Causes of reproductive loss in ewes synchronized and mated during the anestrous season and during the normal breeding season were compared with those for natural cyclic ewes mated in season. Synchronization of ewes in season and out of season with progestogen: pregnant mare serum gonadotropin (PMSG) increased ovulation rate, but the percentage of ewes ovulating did not differ from that noted for untreated ewes mated in season. However, synchronized ewes exhibited markedly higher total reproductive losses, both in season (49%) and out of season (58%), than did untreated ewes mated in season (25%). The two primary sources of the increased reproductive loss in synchronized ewes were increased fertilization failure and increased embryonic mortality, regardless of season. The increased fertilization failure was accompanied by a decrease in the number of accessory sperm per ovum and decreased tubal sperm numbers. The increased embryonic mortality among treated ewes was associated with increased variation in stage of embryo development within ewe and advanced stage of embryo development, which indicated that asynchronies of timing of onset of estrus, ovulation and fertilization may have occurred in synchronized ewes. The high reproductive losses for ewes treated out of season were characterized by a marked increase in fertilization failure, compared with that observed for ewes treated in season, in addition to the relatively high embryonic mortality associated with the synchronization treatment. Semen quality of rams was lower out of season than in season. It was concluded that the reduced and more variable lambing response often obtained for ewes treated with progestogen: PMSG during anestrus may be due to decreased semen quality of rams and increased asynchrony of events in the ewe reproductive tract. (Key Words: Accessory-Sperm, Fertilization, Embryonic Mortality, Ewe, Synchronization.)

Introduction

A means of inducing fertile estrus in anestrous ewes is necessary for sheep producers to increase the efficiency of lamb production. Treatment of ewes with progestogen followed by pregnant mare serum gonadotropin (PMSG) during the normal breeding season results in lambing rates comparable to natural lambing rates (Wishart, 1967; Laster and Glimp, 1974), but treatment of ewes during the anestrous season results in lower and more variable lambing rates (Hulet and Stormshak, 1972; Laster and Glimp, 1974; Christenson, 1976; Lunstra and Christenson, 1981). If lambing rates are to be improved in ewes synchronized during the anestrous season, the causes of the reduced and variable lambing rates must be defined and understood.

The primary objective of this study was to characterize and compare the sources of reproductive losses in naturally cyclic ewes with those observed in ewes synchronized during the normal breeding season (in season) and in ewes synchronized during the anestrous season (out of season).

Materials and Methods

Five hundred crossbred ewes were syn-
chronized with the progestogen:PMSG treat-
ment during the anestrous season (May through
August), and 50 crossbred ewes were synchro-
nized during the normal breeding season
(December). Ewes were synchronized with
intravaginal progestogen-pessaries (Synchro-
Mate, 20 mg) inserted for 16 days. Pro-
gesterone (10 mg) was injected on the day
of pessary removal, and 750 IU PMSG was
injected 1 and 16 days after pessary removal.
All treated ewes were given two injections
of PMSG. Treated ewes were assigned ran-
domly to subgroups of 25, and each subgroup
was exposed to a ram for 30 days, beginning
24 hr after pessary removal. Rams were fitted
with marking harnesses, and estrous data
(crayon marks) were recorded every 4 hr
during the first 6 days and twice daily during
the remaining 9 days after each PMSG in-
jecction. Details of crossbred ewe breeds, the
synchronization technique and collection of
marking data for ewes treated out of season
have been reported (Lunstra and Christenson,
1981). An additional group of 50 un-
treated, cyclic crossbred ewes was ex-
posed to two rams (25 ewes/ram) during the
normal breeding season (November), and
marking data were recorded every 4 hr for
15 days.

