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Genetic and Environmental Impacts on Prenatal Lamb Loss[1]

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Introduction

Four 'facts' apply to most commercial sheep flocks:

1. Number of lambs sold has a greater influence on flock income than any other factor under the producer's control.

2. Ewes producing single lambs are money losers!

3. Producers put in great effort at lambing to maximize lamb survival and then fight predators to keep lambs alive until marketing.

4. **MANY SHEEP FLOCKS LOSE MORE LAMBS BEFORE LAMBING THAN AFTER.**

The average flock loses about 15% of lambs from birth to weaning. Numerous studies have shown that the embryonic loss rate in the first 30 days after mating often exceeds 20%. These are potential lambs which the producer never knew existed; however, they are just as surely lambs not marketed as are lambs eaten by coyotes, although lambs that die after birth will usually represent greater investment of feed and labor than those lost prenatally.

To the producer, the most important prenatal losses occur in ewes that ovulate two eggs but give birth to only one lamb. The ewe's costs for maintenance, labor, and depreciation are unchanged and usually more than the sale value of her resulting single lamb. Research results indicate that the percentage of twin-ovulators that lose one embryo ranges from about 10% to over 40%.

This paper will look at loss of potential lambs before lambing and some of the factors affecting loss rates.

Sequence of Events Before Lambing

Ovulation is the start of the reproductive process, and ovulation rate (number of eggs released by the ewe) sets the potential or upper limit of litter size. Breed, age of ewe, body condition, season, and pre-mating nutrition all influence ovulation rate. Ova have three major hurdles to cross before they appear as lambs - fertilization to become embryos, implantation of embryos, and survival of embryos/fetuses to parturition.

Ram fertility obviously plays a big role in fertilization of ova and resulting conception of ewes. Fertilization of multiple ova tends to be an all-or-none event, i.e. if any eggs are fertilized, they probably all are fertilized (Restall et al., 1976). That means that subfertile rams may reduce conception rates and result in a spread-out lambing, but they will not have a strong effect on twinning rate of pregnant ewes. Studying the reasons for fertilization failure is very difficult since there is no way of knowing which eggs are not fertilized until they are no longer in the system, and then it is too late to examine them.

Fertilized eggs (embryos) implant in the uterus at around 19 days following mating. By then the embryos have become cell masses that have sent out pregnancy signals to the reproductive system resulting in blockage of the next ovulation and estrus, and preparation of the uterus for implantation. Prior to implantation, embryos are distributed between the two uterine horns by an unknown mechanism. In ewes conceiving to a single ovulation, nearly 100% of the lambs develop in the horn adjacent to the ovarian source of the egg. In ewes conceiving to twin ovulations, nearly all ewes implant one embryo in each horn of the uterus, regardless of ovulation site. Since ovulation is a random event between ovaries, half of all twin ovulations are the result of both eggs coming from one ovary. Somehow, one of these eggs is 'sent' to the other horn of the uterus.

Embryos failing to implant at the critical time are lost. If no embryos implant, the ewe will return to service, typically at 24-28 days after the previous estrus. This probably explains many of the 'long cycles' observed in single-sire mating systems.

During a short 'colonization' period, multiple embryos compete for uterine attachment sites (caruncles) through which they will receive all nourishment during gestation. The number of caruncles in the uterus is limited, and it has been shown that there is a positive relationship between the birth weight of a lamb and the number of attachments between its placenta and its mother's uterus. Single lambs are not limited to attachments within one horn of the uterus - a portion of single placentas spread into the other uterine horn.

Real competition arises when ewes have

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multiple embryos within one uterine horn. Embryos with too few attachments ('feeding sites') have increased chance of loss; however, surviving embryos do not benefit greatly from the embryonic loss of sibs since the 'claiming period' for caruncles is past. Our ovulation rate/litter size data suggest that the fairly common observation of twin lambs differing greatly in birth weight is usually the result of a triple ovulation - the larger twin had one uterine horn to itself while the smaller twin is the survivor of two embryos which competed for caruncles in the second uterine horn. Likewise, the observation of light birth weights for single lambs born to Finnsheep or Booroola Merino mothers is probably a case of the lamb being a sole survivor from a high ovulation conception.

