of exogenous progestogens (Robinson et al., 1968; Allison and Robinson, 1970), an effect probably mediated by regulation of tonic secretion of luteinizing hormone (LH; Baird and Scaramuzzi, 1976). In anestrous ewes induced to ovulate by introduction of rams, prior treatment with progesterone appeared to increase ovulation rate compared to ram introduction alone (Knights et al., 2001). More follicles were recruited early and late in the estrous cycle, periods when concentrations of progesterone are low (Brand and de Jong, 1973; Schrick et al., 1993). Bartlewski et al. (1999) found an inverse association of ovulation rates with concentrations of progesterone across breed types, with greater progesterone and fewer ovulations in western white-faced ewes and less progesterone and more ovulations in Finnsheep ewes.

Ewes exposed to low concentrations of progestogens had greater pulse frequencies of LH and concentrations of estradiol, and ovulated older and sometimes had more follicles than control ewes (Johnson et al., 1996; Levya et al., 1998; Viñoles et al., 1999; Bartlewski et al., 2003). These findings might explain reduced pregnancy rates in ewes on low concentrations of progestogens observed by some authors (Johnson et al., 1996; Viñoles et al., 1999), but not by others (Evans et al., 2001), as well as differences in pregnancy rates among exogenous progestogens (Crosby et al., 1991).

In the present study, patterns of follicular development and ovulation and lambing rates were investigated after experimental manipulation of concentrations of progesterone in cycling ewes of a relatively prolific breed, Barbados Blackbelly, in Barbados, where seasonal breeding is not expressed in non-lactating ewes of the breed (Patterson, 1983). The aim was to test the null hypothesis that concentrations of progesterone did not affect numbers or ages of follicles that ovulated or subsequent litter size.

Materials and Methods

The experiment was conducted in Barbados (latitude 10° north) with 168 Barbados Blackbelly ewes in two seasons.

Sixty nine ewes were studied in the dry season (December 2003, season 1) and 99 different ewes were studied in the wet season (July 2004, season 2). The ewes had average ages of 2.5 yr, parities of 1.8, and BW of 43 kg, which did not differ among groups or between seasons. Ewes were penned in an enclosed barn and received a daily ration of 2 kg of concentrates (corn and soybean meal formulated to contain 18 percent crude protein plus minerals), with water and pangola hay available ad libitum.

Ewes were randomized among three groups of 23 or 33 ewes each for seasons 1 and 2, respectively. Ewes in these groups were expected to have low, medium, or high progesterone as a result of treatment. All ewes were treated twice, 8 d apart, to synchronize estrus before the study, each time with two injections of 5 mg PGF₂ α (Lutalyse®, Pfizer Animal Health, New York, N.Y.) 3 h apart (Hawk, 1973). Ewes that would be expected to have medium progesterone received no further treatment; progesterone in those ewes was provided by the corpora lutea (CL) in their ovaries. Each ewe assigned to low progesterone received a progesterone-containing insert (Controlled Internal Drug Releasing Device [CIDR-G; InterAg, Hamilton, New Zealand] containing 0.3 g of progesterone) on d 4 after the synchronized estrus and was given PGF₂ on d 6 (as in the estrous synchronization protocol) to regress the CL and remove endogenous progesterone. These ewes were expected to have low circulating concentrations of progesterone throughout the luteal phase (Van Cleeff et al., 1998). Ewes in the high progesterone group received a CIDR on d 4 to provide additional progesterone to that produced by the CL. In each group, the CIDR was removed on d 14. Because the study was conducted in Barbados, it was not possible to conduct radioimmunoassays to determine exact concentrations of progesterone in peripheral blood. Biological response, as indicated by interval from removal of the CIDR insert to estrus, was used to confirm that concentrations of progesterone differed as expected.

Breeding Soundness Examination, Ram Introduction and Observation for Estrus

A breeding soundness examination

(testicular size, sperm concentration and motility; Salamon, 1976) was performed on six Barbados Blackbelly rams, to verify that each was in breeding condition. On d 7 after estrus, a Sire-Sine® harness with a crayon in the area of the brisket was placed on each of the rams and the rams were allotted to six pens. Each 5 x 9 m pen contained 5 or 6 ewes from each group, for a maximum ewe-to-ram ratio of 17:1. Ewes were observed on d 7 through d 21 at 6:00 a.m. and 6:00 p.m. for crayon marks. Time and date of observed estrus were recorded to determine the interval from CIDR removal to post-treatment estrus (marked by a ram; 0.5 d increments). Once each day, after observation for estrus, crayons on the briskets of the rams were replaced with a different color to distinguish ewes that subsequently came into estrus and to ensure that crayon marks were visible.

