OVULATION RATE, LAMBING RATE, LITTER SIZE
AND EMBRYO SURVIVAL OF RAMBOUILLET SHEEP
SELECTED FOR HIGH AND LOW REPRODUCTIVE RATE

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ABSTRACT

Ewes from lines selected for high and low reproductive rate and a control line bred and selected randomly were endoscopically examined 3 to 5 d after breeding to determine ovulation rates in the fall of 1985, 1986 and 1987. Fertility (ewes lambing per ewe exposed), lambing rate (lambs born per ewe exposed) and litter size (lambs born per ewe lambing) were evaluated at lambing in the spring of each year. Embryonic survival was estimated as the number of lambs born per corpora lutea. Ovulation rates were 1.28, 1.73 and 1.46 for low, high and control lines, respectively. More \( P < .01 \) single ovulations occurred in low-line ewes than in the other two lines; high-line ewes had more \( P < .01 \) twin ovulations than did low- or control-line ewes. Fertility did not differ among lines. Selection line affected \( P < .01 \) lambing rate at first and all services. Control-line ewes had mean lambing rates at first and all services that were intermediate between those of the low and high lines, which were different from each other. Line \( \times \) age of ewe interactions existed \( P < .01 \) for lambing rate at all services and litter size at first and all services. High-line ewes had lower lambing rates and litter sizes as 2-yr-olds than other lines, but their performance increased steadily to 6-yr-olds, whereas the low and control lines remained relatively constant. Embryo survival differed \( P < .10 \) between lines, being 74%, 63% and 67% for low, high and control lines, respectively. However, when ovulation rate was included in the model to assess the effect of selection on embryo survival independent of changes in ovulation rate, no differences among lines were observed. Selection for reproductive rate resulted in a correlated change in ovulation rate.

(Key Words: Sheep, Selection, Reproductive Efficiency, Ovulation Rate.)


Introduction

Lambs weaned per ewe exposed for breeding is the single most important factor associated with profitability of a sheep enterprise in the U.S. Low lambing rates represent a major obstacle to the sheep industry in the U.S. Lambs weaned per ewe exposed for breeding is affected by genetic and environmental factors. The potential for number of lambs born is affected by many components, including ovulation rate, fertilization rate and embryo survival, any or all of which may be under genetic control. Several studies in sheep have shown that selection for reproductive rate or litter size can change litter size (Wallace, 1964; Clark, 1976; Hanrahan, 1976; McGuirk, 1976; Turner, 1978; Atkins, 1980; Hanrahan, 1982; Bradford, 1985; Burfening et al., 1989). However, few studies have been conducted to determine what components of litter size have changed as a result of selection. In sheep, selection for litter size has been shown to alter ovulation rate without affecting embryonic mortality (Bradford et al.; 1986); this is different from results in mice (Bradford, 1969), where selection for high litter size
increased ovulation rate but selection for low litter size increased embryonic mortality.

The purpose of this study was to determine differences in ovulation rate, fertility, lambing rate, litter size and embryo survival among lines of sheep that have been selected for high or low reproductive rate over 19 yr.

Materials and Methods

Sheep. In fall 1968, a selection experiment for reproductive performance in sheep was initiated at the Montana Agricultural Experiment Station. Rambouillet ewes were assigned at random, within age, to one of two selection lines: a high line to be selected for high reproductive rate and a low line to be selected for low reproductive rate. No initial screening of the ewe population was practiced. Rams were selected from the foundation ewes on the basis of a reproductive index, and the four highest and four lowest ranking rams were assigned to the high and low lines, respectively, on the basis of the reproductive index to produce the first ewe lamb progeny (born in 1969). After this time, lines were closed and all selection was from within line. In fall 1972, all remaining foundation ewes were removed from the high and low lines and mated to a random sample of eight rams from the high and low lines to establish a randomly mated, randomly selected control line. Because no selection was practiced among foundation ewes after they were assigned to their respective lines, little difference would be expected between the foundation ewes remaining at this time and those at the start of the experiment. The selection differential of these remaining foundation ewes was \(-.05\) index units (Burfening, unpublished data). Each line was maintained at approximately 100 ewes.

Selection Procedures. Rams were selected within the high and low lines each fall at weaning based on their dam’s past reproductive performance. Selection was based on the following simple index: 

\[ I = \frac{\text{total number of lambs born in lifetime}}{\text{age of ewe}} - 1 \]

The index included lambs from all years that a ewe was exposed for breeding, whether she lambed or failed to lamb. This index discriminates against rams from young ewes that could be genetically better than older ewes but have a lower index because of fewer lambings and because of the age of ewe effect on lambing rate. However, no adjustment for age of ewe was made; generally rams were not selected from 2-yr-old ewes. Four rams with the highest indexes within the high line and four rams with the lowest indexes within the low line were selected for use the following year (at approximately 18 mo of age). In addition, four reserve rams were selected within each line. In the control line, eight rams plus four reserves were selected at random. An additional requirement in all lines was that selected rams could not be paternal half-sibs. The only other restriction placed on rams was that they could not have horns or wool blindness (face score of 5). Selected rams were used for only one breeding season.