Ten mature rams were used for breed-
ing treated ewes during the anestrous season
(May through August; Lunstra and Christenson,
1981). Two of these rams were used for breed-
ing untreated ewes during November and
treated ewes during December. Two ejaculates
were collected from each ram approximately
2 weeks before the beginning of each breeding
period (May, July, October and December).
Each semen sample was evaluated immediately
after collection. Sperm concentration was de-
termined by hemacytometer counts. Percentage
of sperm showing progressive motility was de-
termined after 10-fold dilution of semen
with phosphate-buffered saline (pH 7.4,
37 C). Percentage live sperm and percentage
of sperm having abnormal heads were de-
termined after staining with eosin-fast green
according to the procedure of Hackett and
Macpherson (1965).

Ewes were laparotomized for the determi-
nation of ovulation rate and for recovery of
ova. All laparotomies were performed ap-
proximately 60 hr after the onset of estrus.
Approximately 20% of the ewes synchronized
out of season were laparotomized after the
onset of first induced estrus, and 20% were
laparotomized after the second induced estrus.
Ewes synchronized out of season and not
laparotomized were maintained for the col-
lection of lambing data (Lunstra and Christen-
son, 1981). Thirty-six ewes synchronized
in season were laparotomized (20 after the
first and 16 after the second induced estrus),
and 32 untreated cyclic ewes were laparoto-
mized in-season after the onset of estrus.
The number of ewes not laparotomized in
season (14 treated and 18 untreated ewes)
was too small for accurate lambing informa-
tion to be obtained; hence, lambing data
for untreated and treated ewes in season were
obtained from flocks of similar crossbred
ewes maintained at Clay Center (Dickerson,
1977).

Laparotomy was performed with ewes
under general gas anesthesia (fluothane). The
reproductive tract was exposed by midventral
incision. Ovaries were examined and the num-
ber and diameter of corpora lutea recorded.
Ova were recovered by flushing the oviductal
contents into a collection bowl with sterile
media according to the procedure of Echtern-
kamp and Lunstra (1978). Ova were located
with a stereomicroscope, transferred to a glass
slide and mounted under a coverglass supported
by paraffin strips. The number of accessory
sperm was determined by differential inter-
ference-contrast microscopy at X 400. Ova
were cleared for 24 hr in 25% (v/v) glacial
acetic acid in absolute ethanol and stained
with 1% (w/v) natural orcein in 25% glacial
acetic acid. Fertilization and stage of devel-
opment were determined for each ovum.
Tubal sperm numbers were determined by
hemacytometer counts of flushing media
after removal of ova. Data on semen charac-
teristics, ovulation rate, fertilization, accessory
sperm, tubal sperm, ovum development and
lambing rate were subjected to analysis of
variance, and differences were analyzed by
Student’s t-test. Conception rates were com-
pared by chi-square analysis (Steel and Torrie,
1960).

Results and Discussion

Ewes synchronized with progestogen:PMSG
had higher (P<.01, table 1) average ovulation
\footnote{G. D. Searle Co., Skokie, IL.}
rates (2.5 out of season and 2.9 in season) than untreated ewes at natural estrus (1.9), indicating that treatment stimulated ovulation rate, regardless of season. A significant seasonal difference in ovulation rate was observed at the second induced estrus, with ewes treated in season having a higher (P<.05) ovulation rate than ewes treated out of season (2.7 vs 1.9); no seasonal difference was observed at the first induced estrus (3.0 vs 3.1). These data indicate that ovulation rate was more refractory to a second PMSG injection among ewes treated during anestrus (out of season) than among cyclic ewes treated during the normal breeding season (in season). Regardless of season of treatment, a high percentage (93 to 100%) of ewes in estrus had ovulated, and no synchronized group differed (P>.10) from the untreated group (97%) in percentage of ewes ovulating (table 1). We concluded that anovulatory ewes were not a cause of the reduced conception rate observed among ewes synchronized during the anestrous season.