Observations of Follicular Development and CL

Follicles in the ewe develop at least in part in wave-like patterns, with cohorts growing beyond 3 mm in diameter approximately every four days during the estrous cycle (e.g., Ginther et al., 1995). Follicles that ovulate normally come from the final and the penultimate (next to last) wave (Bartlewski et al., 1999; Gibbons et al., 1999). Thus, it was of interest to determine whether any change in ovulation rate was due to retention of older follicles or recruitment of more follicles in the final follicular wave. Follicular development was observed by transrectal ultrasonography using an Aloka 500 SSD (Corometrics Medical Systems, Wallingford, Conn.) equipped with a 7.5 MHz linear-array transducer, as described by Schrick et al. (1993). Ultrasonographic observations were done by two operators in season 1, but by only one operator in season 2. Ovaries of 10 ewes per group in season 1 and of 8 ewes per group in season 2 were scanned daily from d 6 through subsequent estrus and ovulation (up to d 18 for some ewes). Ovarian follicular diameters were measured and recorded in three categories; small (2 to 3 mm), medium (4 to 5 mm), and large (\geq 6 mm), and their relative positions and those of CL were recorded on an ovarian map.

Data recorded included numbers of

small, medium and large follicles; day of emergence of each ovulatory follicle; and maximum size of each ovulatory follicle prior to ovulation. After estrus, follicles ≥ 4 mm were recorded as ovulated if not observed on the ovary at the subsequent scanning (Schrick et al., 1993). Growth rates of follicles were determined by retrospective comparisons of the follicle sizes recorded up to the point of plateau in diameter or ovulation. The interval (d) from appearance (at 2 or 3 mm in diameter) to disappearance was termed the life span of the follicle. Follicles that were first detected at 4 mm were recorded as 3 mm on the previous day, because average growth rate approximates 1 mm/d (Schrick et al., 1993). The interval from CIDR removal to ovulation was measured from these observations. Ovulation rate was confirmed by the number of CL observed by ultrasonography 7 d after estrus.

Lambing dates and numbers of lambs born were recorded. Conception rate was determined by ewes lambing, as a percentage of ewes in estrus. Pregnancy rate was measured as the percentage of ewes treated that lambed. Prolificacy was expressed as the number of lambs born per ewe that lambed. Lambing rate was defined as lambs born per ewe treated, and lambs born per CL (counted on d 7) also was evaluated.

Statistical Analysis

The basic statistical model used throughout was a two-way analysis of variance or categorical analysis (Chi-square) comparing values in ewes among the three expected concentrations of progesterone, and the two seasons in which the study was conducted. When significant differences were detected by analysis of variance, differences among individual groups were evaluated by Duncan's multiple range test. Transformations were utilized when the raw data were not normally distributed. Linear and quadratic components of the variance were tested when appropriate for continuous variables. All analyses were conducted using SAS version 8.1 (SAS Inst. Inc., Cary, NC). Comparisons of the intervals from CIDR removal to estrus or to ovulation and the growth rate of follicles in the final and penultimate waves utilized Poisson regression in the GENMOD procedure, because

the data followed a Poisson distribution. Average diameter of all ovulatory follicles and growth rates of follicles were analyzed with ANOVA using the MIXED procedure. Counts of follicles were transformed to square roots for analyses. Numbers of follicles in each size class per day and numbers of ovulatory follicles were compared in GENMOD using Poisson regression: in these analyses the model included day as a repeated measure within ewes. The effects of expected progesterone on the numbers of small (2 to 3 mm), medium (4 to 5 mm), large (≥ 6 mm) and total follicles during d 6 through d 14 were determined. Conception and pregnancy rates were examined by Chi-square analyses using the FREQ procedure. Lambs born per CL and per ewe lambing (prolificacy), and partial embryonic loss were compared in GENMOD using logistic regression. Numbers of follicles in the final and penultimate waves and the interval (d) that each follicle was observed were examined using analysis of variance in the MIXED procedure. Effects of expected progesterone on proportions of disappearing large (ovulatory) follicles arising from the final and penultimate follicular waves were examined by Chi Square. A correlation coefficient was calculated to examine the relationship between numbers of CL formed and numbers of follicles that disappeared.