Embryos that successfully implant and survive to 30 days seem to suffer little mortality thereafter. We have seen very little loss after 30 days, the earliest time that embryos can be reliably counted by ultrasound.

Defining Embryo Loss

Embryonic losses might be considered in two categories - total loss and partial loss. Even when ewes are group mated to semen-tested high-fertility rams, a substantial proportion do not conceive at a single estrus. Results from large studies typically show 80% of ewes lambing in the first cycle; however, 80% of the remainder (i.e. about 16%) lamb in the second cycle and a portion of remaining ewes will lamb to matings in the third cycle if mating continues that long. As mentioned previously, some returning ewes had fertilized ova and were temporarily pregnant, however implantation failure resulted in the ewe returning to service in what would appear as a long cycle. The net portion of a ewe flock with total loss of all embryos is typically 2-5%.

A greater proportion of ewes are multiple ovulators who successfully implant at least one embryo but also lose at least one potential lamb. Current techniques do not allow determination of whether the loss of potential lamb(s) is due to failure in fertilization, implantation failure, or loss post-implantation.

One approach to addressing this difficulty on a flock or group basis is to combine all losses and analyze litter size relative to ovulation rate for ewes conceiving to multiple ovulations. Since it takes one embryo to establish pregnancy, one can then look at the success of turning additional eggs into lambs. This has been termed uterine efficiency (UE) by Meyer (1985) and defined as the mean increase in litter size resulting from ovulation of one additional egg. For twin ovulators, this amounts to the proportion of ewes that give birth to twins (since all had to be successful with at least one egg). For triple ovulators, UE is the difference in mean litter size between triple ovulators and twin ovulators. The same calculation is extended to higher ovulation records for studies involving prolific breeds.

Sources of Variation Affecting Embryo Loss

Ovulation Rate

Since ewes lambing as a result of conception to a single ovulation must produce one lamb, they are, by definition, 100% efficient. If they failed to produce a lamb, they would be counted as dry ewes. As described above, ewes conceiving to twin ovulation must be successful with one egg, but a proportion are not successful with both. As ovulation rate increases, success of additional eggs declines so that the difference in litter size between triple and twin ovulators (advantage due to third egg) will be less than the difference in litter size between twin and single ovulators (advantage of second egg) (Meyer, 1985; Robinson and Scaramuzzi, 1986; Meyer et al, 1994). It has been shown with prolific breeds that litter size peaks at about five ova - at higher ovulation rates litter size actually declines (Hanrahan, 1976; Piper and Bindon, 1981). This is probably due to the embryo competition for limited numbers of caruncles resulting in high embryonic losses (mentioned earlier).

Management Stress

Circumstantial evidence from New Zealand indicates that pre-implantation embryos may be especially susceptible to losses due to ewe stress occurring 10 to 15 days post-mating. Flocks that have been shorn during the mating season often exhibit a break in the lambing pattern. In some cases, lambing virtually ceases for several days. The lambing break occurs 132 to 137 days after shearing, corresponding to a time when shorn ewes would have been 10 to 15 days post-mating. Ewes either side of this time window seem to be largely unaffected.

Nutritional Stress/Body Condition

Ewes in poor body condition at mating, in addition to having lower ovulation rates, also experience increased embryo loss compared to ewes in good body condition. The impact of poor body condition may depend upon the genotype of the ewe.