Ova recovery rate was 98% for untreated ewes in season and 87% for synchronized ewes (P<.05, table 2). Recovery of ova from synchronized ewes was lower (P<.05) at the first induced estrus (83 and 81%) than at the second (92 and 95%), both out of season and in season, respectively. Recovery of ova from synchronized ewes at the second induced estrus did not differ (P>.10) from the recovery from untreated ewes. Recovery rates of ova were equal to or greater than those reported in other studies (75%, Hart, 1956; 91 to 94%, Mattner and Braden, 1967; 83 to 94%, Cullen et al., 1968; 72%, Trounson and Moore, 1974; 67%, Cognie et al., 1975).

Fertilization rate averaged 93% for untreated ewes in season (table 2), but was lower for ewes synchronized in season (80%, P<.05) and markedly lower for ewes synchronized out of season (58%, P<.01). A negative influence of synchronization treatment on fertilization rate, regardless of season, was clearly demonstrated. An effect of season was observed among synchronized ewes, as average fertilization rate was lower (P<.01) out of season (58%) than in season (80%). Other researchers have reported that fertilization rate is reduced at the first estrus following progestogen treatment (Foote and Waite, 1965; Cullen et al., 1968; Allison and Robinson, 1970; Quinlivan, 1970; Trounson and Moore, 1974; Cognie et al., 1975), but no reports were found concerning fertilization rate at two consecutive estrous periods following progestogen:PMSG synchronization. Fertilization rate for ewes treated in season was significantly lower than that

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**Table 1. Ovulation Rate for Ewes Synchronized Out of Season and In Season and for Untreated Ewes In Season**

<table>
<thead>
<tr>
<th>Group</th>
<th>No. of ovulation sites/estrous ewe</th>
<th>% ewes ovulating</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Synchronized:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Out of season (May-August)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>First induced estrus</td>
<td>3.0 ± .2 (111)</td>
<td>98.2 (109)</td>
</tr>
<tr>
<td>Second induced estrus</td>
<td>1.9 ± .2 (94)</td>
<td>92.6 (87)</td>
</tr>
<tr>
<td>Avg</td>
<td>2.5 ± .1 (205)</td>
<td>95.6 (196)</td>
</tr>
<tr>
<td>In season (December)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>First induced estrus</td>
<td>3.1 ± .6 (20)</td>
<td>100.0 (20)</td>
</tr>
<tr>
<td>Second induced estrus</td>
<td>2.7 ± .4 (16)</td>
<td>100.0 (16)</td>
</tr>
<tr>
<td>Avg</td>
<td>2.9 ± .3 (36)</td>
<td>100.0 (36)</td>
</tr>
<tr>
<td><strong>Nonsynchronized:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>In season (November)</td>
<td>1.9 ± .1 (32)</td>
<td>96.9 (31)</td>
</tr>
</tbody>
</table>

*a* Means ± SE. Number of estrous ewes laparotomized is given in parentheses.

*b* Number of ewes ovulating is given in parentheses.

*c* Synchronized with progestogen:PMSG treatment.

*d* Untreated ewes exhibiting natural estrus.

*e, f, g* Means in the same column with no common superscript are different (P<.05).
TABLE 2. OVA RECOVERY, FERTILIZATION AND ACCESSORY SPERM NUMBERS FOR EWES SYNCHRONIZED OUT OF SEASON AND IN SEASON AND FOR UNTREATED EWES IN SEASON*