Results and Discussion

None of the variables examined differed between seasons or revealed interactions of season with expected concentration of progesterone. Therefore all data are reported as means over both the dry and wet seasons.

Intervals to Estrus and Ovulation

The percentage of ewes marked by rams (mean 90 percent) and the percentage of scanned ewes observed to ovulate (mean 85 percent), did not differ with expected concentration of progesterone. Intervals from removal of the CIDR to estrus exhibited a quadratic pattern ($P < 0.005$) over groups expected to provide increasing concentrations of progesterone (low 1.5 ± 0.1 , medium 2.2 ± 0.2 and high 1.9 ± 0.1 d, respectively). Likewise, intervals from CIDR removal to ovulation increased

linearly ($P < 0.05$) with increasing expected concentrations of progesterone (2.0 ± 0.3 , 2.9 ± 0.6 and 3.2 ± 0.2 d, respectively). These data, in agreement with those of Deaver et al. (1986), confirmed that the treatments applied altered progesterone in the manner expected.

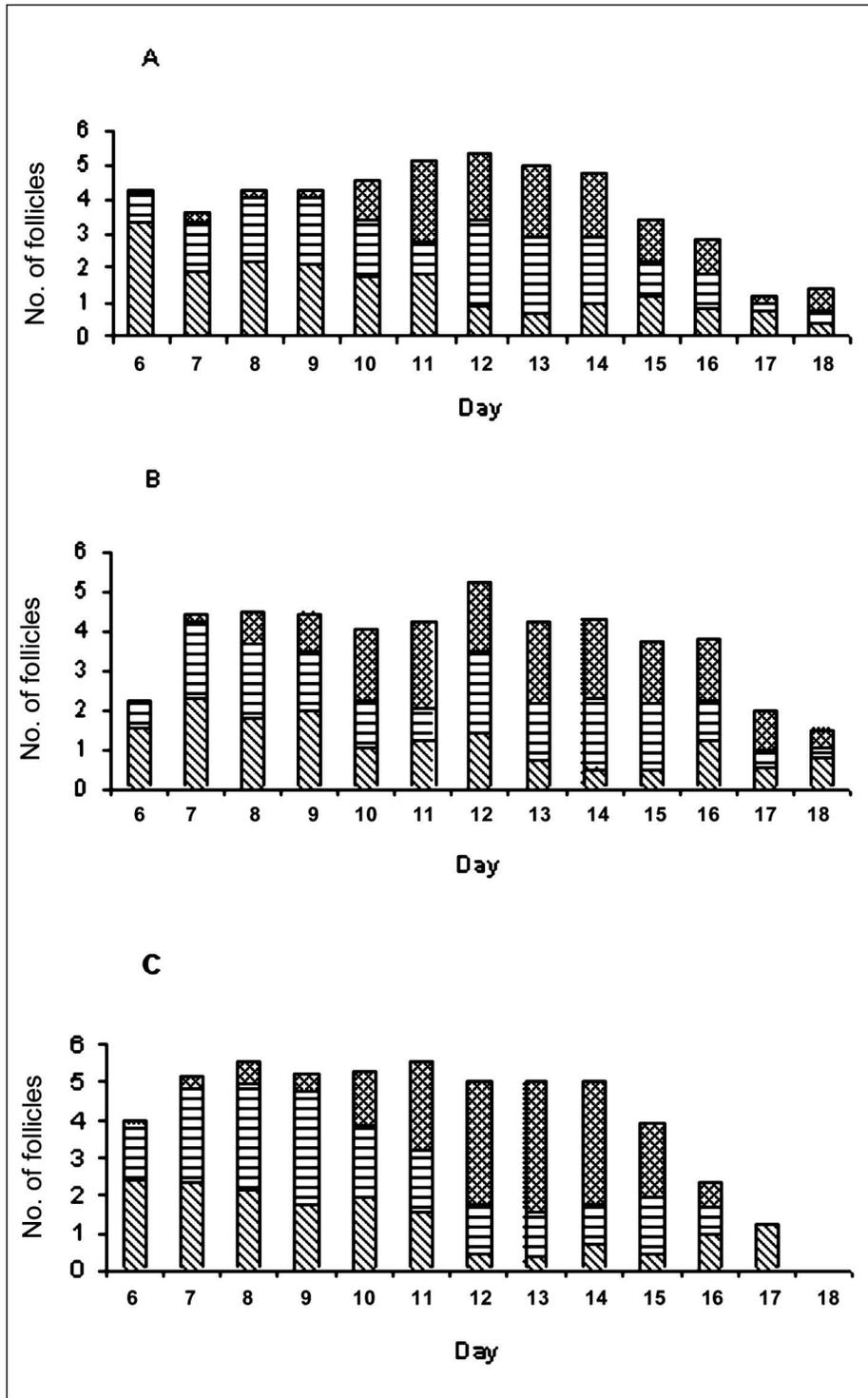
Numbers of Follicles, Growth Rates, and Lifespan of Ovulatory Follicles