Two studies conducted at Oregon State University produced ewes that were in either good or poor or body condition at mating (West, et al., 1991). Ewes in each group were then subjected to either good or poor nutrition for a period immediately following mating. In addition to the expected result that ewes in good body condition had higher ovulation rates than ewes in poor body condition, effects of body condition and post-mating nutrition on uterine efficiency of multiple-ovulating ewes were:

1. Body condition affected uterine efficiency:
   - Ewes in good body condition at mating produced more lambs from the same number of eggs than did ewes in poor body condition at mating.
   - Poor body condition reduced litter size more in triplet ovulators (by .35 lambs) than in twin ovulators (.15 lambs).
2. Post-mating nutrition affected uterine efficiency:
   - Dropping the nutrition level of good condition ewes resulted in lower uterine efficiency.
   - Returning flushed low condition ewes to poor nutrition resulted in loss of most of the lambs potentially gained from flushing.
3. Post-mating nutrition could not overcome the effects of pre-mating body condition:
   - Good feeding of poor condition ewes after conception did not overcome the effects of their poor body condition.

4. Effect of body condition on uterine efficiency depended upon ewe genotype:
   - Among ewes conceiving to twin ovulations, poor body condition reduced litter size of Coopworth x Polypay ewes but did not reduce litter size of Polypay ewes; however, poor body condition did reduce litter size among Polypay ewes conceiving to triple ovulations.

Similar effects of body condition on UE have been observed in Targhee and Finn x Targhee ewes (Meyer and Bradford, 1973): both genotypes exhibited reduced UE when in poor body condition; the effect was greater for triple than for twin ovulators; and negative effects on UE were less for the more prolific genotype.

Ewe Genotype

Numerous studies have shown that breeds differ in uterine efficiency. Initial studies indicated that genotypes of typically low litter size had both lower ovulation rates than other breeds and then produced fewer lambs even when they conceived to multiple ovulations. This has been reported in Australia for Merinos vs. Merino crossbred ewes and in New Zealand for Romneys vs. Romney crosses. In both cases, purebred ewes had both lower ovulation rates and lower litter size even when conceiving to twin ovulations. In Australia, as few as 50% of Merinos conceiving to twin ovulations produce twins (Kleeman et al., 1990; Wilkins, 1989). A study comparing Merinos and their crosses reported a UE value of .58 for purebred Merinos vs. .67 for Dorset crosses and .77 for Border Leicester crosses (Meyer et al., 1994). Data from New Zealand indicate that the portion of twin-ovulating Romneys producing twins may be as low as 50-60% (Quinlivan et al., 1966; Meyer and Clarke, 1982; Meyer et al., 1983). In a study where higher UE values were observed, litter size of twin-ovulating ewes ranged from 1.71 for Romneys to 1.75 for Dorset x Romneys, 1.88 for Border Leicester x Romneys and 1.93 for Finn x Romneys (Meyer, 1979).

The above results with ewes of Border Leicester or Finn breeding warrant further comment. The consistently high UE for Border Leicester crosses among non-exotic breeds (see also Cummings et al., 1975, and Meyer and Clarke, 1982) explains in part their popularity as a ewe sire breed in different countries and has served as the basis for their choice as recipients in several embryo transfer/multiplication programs.

The very positive effect of Finnsheep on embryo survival likewise appears to be a consistent breed characteristic. In a study of Targhee and Finn x Targhee ewes conceiving to twin ovulations, 90% of the Finn crosses managed to produce twins compared to only 70% of the straightbred Targhees (Meyer and Bradford, 1973). The previously mentioned body condition study including Polypay ewes (which are 1/4 Finn) also found an advantage of Polypays over Polypay crosses in which the Finn component is reduced. This was supported in a subsequent study (Nawaz and Meyer, 1991) in which purebred Polypay ewes conceiving to twin ovulations exhibited a mean UE of .96 compared to .85 for three Polypay crossbred genotypes and .74 for two genotypes containing no Polypay breeding.

Reports concerning other prolific sheep such as the Romanov (Ricordeau et al., 1982) and Javanese breeds (Bradford et al., 1986) suggest that the effect noted in the Finn may be common to prolific breeds. The highly prolific Booroola Merino in which prolificacy is due to a single allele shows a substantial UE superiority over other Merinos (Bindon et al., 1980) but does not achieve the levels seen in other prolific breeds (Meyer et al., 1994). The previously mentioned Border Leicester effect was quite evident in Border Leicester x Booroola crosses with the crosses having higher UE than purebred Booroolas at ovulation rates of two, three and four.