<table>
<thead>
<tr>
<th>Group</th>
<th>% ova recovered per ewe</th>
<th>% ova fertilized per ewe</th>
<th>No. of accessory sperm/ovum</th>
<th>No. of tubal sperm/ewe</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Synchronized</strong>d:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Out of season (May-August)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>First induced estrus</td>
<td>83 ± 3 (272)**</td>
<td>53 ± 4**</td>
<td>13 ± 2**</td>
<td>4 ± 2**</td>
</tr>
<tr>
<td>Second induced estrus</td>
<td>92 ± 3 (184)</td>
<td>64 ± 4**</td>
<td>43 ± 5*</td>
<td>36 ± 12**</td>
</tr>
<tr>
<td>Avg</td>
<td>87 ± 3 (456)*</td>
<td>58 ± 3**</td>
<td>25 ± 3**</td>
<td>19 ± 6**</td>
</tr>
<tr>
<td>In season (December)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>First induced estrus</td>
<td>81 ± 4 (49)**</td>
<td>74 ± 9*</td>
<td>32 ± 5*</td>
<td>5 ± 3**</td>
</tr>
<tr>
<td>Second induced estrus</td>
<td>93 ± 3 (41)</td>
<td>87 ± 7</td>
<td>46 ± 8</td>
<td>452 ± 110*</td>
</tr>
<tr>
<td>Avg</td>
<td>87 ± 4 (90)*</td>
<td>80 ± 5*</td>
<td>38 ± 5*</td>
<td>209 ± 30**</td>
</tr>
<tr>
<td><strong>Nonsynchronized</strong>e:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>In season (November)</td>
<td>98 ± 2 (59)</td>
<td>93 ± 4</td>
<td>60 ± 11</td>
<td>2,519 ± 822</td>
</tr>
</tbody>
</table>

*aData presented as mean ± SE.

*bBased on number of recent ovulation sites per ewe at laparotomy. Total number of ova recovered is given in parentheses.

*cBased on number of recovered ova per ewe.

*dSynchronized with progestogen:PMSG treatment.

*eUntreated ewes mated at natural estrus.

*Mean differs (P<.05) from that for nonsynchronized ewes within column.

**Mean differs (P<.01) from that for nonsynchronized ewes within column.

for untreated ewes only at the first induced estrous period (table 2); fertilization rate at the second induced estrous period appeared normal. Fertilization rate was lower at the first (P<.05) and second (P<.01) induced estrous periods for ewes treated out of season than for ewes treated in season.

Number of accessory sperm per ovum averaged 60 ± 11 for untreated ewes in season (table 2), and was reduced in synchronized ewes, both in season (38 ± 5) and out of season (25 ± 3). Average number of accessory sperm was lower (P<.05) for ewes treated out of season than for ewes treated in season. Accessory sperm numbers were reduced at both the first (P<.01) and second (P<.05) induced estrous periods for ewes synchronized out of season, but were reduced (P<.05) only at the first induced estrus for ewes synchronized in season, by comparison with the numbers for untreated ewes.

Several researchers have shown that a positive relationship exists between the number of sperm in the oviduct around the time of ovulation and the number of accessory sperm per ovum (Braden and Austin, 1954; Mattner, 1963; Lightfoot and Salamon, 1970) and the percentage of ova fertilized (Braden and Austin, 1954; Lightfoot and Salamon, 1970; Vander-Vliet and Hafez, 1974). Our data confirm the relationship between fertilization and number of accessory sperm; increased fertilization rates were associated with increased numbers of accessory sperm per ovum (table 2). Moreover, the accessory sperm data imply that the number of sperm in the oviduct around the time of ovulation were reduced in treated ewes, in comparison to untreated ewes, and that this reduction was greater in ewes treated out of season than in ewes treated in season.

High numbers of spermatozoa were present in fluids flushed from the oviducts of untreated ewes (table 2) at approximately 60 hr after onset of estrus, but tubal sperm numbers were reduced markedly in flushings from synchronized ewes, both in season (209 ± 30) and out of season (19 ± 6). Quinlivan and Robinson (1969) reported that there are fewer sperm in the oviducts of progestogen-treated ewes than in the oviducts of untreated ewes, and that tubal sperm numbers decline.
more rapidly in treated ewes than in untreated ewes. They attribute the reductions to a detrimental effect of progestogen. While tubal sperm numbers were significantly reduced in all synchronized ewes, regardless of season of treatment, the greatest reduction was observed at the first induced estrus (table 2), which is consistent with the suggested detrimental effect of progestogen. At the second induced estrus, tubal sperm numbers were more than 10-fold lower in ewes treated out of season than in ewes treated in season (table 2), indicating that a detrimental out-of-season effect extended through the second induced estrous period for sperm transport and survival in treated ewes.