Numbers of large (≥ 6 mm in diameter) and medium (4 to 5 mm) follicles present during d 6 to d 14 varied, and the pattern differed, as indicated by the day \times expected progesterone interaction ($P < 0.0001$), but number of small (2 to 3 mm) follicles did not differ (Figure 1). A day \times expected progesterone interaction was observed for total number of follicles on the ovary ($P < 0.001$; Figure 1). Specifically, numbers of medium follicles on d 6 through d 9 and of large follicles on d 9 through d 13 increased as concentrations of progesterone decreased.

Last diameters of ovulatory follicles did not differ among expected concentrations of progesterone (4.8 ± 0.6 mm). In contrast, Johnson et al. (1996) observed that diameters of ovulatory follicles were greater in ewes that had concentrations of progesterone < 1 ng/mL from d 6. In the present study, growth of follicles in the penultimate wave might have been limited by relatively greater concentrations of progesterone during the mid- to late-luteal phase of the cycle. In comparison, most growth of ovulatory follicles from the final wave occurred during the very late luteal and follicular phases of the estrous cycle, when progesterone concentrations were waning and frequency of pulsatile secretion of LH would have increased.

Mean intervals from detection at 2 or 3 mm to ovulation were 9.0 ± 0.2 and 5.0 ± 0.3 d for ovulatory follicles of the penultimate and final waves, respectively ($P < 0.05$). Mean intervals that ovulatory follicles from both waves were present prior to ovulation increased linearly ($P < 0.05$) as concentrations of progesterone decreased (5.7 ± 0.6 , 7.6 ± 0.6 and 8.1 ± 0.2 d for ewes with high, medium and low progesterone, respectively). Thus, follicles from the penultimate wave were an average of 4 d older at ovulation than follicles from the final

Figure 1. Numbers of total follicles (height of each bar at each day) and numbers in each size class summed over both ovaries (diagonal bars - 2 and 3 mm [small]; horizontal bars - 4 and 5 mm [medium]; and cross hatched - ≥ 6 mm [large]) on d 6 through estrus and ovulation (up to d 18) in ewes with expected high (A), medium (B), or low (C) progesterone. Numbers of medium, large, and total follicles varied with the day by expected progesterone interaction ($P < 0.001$, 0.001 , and 0.0001 , respectively). Note the patterns by which follicles moved from smaller to larger categories as the cycle progressed and that more large follicles were present later in the cycle in groups with expected lower progesterone. Then as ewes returned to estrus, the total number and the numbers of medium and large follicles decreased due to ovulation.



wave, and ovulatory follicles were retained on the ovary for about 1.5 d longer in ewes with low concentrations of progesterone than in ewes with high or medium progesterone. Similarly, in earlier studies, lifespan of the largest follicles in the penultimate wave (Bartlewski et al., 1999) or that arose earlier (Johnson et al. 1996) was increased, which allowed them to ovulate with follicles from the final wave.

