

A Model of Litter Size Distribution in Cattle

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ABSTRACT: Genetic increases in twinning of cattle could result in increased frequency of triplet or higher-order births. There are no estimates of the incidence of triplets in populations with genetic levels of twinning over 40% because these populations either have not existed or have not been documented. A model of the distribution of litter size in cattle is proposed. Empirical estimates of ovulation rate distribution in sheep were combined with biological hypotheses about the fate of embryos in cattle. Two phases of embryo loss were hypothesized. The first phase is considered to be preimplantation. Losses in this phase occur independently (i.e., the loss of one embryo does not affect the loss of the remaining embryos). The second phase occurs after implantation. The loss of one embryo in this stage results in the loss of all embryos. Fewer than 5% triplet births are predicted when 50% of births are twins and triplets. Above 60% multiple births, increased triplets accounted for most of the increase in litter size. Predictions were compared with data from 5,142

calvings by 14 groups of heifers and cows with average litter sizes ranging from 1.14 to 1.36 calves. The predicted number of triplets was not significantly different ($\chi^2 = 16.85$, $df = 14$) from the observed number. The model also predicted differences in conception rates. A cow ovulating two ova was predicted to have the highest conception rate in a single breeding cycle. As mean ovulation rate increased, predicted conception to one breeding cycle increased. Conception to two or three breeding cycles decreased as mean ovulation increased because late-pregnancy failures increased. An alternative model of the fate of ova in cattle based on embryo and uterine competency predicts very similar proportions of singles, twins, and triplets but different conception rates. The proposed model of litter size distribution in cattle accurately predicts the proportion of triplets found in cattle with genetically high twinning rates. This model can be used in projecting efficiency changes resulting from genetically increasing the twinning rate in cattle.

Key Words: Cattle, Multiple Births, Prediction, Conception, Models, Genetics

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Introduction

Increased twinning in beef cattle is predicted to improve the efficiency of beef production (Guerra-Martinez et al., 1990). Along with genetic increases in twinning comes the possibility of increases in triplets and quadruplets. Even though management may be able to adapt to the increased requirements of twinning, triplets and quadruplets require even greater management inputs.

The prediction of the distribution of litter sizes in cattle is needed to assess the bioeconomic consequences of genetically increased twinning in cattle. Current levels of twinning in beef cattle are low, and even experimental herds with increased twinning are

unlikely to have reached optimal levels of twinning. Models need to predict litter size distribution at mean genetic levels higher than current genetic levels of twinning. The purpose of this research is to predict the number of triplet births at different mean litter sizes in cattle.

Materials and Methods

A model that combines empirical and biological components was developed for prediction. The model begins with an empirically derived distribution of ovulation rate and then reduces ovulation rate to litter size by a series of biologically motivated steps and rules.

Ovulation Rate. No populations of cattle with natural ovulation rates at the levels that need to be predicted have ever been documented. Both sheep and cattle have phylogenetic origins in the family Bovidae. Some populations of sheep have ovulation rates

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ranging from one to five or more. This is a useful range for predicting twins and triplets in cattle. Therefore, data from sheep were used to predict the distribution of ovulation rate in cattle.

Ovulation rates for Romanov ewes at four ages (8 to 10 mo, 1 to 2 yr, 2 to 3 yr, and 3 to 5 yr) reported by Ricordeau et al. (1982) were used. The assumed model for ovulation rate was the threshold model for ordered categorical data (Pérez-Enciso et al., 1994). This model transforms a normal distribution of liability into proportions of ordered categories (ovulation rate). (See Figure 1.) The method of Gianola and Foulley (1983) was used to fit the four thresholds defining ovulation rates of 1, 2, 3, 4, and 5 or more simultaneously with the mean liabilities for the four age groups. The four thresholds were estimated to be $-1.9296 \pm .1007$, $-.0062 \pm .0476$, $1.8221 \pm .0710$, and $2.9864 \pm .1016$, respectively. Only the differences between thresholds are important, so for convenience the thresholds were centered on the threshold between two and three ova to yield thresholds (δ_i , $i = 1 - 4$) of -1.9234 , 0 , 1.8283 , and 2.9926 . The formula for the proportion of i ova is

$$\Phi(\delta_i - \eta) - \Phi(\delta_{i-1} - \eta) \quad [1]$$

Thresholds δ_0 and δ_5 equal $-\infty$ and $+\infty$, respectively; Φ is the standardized cumulative normal distribution; and η is the mean of the underlying standard normal liability distribution.

Initially, the thresholds for ovulation rate were based on an unreported number of Lacaune sheep used by Pérez-Enciso et al. (1994). Ovulation rate thresholds were much narrower than those derived from the Romanov data reported by Ricordeau et al. (1982) and resulted in many more singles and triplets and fewer twins than were found in the cattle twinning data. Consequently, the Romanov data were used to parameterize ovulation rate.