Among the rams used for breeding, total sperm per ejaculate, percentage motile sperm, percentage live sperm and percentage normal sperm were lower (P<.05) out of season than in season (table 3). A reduction in the semen quality of rams during the nonbreeding season has been reported by others (Cupps et al., 1960; Lodge and Salisbury, 1970). Schanbacher (1979) treated rams during the nonbreeding season to improve semen quality and obtained a two-fold increase in conception rate and a 2.5-fold increase in number of lambs born to ewes synchronized with progestogen:PMSG treatment. The greatest decreases in fertilization rate, accessory sperm numbers and tubal sperm numbers in treated ewes were observed out of season (table 2), a time when semen quality of rams was lowest (table 3). We concluded that the out-of-season reduction in semen quality of rams may have been a major factor in the reduced conception rate observed among ewes treated with progestogen:PMSG and mated during the anestrous season. Characteristics of semen from rams used during the normal breeding season were similar (table 3), but fertilization rate, accessory sperm numbers and tubal sperm numbers were significantly lower in treated ewes than in untreated ewes in season (table 2). Since these differences could not be attributed to changes in semen quality in season, we concluded that the progestogen:PMSG treatment has a detrimental effect on transport, survival or fertilizing ability of sperm in the ewe.

Asynchrony of timing of mating, ovulation and ovum transport can cause reduced fertility (Blandau, 1961). Echternkamp and Lunstra (1978) indicated that the normal interval from onset of estrus to ovulation in ewes may be shortened by progestogen:PMSG treatment. Most of the fertilized ova collected from nonsynchronized ewes at approximately 60 hr after the onset of estrus were at the two- to four-cell stage, while ova collected from synchronized ewes were at the four- to eight-cell stage (table 4). Developmental stage of fertilized ova, expressed as number of mitotic divisions per ovum, was advanced (P<.01) in synchronized ewes, regardless of season of treatment. In addition, fertilized ova showed more advanced development (P<.01; table 4) in ewes treated in season (2.3 cell divisions)...

### Table 3. Semen Characteristics of Rams Used for Breeding

<table>
<thead>
<tr>
<th>Month of evaluation</th>
<th>Total sperm per ejaculate (× 10⁹)</th>
<th>% progressively motile sperm</th>
<th>% live sperm</th>
<th>% sperm with abnormal heads</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Out of season</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>2.49 ± .45 e</td>
<td>52 ± 3 e</td>
<td>64 ± 2 d</td>
<td>7 ± 1 d</td>
</tr>
<tr>
<td>July</td>
<td>1.54 ± .24 d</td>
<td>41 ± 5 d</td>
<td>58 ± 5 d</td>
<td>10 ± 1 d</td>
</tr>
<tr>
<td>Avg</td>
<td>2.02 ± .27 de</td>
<td>46 ± 3 de</td>
<td>61 ± 2 d</td>
<td>8 ± 1 de</td>
</tr>
<tr>
<td><strong>In season</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>November</td>
<td>4.58 ± 1.68 ef</td>
<td>65 ± 5 f</td>
<td>78 ± 2 e</td>
<td>7 ± 4 def</td>
</tr>
<tr>
<td>December</td>
<td>4.35 ± .35 f</td>
<td>53 ± 10 def</td>
<td>76 ± 1 e</td>
<td>1 ± 1 f</td>
</tr>
<tr>
<td>Avg</td>
<td>4.46 ± .70 f</td>
<td>59 ± 6 f</td>
<td>77 ± 1 e</td>
<td>4 ± 2 f</td>
</tr>
</tbody>
</table>

aSemen was collected by artificial vagina 2 weeks prior to use of rams for natural mating. Two ejaculates from each ram were evaluated. Values are expressed as mean ± SE per ram.

bTen mature rams were evaluated and used for out-of-season matings (25 ewes per ram).

cTwo mature rams were evaluated and used for in-season matings (25 ewes per ram).