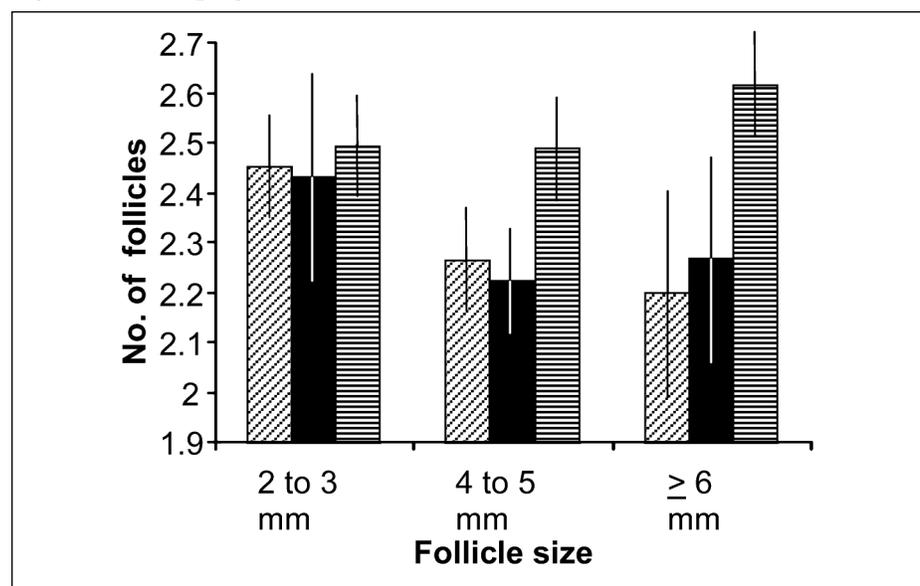
Ewes with low progesterone had more ($P < 0.01$) medium and large follicles prior to ovulation than ewes with high or medium concentrations of progesterone (Figure 2). Follicles from the penultimate wave that disappeared after estrus had grown more slowly (0.7 ± 0.1 mm/day) than those from the final wave (0.9 ± 0.1 mm/d; $P < 0.05$). However, mean growth rates of follicles that disappeared after estrus did not differ with expected progesterone within either wave, or for both waves combined (high, 0.7 ± 0.1 , medium, 0.8 ± 0.1 , low, 0.6 ± 0.2 mm/d).

In cows, lower progesterone led to increased pulse frequency of LH, maintenance of dominant follicles, and greater secretion of estradiol (Stock and Fortune, 1993; Kinder et al., 1996). Taft et al. (1996) found that frequent injections of bovine LH during normal luteal phases maintained the largest (dominant) follicle and suppressed recruitment of other follicles in cows. Although follicles are recruited in the ewe despite the presence of other large follicles (Duggavathi et al., 2003, 2005), follicles in the penultimate wave might have been protected from atresia by a greater frequency of secretion of pulses of LH in ewes with lower concentrations of progesterone (Johnson et al., 1996 and Van Cleeff et al., 1998). In contrast, more follicles in the 2-mm to 5-mm classes during the mid-luteal phase were observed in Merino ewes with 2 CL than in ewes with 1 CL (Turnbull et al., 1978).

Ovulation Rates

As shown in Table 1, the increase in ovulation rate as progesterone decreased was clearly due to greater persistence of follicles from the penultimate wave. The proportion of disappearing large follicles that came from the penultimate wave increased from 36.3 percent in the high progesterone group to 53.7 percent in

Figure 2. Mean (\pm SEM) numbers of follicles in each size class on the day prior to ovulation by expected concentrations of progesterone (diagonal bars - high; solid bars -medium; horizontal bars - low). Numbers of medium and large follicles were greater in ewes with expected low progesterone than in ewes with expected high or medium progesterone ($P < 0.01$).



ewes on medium progesterone and 76.7 percent in ewes on low progesterone ($P < 0.005$). The effect of expected progesterone on ovulation rate was linear ($P < 0.01$), regardless of whether ovulation rate was estimated by disappearance of follicles after estrus (Figure 3 A) or numbers of CL on d 7 after estrus (Figure 3 B). The number of follicles (≥ 4 mm) that disappeared in relation to estrus

increased linearly ($P < 0.05$) with decreasing concentrations of progesterone. Number of CL formed was correlated to number of follicles that disappeared ($r = 0.53$; $P < 0.0001$).

The increase in ovulation rate in ewes with lower expected concentrations of progesterone was due to retention and ovulation of more follicles from the penultimate wave of follicular devel-

opment. This finding is in agreement with Johnson et al. (1996) and Bartlewski et al. (1999; 2003), who reported that follicles of varying ages, or originating from both the penultimate and final follicular waves, ovulated in the cycling ewe. Additionally, it extends to a relatively prolific breed of ewes the finding by Bartlewski et al. (1999) in less prolific ewes that exposure to low concentrations of progestogens during the luteal phase can increase ovulation rate.