Ewes in the high, low and control lines were selected at approximately 16 mo of age on the same basis as rams. Ewes were bred to lamb first at 2 yr of age and all ewes were removed from the flock at 6 yr of age. The only other reasons for disposal of ewes were failure to lamb for two consecutive years and/or physical problems such as mastitis.

Management and Environment. The experiment was carried out at Red Bluff Research Ranch near Norris, Montana. Elevation ranges from 1,280 to 1,900 m, and precipitation ranged from 25 to 48 cm, with an average of 42 cm. Shed lambing was practiced, and ewes were brought to the ranch headquarters for breeding, lambing and data collection.

Ewes and lambs were managed as one group throughout the experiment except at breeding when ewes were assigned to single-sire breeding pens. The breeding season was from mid-November to early December. Lambing occurred in April and May.

Ewes were maintained together on winter range composed primarily of blue-bunch wheatgrass and Idaho fescue. While on winter range, ewes were supplemented with 0.15 kg of a 20% protein pellet. Although supplementation varied somewhat from year to year, the approximate composition of the protein supplement was 48% barley, 5% wheat millrun, 27% soybean meal, 5% dehydrated alfalfa, 6% molasses, 7.5% dicalcium phosphate and salt. Ewes were fed mixed alfalfa and grass hay when snow cover was too deep to permit grazing or sufficient feed was not available on the range (5 to 7 d per winter).

Ewes were moved to large pens to lamb and observed 24 h per day. Upon lambing, ewes and lambs were placed in individual pens, approximately 1.3 m². Lambs were ear-tagged and weighed within 24 h of birth.
Data. Ovulation rate was evaluated for three consecutive years (1985 to 1987). Each ram was fitted with a marking harness to aid in detection of estrus. Ewes in each pen were checked twice weekly for estrus. Ovaries of ewes that were marked by rams were examined via midventral laparoscopy 3 to 5 d postmating. Only ewes that were clearly marked by the rams were included in this study. This was because daily estrus detection was not practiced, and weather conditions (snow on the backs of the ewes and extreme cold caused the marking crayons to not work well) sometimes made it difficult to determine positively whether a ewe had been marked by the ram. Ewes were held off feed and water 24 h prior to laparoscopy. Just prior to laparoscopy, each ewe was injected with 10 mg acepromazine maleate i.m. and local anesthesia was induced by use of 5 ml lidocaine (2%) at each probe site. Ewes also were treated with penicillin G procaine. The number of corpora lutea observed on each ovary was recorded; it was assumed to represent ovulation rate for a particular ewe. Oldam et al. (1976) reported that this technique did not reduce reproductive performance of the ewes.

To ensure that lambing data could be related to the observed ovulation rate, ewes were returned to range after laparoscopy and exposed to blackface rams for the remainder of the breeding season. Birth of a crossbred lamb indicated that mating to the Rambouillet ram and the ovulation observed did not result in pregnancy.

Subsequent lambing record for each ewe was examined to assess fertility (lambing status of each ewe exposed), lambing rate (number of lambs born per ewe exposed) and litter size (number born per ewe lambing at first, to the Rambouillet ram, and all services [to the Rambouillet or blackface ram]). Estimated embryo survival (fertilization success and embryo survival) was the percentage of corpora lutea represented by live lamb(s) from the Rambouillet rams.

Embryonic survival data from ewes giving birth to crossbred lambs was taken to be zero. Ewes giving birth to more lambs than the observed ovulation rate had their ovulation rates adjusted upward to match the lambing record (Bradford, personal communication), which occurred in 7.1, 10.8 and 9.8% of the low-, high- and control-line ewes, respectively.

Statistical Analyses. Ovulation rate, fertility, lambing rate, litter size and embryo survival were analyzed using the GLM procedure of SAS (1985). Our model had the independent effects of line, year of birth of the ewe, age of the ewe and the random effects of sire of the ewe within line x year of birth and ewe within sire (line x year of birth). Line was tested by sire within line x year of birth; sire was tested by ewe within sire (line x year of birth). To study the effect of selection on embryo survival independent of changes in ovulation rate, ovulation rate was included in the model, and the data were reanalyzed. The effect of type of twin ovulation, unilateral (both ovulations occurring on one ovary) or bilateral (one ovulation on each ovary), on fertility, lambing rate and embryo survival was studied by including categories of unilateral or bilateral ovulations in an analysis of the ewes that had twin ovulations. The ewes with three ovulations were deleted from this analysis because of the small numbers in this subclass.