d, e, fMeans in the same column without common superscripts are different (P<.05).
TABLE 4. VARIATION IN DEVELOPMENTAL STAGE OF FERTILIZED OVA AND OVARIAN STATUS OF EWES SYNCHRONIZED OUT OF SEASON AND IN SEASON AND OF UNTREATED EWES IN SEASON

<table>
<thead>
<tr>
<th>Group</th>
<th>Interval from onset of estrus to ovum recovery, hr</th>
<th>No. of ova fertilized&lt;sup&gt;a&lt;/sup&gt;</th>
<th>No. of mitotic divisions per fertilized ovum&lt;sup&gt;b&lt;/sup&gt;</th>
<th>% ewes with fertilized ova differing by one or more mitotic divisions&lt;sup&gt;c&lt;/sup&gt;</th>
<th>% ewes with corpora luteal diameters differing by ≥ 3 mm&lt;sup&gt;d&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Synchronized&lt;sup&gt;e&lt;/sup&gt;:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Out of season (May-August)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>First induced estrus</td>
<td>60 ± 1</td>
<td>155</td>
<td>2.1 ± .1&lt;sup&gt;**&lt;/sup&gt;</td>
<td>35.6 (45)&lt;sup&gt;**&lt;/sup&gt;</td>
<td>27.2 (92)</td>
</tr>
<tr>
<td>Second induced estrus</td>
<td>57 ± 1</td>
<td>119</td>
<td>1.5 ± .1&lt;sup&gt;*&lt;/sup&gt;</td>
<td>44.1 (34)&lt;sup&gt;**&lt;/sup&gt;</td>
<td>44.8 (58)&lt;sup&gt;**&lt;/sup&gt;</td>
</tr>
<tr>
<td>Combined</td>
<td>59 ± 1</td>
<td>274</td>
<td>1.8 ± .1&lt;sup&gt;**&lt;/sup&gt;</td>
<td>39.2 (79)&lt;sup&gt;**&lt;/sup&gt;</td>
<td>34.0 (150)&lt;sup&gt;*&lt;/sup&gt;</td>
</tr>
<tr>
<td>In season (December)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>First induced estrus</td>
<td>64 ± 2</td>
<td>39</td>
<td>2.5 ± .1&lt;sup&gt;**&lt;/sup&gt;</td>
<td>40.0 (10)&lt;sup&gt;*&lt;/sup&gt;</td>
<td>53.3 (15)&lt;sup&gt;**&lt;/sup&gt;</td>
</tr>
<tr>
<td>Second induced estrus</td>
<td>62 ± 1</td>
<td>34</td>
<td>2.1 ± .1&lt;sup&gt;**&lt;/sup&gt;</td>
<td>54.6 (11)&lt;sup&gt;**&lt;/sup&gt;</td>
<td>64.3 (14)&lt;sup&gt;**&lt;/sup&gt;</td>
</tr>
<tr>
<td>Combined</td>
<td>63 ± 1</td>
<td>73</td>
<td>2.3 ± .1&lt;sup&gt;**&lt;/sup&gt;</td>
<td>47.6 (21)&lt;sup&gt;**&lt;/sup&gt;</td>
<td>58.6 (29)&lt;sup&gt;**&lt;/sup&gt;</td>
</tr>
<tr>
<td>Nonsynchronized&lt;sup&gt;f&lt;/sup&gt;:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>In season (November)</td>
<td>58 ± 3</td>
<td>53</td>
<td>1.1 ± .2&lt;sup&gt;**&lt;/sup&gt;</td>
<td>4.8 (21)</td>
<td>13.0 (23)</td>
</tr>
</tbody>
</table>

<sup>a</sup>Ova were fixed, cleared and stained before classification.

<sup>b</sup>Data presented as mean ± SE. Fertilized one cell = 0, two cell = 1.0, four cell = 2.0 and eight cell = 3.0.

<sup>c</sup>Number of ewes with two or more fertilized ova is given in parentheses.