The number of follicles that disappeared and was presumed to have ovulated was an overestimate of the number of CL observed on d 7 after estrus, which was used as a final measure of ovulation rate. Similarly, Bartlewski et al. (2003) observed that not all follicles that disappeared at estrus formed CL. The accuracy of observation of disappearance of follicles as a measure of ovulation rate might have been reduced, because some follicles ≥ 4 mm did not ovulate, but regressed in size and might have been assumed to be new 2 or 3 mm follicles. Alternatively, some ovulated follicles might not form a CL. In earlier research, Murdoch et al. (1983) observed that ewes injected with LH or FSH on d 15 ovulated, but were unable to develop sufficient luteal function. They suggested that the pre-ovulatory follicle was forced to ovulate prematurely and lacked gonadotropin receptors on follicular cells, which reflected follicular maturity

Table 1. Intervals from emergence to disappearance of presumed ovulatory follicles from the final or penultimate waves.

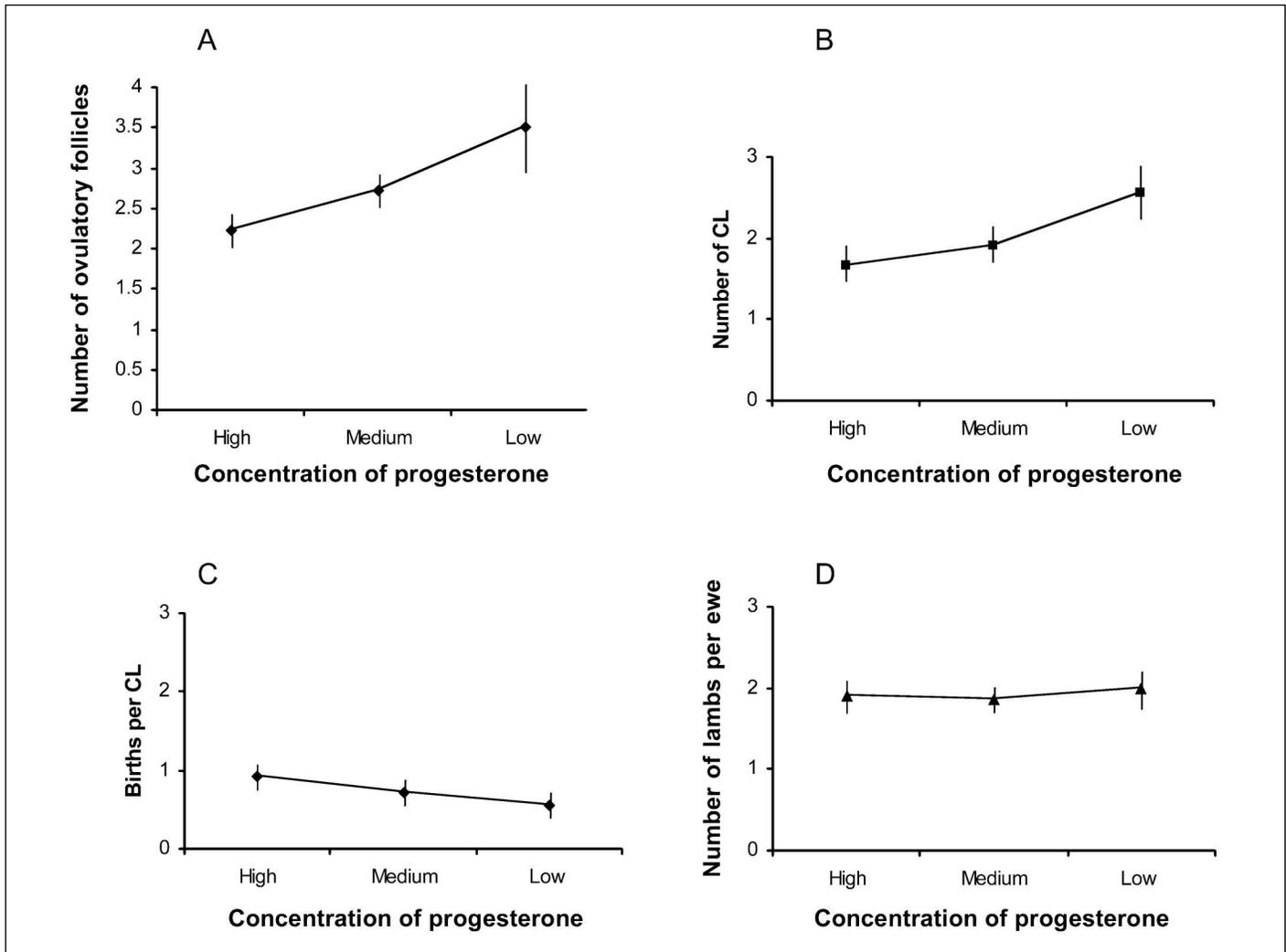
	Expected concentration of progesterone			All Groups
	High	Medium	Low	
Number of ewes observed	15	15	16	46
Time from emergence to ovulation:				
Final follicular wave:				
Total number of follicles observed	21	19	13	53
Interval (days \pm SEM)	4.6 \pm 0.5	5.2 \pm 0.3	5.5 \pm 0.3	5.0 \pm 0.3 ^c
Penultimate follicular wave:				
Total number of follicles observed	12	22	43	77
Interval (days \pm SEM)	8.2 \pm 0.3	9.0 \pm 0.3	9.2 \pm 0.2	9.0 \pm 0.2 ^d
Both waves:				
Total number of follicles observed	33	41	56	130
Interval (days \pm SEM)	5.7 \pm 0.6 ^a	7.6 \pm 0.6 ^b	8.1 \pm 0.2 ^b	7.2 \pm 0.4