Results and Discussion

Ovulation Rate. Ovulation rate was affected (P < .01) by line and age of ewe. Response in ovulation rate followed selection for reproductive rate. Mean ovulation rates for the three lines were different from each other (Table 1). More (P < .01; chi-square analysis) single ovulations were observed in low-line ewes than in the other lines, and high-line ewes had more (P < .01; chi-square analysis) twin ovulations than did low- or control-line ewes (Figure 1).

Ovulation rate was lowest for 2-yr-old ewes (1.08) and increased with age to 5-yr-old ewes (1.66), but it declined in 6-yr-old ewes (1.62). No line x age of ewe interaction (P > .05) was observed.

Fertility. Ewe within sire (line x year of birth) was the only significant source of variation affecting fertility. Thus, selection for reproductive rate did not produce a correlated response in fertility. Other studies have reported improved conception rates for sheep selected for multiple births (Wallace, 1964; Clarke, 1976; McGuirk, 1976; Turner, 1978; Bradford et al., 1986).

Fertility was not different between ewes that had one corpus luteum vs ewes with two or three corpora lutea (Table 2). This result is different from that observed by Bradford et al. (1986), who reported a 19% advantage for ewes with two corpora lutea. Among ewes with two corpora lutea, those with bilateral
TABLE 1. LEAST SQUARES MEANS FOR THE EFFECT OF SELECTION LINE ON OVULATION RATE, FERTILITY, LAMBING RATE AND LITTER SIZE

<table>
<thead>
<tr>
<th>Trait</th>
<th>Selection line</th>
<th></th>
<th></th>
<th>Mean square^d</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low</td>
<td>High</td>
<td>Control</td>
<td>Mean square^d</td>
</tr>
<tr>
<td></td>
<td>No. of ewes</td>
<td>Mean</td>
<td>Mean</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>226</td>
<td>241</td>
<td>233</td>
<td>.31</td>
</tr>
<tr>
<td></td>
<td>1.25^a</td>
<td>1.67^b</td>
<td>1.43^c</td>
<td>.19</td>
</tr>
<tr>
<td>Fertility (no. lambing per ewe exposed)</td>
<td>No. of ewes</td>
<td>Mean</td>
<td>Mean</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>224</td>
<td>238</td>
<td>225</td>
<td>.13</td>
</tr>
<tr>
<td></td>
<td>.78^a</td>
<td>.70^a</td>
<td>.71^a</td>
<td>.17</td>
</tr>
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<td></td>
<td>All services</td>
<td>.85^a</td>
<td>.85^a</td>
<td>.80^a</td>
</tr>
<tr>
<td>Lambling rate (no. born per ewe exposed)</td>
<td>No. of ewes</td>
<td>Mean</td>
<td>Mean</td>
<td>Mean</td>
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<td>224</td>
<td>238</td>
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<td>.42</td>
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<td>1.05^b</td>
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</tr>
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<td></td>
<td>All services</td>
<td>.95^a</td>
<td>1.23^b</td>
<td>1.07^b</td>
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<tr>
<td>Litter size (no. born per ewe lambing)</td>
<td>No. of ewes</td>
<td>Mean</td>
<td>Mean</td>
<td>Mean</td>
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<td>167</td>
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<td>1.45^b</td>
<td>1.32^c</td>
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<tr>
<td></td>
<td>All services</td>
<td>190</td>
<td>198</td>
<td>189</td>
</tr>
<tr>
<td></td>
<td>1.04^a</td>
<td>1.43^b</td>
<td>1.33^b</td>
<td>.19</td>
</tr>
<tr>
<td></td>
<td>Mean square used to test line (sire within line x year).</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

^a,b,c,d Means with different superscripts within the same row were different (P < .05).

TABLE 2. EFFECT OF TYPE OF OVULATION RATE ON FERTILITY LAMBING RATE AND EMBRYONIC SURVIVAL AT FIRST SERVICE

<table>
<thead>
<tr>
<th>Type of ovulation</th>
<th>Fertility</th>
<th>Lambing rate</th>
<th>Embryonic survival</th>
</tr>
</thead>
<tbody>
<tr>
<td>Single</td>
<td>.73</td>
<td>.73^b</td>
<td>.73^b</td>
</tr>
<tr>
<td>Twin</td>
<td>.72</td>
<td>1.23^c</td>
<td>.61^c</td>
</tr>
<tr>
<td>Unilateral^a</td>
<td>.64^b</td>
<td>1.16^b</td>
<td>.57</td>
</tr>
<tr>
<td>Bilateral^a</td>
<td>.80^c</td>
<td>1.31^c</td>
<td>.66</td>
</tr>
<tr>
<td>Triplet</td>
<td>.67</td>
<td>1.20^f</td>
<td>.40^f</td>
</tr>
</tbody>
</table>

^a From a model that only contained the ewes that had two ovulations.
^b,c,dMeans with different superscripts within the same column were different (P < .05).
ewes was lowest in 2-yr-old ewes and increased steadily until 6 yr of age. However, in the other two lines, little change occurred with age of ewe.