<sup>d</sup>Number of ewes with two or more ovulation sites (corpora lutea) is given in parentheses.

<sup>e</sup>Progestogen-PMSG treated ewes.

<sup>f</sup>Untreated ewes mated at natural estrus.

*Mean differs (P<.05) from that for nonsynchronized ewes within column.

**Mean differs (P<.01) from that for nonsynchronized ewes within column.

than in ewes treated out of season (1.8 divisions). This seasonal difference in stage of ovum development was apparent at both the first (P<.05) and the second induced estrus (P<.01). The differences in stage of development of fertilized ova suggest that ovulation occurred earlier in synchronized ewes than in naturally cyclic ewes and that ovulation occurred earlier in relation to the onset of estrus in ewes synchronized in season than in ewes synchronized out of season. Stage of embryonic development was more advanced (P<.05) in treated ewes at the first induced estrous period than at the second, regardless of season (table 4). The marked advance observed at the first induced estrus may indicate that the effect is related to the progestogen employed before onset of first estrus (Cumming et al., 1970; Echtern- kamp and Lunstra, 1978), or it may reflect the decreased efficacy of the second PMSG injection (Lunstra and Christenson, 1981).

Fertilized ova differing in stage of development were recovered from synchronized ewes. Occasionally, two-cell and eight-cell ova were recovered from the same oviduct. The percentage of ewes having fertilized ova that differed by one or more mitotic divisions was low among untreated ewes (4.8%) but high among ewes synchronized out of season (39.2%) and in season (47.6%; table 4). The high incidence among treated ewes may indicate that the induced multiple ovulations did not occur simultaneously or that delayed fertilization occurred in some of the ova. If differences in stage of development within ewes were due to delayed fertilization of some ova because of limited sperm numbers in the oviduct at ovulation, the incidence of different stages of development within treated ewes should have been highest at the first induced estrus (i.e., when accessory sperm numbers were lowest; table 2). However, the incidence of differing developmental stages at the second induced estrus was as high as, or higher than, that at the first induced estrous period (table 4), indicating that restricted sperm numbers in the oviduct were not
a factor. Variation in time of ovulation within ewe could explain the differing stages of development observed within ewes. Diameters of corpora lutea differed within ewes having two or more recent ovulations (table 4), and the percentage of ewes possessing corpora lutea differing by at least 3 mm in diameter was similar to the percentage of ewes having fertilized ova differing by one or more stages of development. It has been reported that the diameter of corpora lutea increases steadily during the first 2 to 3 days after ovulation in normal cyclic and PMSG-superovulated ewes (McClellan et al., 1975). If diameter of corpora lutea is directly related to time since ovulation, the data on differing corpora luteal diameters and differing developmental stages of fertilized ova indicate that considerable variation in time of ovulation occurred within synchronized ewes, regardless of season of treatment.

Total reproductive losses per ewe (expressed as a percentage of total potential ova per estrus) ranged from 45 to 62% for synchronized ewes, but were only 25% for untreated cyclic ewes (table 5). Fertilization failure was a major source of reproductive loss among all synchronized ewes, and average reproductive losses due to fertilization failure were significantly higher for treated (20% and 42%) than for untreated ewes (7%). Fertilization failure represented 72% of total reproductive losses for ewes synchronized out of season, 41% for ewes synchronized in season and 28% for untreated ewes in season. Fertilization failure was the primary source of reproductive loss at both the first (85% of total losses) and second (58%) induced estrous periods among ewes synchronized out of season (table 5).