*Proportions of disappearing follicles arising from the penultimate and final waves differed with expected concentration of progesterone ($\chi^2 = 14.76$, 2 df, $P < 0.005$).

^{a,b} Means in the same row with different superscripts differed ($P < 0.05$; Duncan's multiple range test).

^{c,d} Overall means for waves differed ($P < 0.05$).

Figure 3. Characteristics (mean \pm SEM) of ewes with expected high, medium or low concentrations of progesterone. A. Numbers of follicles disappearing after estrus in 15, 15, and 16 ewes, respectively, observed by ultrasonography. The number of follicles that disappeared increased linearly with decreasing expected concentrations of progesterone ($P < 0.02$). B. Numbers of CL in ewes that lambed to first service ($n = 39, 44, \text{ or } 41$ ewes, respectively) increased linearly with decreasing expected concentrations of progesterone ($P < 0.001$). C. Numbers of lambs born per CL in ewes that lambed to first service decreased linearly with decreasing expected concentrations of progesterone ($P < 0.01$). D. Numbers of lambs born per ewe lambing (prolificacy) did not differ with expected progesterone.



and inherent ability to luteinize. When follicular synthesis of estrogen was reduced by treatment with an aromatase inhibitor and follicles were ovulated/luteinized by injection of hCG (Benoit et al., 1992), estrus did not occur and the onset of luteal function was delayed. However, ewes showed estrus naturally after withdrawal of progesterone in the present study, and, as discussed below, pregnancy rates in the normal range indicated that functional CL were formed.

Conception and Pregnancy Rates, Embryonic and Fetal Losses, Prolificacy and Lambing Rates

Conception and pregnancy rates to the single service averaged 76 percent and 74 percent, respectively, and did not differ with expected concentrations of progesterone during the pre-breeding cycle in the present study. Evans et al. (2001) found that lower dosages of progesterone had no deleterious effects on embryo quality or fertility and concluded that age of follicles was less critical in sheep than in cattle. In contrast, reduced conception and pregnancy rates in ewes were associated with lower-luteal-phase concentrations of progesterone or progestogens before breeding and the ovulation of older follicles

(Johnson et al., 1996; Ungerfeld and Rubianes 1999; Viñoles et al., 2001). Similarly, cows with low concentrations of progesterone during the luteal phase ovulated an older follicle and had decreased pregnancy rates (Cooperative Regional Research Project, NE-161, 1996) due to death of embryos during the 2 to 16 cell stage (Ahmad et al., 1995). Lower conception rates were observed in studies using immunization against androgens to increase ovulation rate (Boland et al., 1986; Meyer and Lewis, 1988; Wilkins, 1997), but not in trials using immunization against inhibin (Kusina et al., 1995a,b). Wilkins

(1997) reported that some nutritional treatments that increased ovulation rate depressed conception rates, but in his study, ewes with twin ovulations had a greater conception rate than ewes with single ovulations.