Our data are in agreement with other studies on selection for reproduction. Clarke (1976) reported litter sizes of 1.13, 1.62 and 1.22 for their low, high and control lines, respectively. Turner (1978) reported litter sizes of 1.18 and 1.70 for the 0 and T lines, respectively. Response in other studies has been smaller, but most other studies have been of shorter duration and have been for litter size (Mann et al., 1978; Atkins, 1980; Bradford, 1985).

Figure 1. Distribution of ovulations among selection lines.

Figure 2. Least squares means for the age of ewe x selection line interaction for lambing rate at all services.
Embryo Survival. Embryo survival was only affected by line (P < .10). The general trend was for lowest survival in high-line ewes and highest survival in low-line ewes, with control line ewes intermediate (Table 1). Because data on fertilization rates were unavailable, embryo survival includes fertilization failure. However, as the number of eggs entering the uterus increases, embryo survival declines (Fogarty, 1984); therefore, high-line ewes, because of their higher ovulation rate, might be expected to have lower embryo survival. Nonetheless, fertilization failure also may have contributed to the low value observed in the high-line ewes. The data were reanalyzed with ovulation rate included in the model to examine the effect of selection on embryo survival independent of ovulation rate. There was no effect of line (P = .85) when ovulation rate was included in the model, nor was the line × ovulation rate interaction important. Therefore, any effect of line on embryo survival appeared
to be associated with the correlated response in ovulation rate that was a result of selection for reproductive rate rather than a correlated response in embryo survival to selection for reproductive rate. Thus, if the primary response to selection for increased reproductive rate is an increase in ovulation rate, only a portion of that increase in ovulation will be detected as an increased lambing rate or increased litter size.

Ewes with single ovulations had a higher (P < .01) embryo survival rate (73%) than did ewes with twin ovulations (61%), which was higher (P < .01) than the embryo survival rate for ewes with three ovulations (40%, Table 2). Embryo survival in unilaterally twin ovulating ewes was 57% compared with 66% for bilaterally ovulating ewes, but this difference was not significant (P > .10).

The effect of type of ovulation (unilateral or bilateral) on embryo survival has been studied on many occasions. Several experimenters reported little, if any, effect of type of ovulation in twin ovulating ewes (Sittman, 1972; Kelly and Johnston, 1983; Meyer, 1985; Bradford et al., 1986), whereas others (Casida et al., 1966; Doney et al., 1973; White et al., 1981) indicated an effect of type of ovulation in favor of those with bilateral ovulations. This difference may be related to migration of embryos between uterine horns (Scanlon, 1972; Sittman, 1972; Doney et al., 1973). Presumably, transuterine migration is routine in ewes with two ovulations on one ovary, but whereas migration decreases the effects of uterine crowding, failure to successfully migrate may cause embryo mortality (Scanlon, 1972).

![Figure 4. Relationship between ovulation rate and predicted litter size.](image-url)
To study the effect of adding one or two embryos to the pregnant ewe, prediction equations similar to those of Hanrahan (1982) and Bradford et al. (1986) were developed to predict litter size from ovulation rate. Restrictions imposed to make the equations comparable to those in the literature were: 1) records from ewes that failed to lamb were deleted and 2) predicted litter size of ewes with one corpus luteum was set to unity (i.e., the regression was forced through the point 1,1). There was no difference \((P > .10)\) between regression equations for high and control lines, but equations for both of them were different \((P < .05)\) from those for the low line (Table 3 and Figure 4). The increase in uterine efficiency (the percentage increase in litter size due to each unit increase in ovulation rate; Meyer 1985) from increasing ovulation rate from one to two was 62, 77 and 69% for low, high and control lines, respectively. However, the increase in uterine efficiency from increasing ovulation rate from two to three corpora lutea was \(-.35, .13 \text{ and } .18\) for the low, high and control lines, respectively. The first value represents very few observations. This compares to a uterine efficiency from the prediction equations of Hanrahan (1982) and Bradford et al. (1986) of 68 and 71% from increasing ovulation rate from one to two and 33 and 27% from increasing ovulation rate from two to three, respectively.

**Implications**

Selection based on high and low reproductive rate in the Rambouillet flock resulted in a change in lambing rate and litter size. These changes were due primarily to a correlated change in ovulation rate and not to changes in embryo survival. However, not all of the correlated change in ovulation rate resulted in more lambs because embryonic mortality and/or fertilization failure was higher in ewes with higher ovulation rates.

**Literature Cited**