Further evidence of an effect of ewe genotype on uterine efficiency comes from a two-year study of immunization to increase litter size (Meyer et al., 1988). The study was conducted in a large crossbred commercial flock in which ewes were identified as to whether they were heavily blackface or showed no sign of blackface breeding - 'smutface' and brockle-face ewes were excluded from the study. Among ewes conceiving to twin ovulations, mean litter size of whiteface ewes (1.84) was .12 lambs greater than the average for blackface ewes (1.72) over two years. All ewes had been run together since birth and were group mated to the same rams.

Our ongoing studies with various ewe genotypes reinforce the above observation. In a recently completed five year study, whiteface ewes consistently demonstrated equal or higher uterine efficiency than Hampshire x whiteface crosses. In every year of the study, purebred Hampshires demonstrated the lowest uterine efficiency. Apart from the second year of the study (in which all ewes were in poor body condition at mating), whiteface ewes have averaged 89% of twin ovulators producing twin lambs compared to 83% for Hamp crosses and only 64% for purebred Hamps. In the second year of the study, all three groups ranged from 60 to 64% twinning, reflecting the earlier observation that poor body condition can have major negative effects on uterine efficiency.

Embryo Genotype

Although the effect appears to be smaller, there is evidence that genotype of the embryo (i.e. breed of ram used) may also affect embryo success. In the above study with whiteface, Hamp crossbred and purebred Hampshire ewes, a variety of sire breeds were randomized across ewe genotypes. However, in each of the five years, one of the sire breeds used was Suffolk with the rams used each year coming from the same large purebred flock with care taken to insure that rams were unrelated. In every year, twin-ovulating ewes mated to Suffolk rams have had lower litter size than ewes mated to whiteface rams.

In the second year of the above trial, when body condition of ewes was low, twin-ovulators conceiving to Suffolk rams had a mean litter size of only 1.46 compared to 1.73 and 1.81 for ewes mated to Texel and Dorset rams, respectively. The low UE of ewes mated to Suffolk rams was not due to low values for a single ram, since the three Suffolk rams had values of 1.43, 1.45, and 1.50 lambs born from conceptions to twin ovulations - all were below the lowest value for any Texel or Dorset ram.

The effects of embryo genotype and ewe genotype may be additive. The lowest UE observed for any ewe x sire combination consistently came from purebred Hampshire ewes mated to Suffolk rams - only 40% of these ewes produced twins after conceiving to twin ovulations.

Ewe Age

Few studies of embryo loss have been large enough to examine the effect of ewe age on loss rates. An exception was a large trial involving 2246 ovulation/lambing records of Booroola and Merino-derived genotypes (Meyer et al., 1994). Young (two- and three-yr.-old) ewes consistently exhibited the lowest UE with litter sizes averaging 10% below the overall means for respective ovulation rates. Within ovulation classes, four-through six-year-old ewes exhibited comparable mean litter sizes with litter size dropping off among seven-year-old ewes.

Summary/ Recommendations

1. Recognize that body condition affects uterine efficiency and that while flushing increases ovulation rate, only a portion of the extra eggs will be realized as lambs.

2. Post-mating nutrition is important for embryonic success, especially if ewes are in poor body condition. Good nutrition should extend as least three weeks beyond mating. It is better to sort off the 50% of ewes in poorest body condition and flush them both before and after mating rather than to flush all of the flock before mating and discontinue the extra nutrition early.

3. Among genetic effects, both Border Leicester and Finn genes increase embryonic survival with Finn genes having the larger effect.

4. Choice of ram breeds may influence embryo loss (and definitely affects post-natal losses), especially if ewes are in poor body condition. Blackface breeding seems to be detrimental to embryo survival compared to white-face breeding.

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