Births per CL decreased linearly ($P < 0.001$) with decreasing concentrations of progesterone (Figure 3 C) during the luteal phase preceding ovulation. Thus, reproductive wastage (CL not represented by lambs born) was greater for ewes with low (1.3 ± 0.2 ; $P < 0.01$) than for ewes with either high (0.8 ± 0.2) or medium (0.9 ± 0.2) concentrations of progesterone. As a result, the greater ovulation rates (Figure 3 B) observed with lower concentrations of progesterone did not produce a corresponding increase in number of lambs born per ewe lambing (Figure 3 D). Prolificacy (lambs born per ewe lambing) did not differ among groups and averaged 1.90 ± 0.12 , 1.86 ± 0.11 and 2.00 ± 0.14 for ewes with high, medium or low progesterone, respectively. Lambing rate (lambs born per ewe treated) did not differ among ewes on high (1.3 ± 0.1), medium (1.5 ± 0.1) or low (1.5 ± 0.2) concentrations of progesterone. Quintuplets were born to one ewe with high and one ewe with low concentrations of progesterone and quadruplets were born to one ewe with medium concentrations of progesterone.

An increase in partial rather than total pregnancy loss was associated with decreasing progesterone in the cycle before ovulation, because pregnancy rates did not differ with concentrations of progesterone, older ovulatory follicles (oocytes) originating from the penultimate wave may not be as healthy and may be a causative factor of more reproductive wastage. Greater reproductive wastage in ewes with lower-luteal-phase concentrations of progesterone, which ovulated more follicles from the penultimate wave, might have been due to reduced fertilization rate (Hulet et al., 1956; Boland et al., 1986; Mitchell et al., 2002), greater embryonic death (Hulet et al., 1956), delayed embryonic development (Boland et al., 1986), greater fetal death (Dixon et al., 2007), or a combination of those factors (Kleemann and Walker, 2005a,b). It may be important to note the report by Carrillo et al. (2006) that both lambing rate and pro-

lificacy were increased by treatment with 125 mg bovine GH 5 d before the end of treatment with intravaginal sponges containing 45 mg flurogestone acetate. Growth hormone is required in addition to FSH and LH in order to produce ovulable follicles in the ewe (Eckery et al., 1993).

Negative relationships between ovulation rate and lambs born per ovulation have been reported in numerous studies (Meyer, 1985; Knights et al., 2003; Dixon et al., 2007). In addition to the effects on follicles and oocytes discussed above, uterine capacity might have influenced litter size through the inability to sustain additional embryos. Nawaz and Meyer (1991) and Meyer et al. (1994) observed differences among breed-types in "uterine efficiency" (lambs born per CL), with greater efficiency in genotypes known to have larger litter sizes in each study.

Other Considerations

Rams were introduced to the ewes in this study 7 d before withdrawal of progesterone or regression of CL. Based upon a study by Evans et al. (2004), exposure to rams for 3 d before progesterone withdrawal might have been expected to limit fertility or prolificacy. They found 14-percentage- and 9-percentage-point reductions in ewes lambing to first service in two trials and 0.23 fewer lambs born per ewe lambing in one of those trials, which they attributed to increased LH pulse frequency in response to ram introduction during treatment with progestogen. However, their results might have been influenced in part by the fact that they delayed introduction of intact rams for breeding until 48 h after sponge withdrawal (Hawken et al., 2005). In the present study, the same intact rams remained with the ewes throughout and overall pregnancy rate was quite acceptable, similar to that reported for hair sheep in the tropics (74 percent; Godfrey et al., 1997), and greater than that observed in ewes treated with intravaginal inserts (CIDRs) in the breeding season (57 percent; Rhodes and Nathanielsz, 1988).

Conclusions

In summary, removal of endogenous progesterone and use of intravaginal

inserts to lower circulating concentrations of progesterone increased ovulation rate through more follicles being maintained from the penultimate wave, likely due to greater LH pulse frequency, which regulates follicular and oocyte maturation. However, increased ovulation rate did not increase litter size. Older oocytes, from follicles of the penultimate wave, might have been incapable of either fertilization or embryonic development, the latter being more likely, based upon the research with cows. Furthermore, uterine capacity might have limited litter size. In practical terms, even though most progesterone delivery systems provide lower progesterone than the corpora lutea in a ewe's ovaries, and lower progesterone raised ovulation rate, there was no net gain or loss in lambs born.

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