Embryonic mortality expressed as a percentage of total potential ova per ewe was 12% for ewes synchronized out of season and 29% for ewes synchronized in season, compared to 15% for untreated ewes in season (table 5). However, embryonic mortality expressed as a percentage of fertilized ova averaged 27% for ewes synchronized out of season and 36% for ewes synchronized in season, values significantly higher than the 16% for untreated ewes in season (table 5). There is evidence that embryonic mortality

| TABLE 5. REPRODUCTIVE LOSSES FOR EWES SYNCHRONIZED OUT OF SEASON AND IN SEASON AND FOR UNTREATED EWES IN SEASON |
|--------------------------------------------------|--------------------------------------------------|------------------|------------------|---------|
| Group                                             | No. of fertilized ova per estrous ewe | No. of lambs born per estrous ewe | Source of reproductive loss per ewe* | Total % lost |
|                                                   |                                     |                                 | % ovulation failure | % fertilization failure | % embryonic mortality |                      |
| Synchronized** C:                                 |                                      |                                 |                      |                      |                      |                      |
| Out of season (May-August)                        |                                      |                                 |                      |                      |                      |                      |
| First induced estrus                              | 1.6 ± .2                             | 1.4 ± .1                         | 2                    | 47**                 | 6 (15)                | 55**                 |
| Second induced estrus                             | 1.2 ± .2*                            | .7 ± .1**                        | 7                    | 36**                 | 19 (40*)              | 62**                 |
| Avg/estrus                                        | 1.4 ± .1*                            | 1.0 ± .1*                        | 4                    | 42**                 | 12 (27*)              | 58**                 |
| In season (December)                              |                                      |                                 |                      |                      |                      |                      |
| First induced estrus                              | 2.3 ± .5                             | 1.5 ± .1                         | 0                    | 26*                  | 26 (35*)              | 52*                  |
| Second induced estrus                             | 2.4 ± .3*                            | 1.5 ± .1                         | 0                    | 13                   | 32 (38*)              | 45*                  |
| Avg/estrus                                        | 2.3 ± .3*                            | 1.5 ± .1                         | 0                    | 20*                  | 29 (36*)              | 49*                  |
| Nonsynchronized** D:                              |                                      |                                 |                      |                      |                      |                      |
| In season (November)                              | 1.7 ± .1                             | 1.5 ± .1                         | 3                    | 7                    | 15 (16)               | 25                   |

aPercentage values are based on total ova that would have been produced per ewe had all ewes in estrus ovulated (potential ova).

bEmbryonic mortality expressed as percentage of total potential ova per ewe. Embryonic mortality expressed as a percentage of fertilized ova per ewe is given in parentheses.

cSynchronized with progestogen: PMSG treatment.

dUntreated ewes mated at natural estrus.

*Value differs (P<.05) from value for nonsynchronized ewes within column.

**Value differs (P<.01) from value for nonsynchronized ewes within column.
increases as ovulation rate increases (Casida et al., 1966; Edey, 1969), and differences between average ovulation rates for treated and untreated ewes (table 1) tended to confirm this relationship. The high embryonic mortality in treated ewes may have been related to the increased ovulation rate, the advanced stage of embryonic development and the increased variation within ewe observed for stage of embryonic development and diameter of corpora lutea.

In conclusion, synchronization of ewes with progestogen: PMSG produced an acceptable percentage of ewes ovulating and an increased ovulation rate, but treated ewes suffered a marked increase in reproductive losses. The two primary sources of reproductive loss were decreased fertilization rate and increased embryonic mortality. The decreased fertilization rate and embryonic survival in treated ewes were accompanied by decreased numbers of accessory sperm per ovum, decreased numbers of tubal sperm per ewe, advanced stage of early embryo development and increased variation in stage of embryonic development and size of corpora lutea within ewe. Reproductive losses among ewes treated during the anestrous season were characterized by a markedly higher incidence of fertilization failure than observed among ewes treated in season. The high incidence of fertilization failure among ewes treated out of season was associated with reductions in accessory and tubal sperm numbers. Since embryonic mortality and within-ewe variation in stage of embryonic development were high among treated ewes, regardless of season, it was concluded that the reduction in lambing response observed among ewes treated out of season was primarily due to reduced fertilization rate. The reduced fertilization rate was associated with a decrease in the quality of rams semen used for breeding during the anestrous season.

**Literature Cited**