Changing the mean of the underlying standard normal liability distribution changes the proportions of 1, 2, 3, 4, and 5 ova and therefore the mean ovulation rate. The mean ovulation rate is much lower in cattle than in Romanov sheep, so lower mean liabilities were used for cattle. This difference is illustrated in Figure 1.

Embryo Survival. The success of an embryo in producing a calf at birth was determined by a series of simple steps and rules. These steps were motivated by hypotheses about the functional interactions of embryo and the uterus in the reproductive physiology of cows but not including all of the known complexity. A central tenet is that embryo loss can be divided into two stages (Echternkamp et al., 1990). Each embryo has a probability of failure in each of the two phases. Loss of one or more embryos in the early, preimplantation phase does not affect the remaining embryos (independent loss). Loss of one or more embryos in the later, postimplantation phase causes the loss of all the remaining embryos as well (dependent loss) as a result of placental anastomosis. Also, more than three

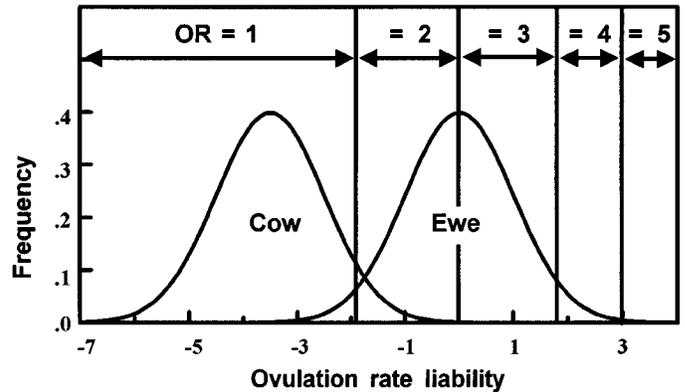


Figure 1. Estimated underlying distribution for ovulation rate (OR) in Romanov ewes and representative predicted underlying distribution in cows with a moderate level of twinning. Thresholds between different OR are indicated by vertical lines.

surviving embryos in the same uterine horn cause the loss of the entire litter (Echternkamp, 1992).

Initially, all losses of embryos are assumed to be independent. Later, the dependent loss is calculated. The combinations of embryos that independently survive or fail in the two phases can be determined from a trinomial distribution given the probabilities of early and late embryo loss. The trinomial distribution for the probabilities of $M1$ embryos failing in the early period, $M2$ embryos independently failing in the second period, and S embryos surviving both periods given probabilities of $m1$ for failing in the early phase and $m2$ for independently failing in the later phase is

$$\frac{(M1 + M2 + S)!}{M1! M2! S!} m1^{M1} m2^{M2} (1 - m1 - m2)^S \quad [2]$$

The probability of early-phase and late-phase independent losses were estimated to be .209 and .098 from an earlier stage of the experiment (Echternkamp et al., 1990).

Dependent loss can then be simulated by removing all litters with at least one fetus lost in the late phase. Additionally, proportions of litters with four and five surviving fetuses are removed, which reflects the probability of having more than three fetuses in one horn. These proportions were based on the binomial distribution assuming the probability of an ovum on the right side is .6 and on the left side is .4. The probabilities of right- and left-side ova approximate those found in Echternkamp et al. (1990). The proportion of four surviving fetuses all on the right side is $.6^4$ and all on the left side is $.4^4$, which totaled .1552. The proportion of five surviving fetuses with either four or five on the right side is $.6^5 + 5 \cdot .6^4 \cdot .4^1$ and with four or five on the left side is $.4^5 + 5 \cdot .4^4 \cdot .6^1$, which totaled .4240.

Litter Size Model. The ovulation rate distribution and embryo survival components were combined to

develop a model to predict the distribution of litter size. The steps and rules are described and incorporated in the following algorithm.

- Step 1. Determine the proportions of 1, 2, 3, 4, and 5 ova based on a mean liability and the thresholds described above.
- Step 2. Use a trinomial distribution with probabilities for loss in the early and late phases to determine the proportions of embryos lost in each phase for each ovulation rate. Temporarily assume all losses are independent.
- Step 3. Determine the dependent loss of embryos resulting from the independent loss of embryos in the late phase.
- Step 4. Determine the dependent loss that is due to having more than three fetuses in the same uterine horn by removing .1552 of litters with four surviving fetuses and .4240 of litters with five surviving fetuses.
- Step 5. Multiply the proportions of each ovulation rate by the probabilities of 0, 1, 2, 3, 4, or 5 fetuses surviving to term.
- Step 6. Sum the probabilities of 0, 1, 2, 3, 4, or 5 fetuses across all ovulation rates.

The preceding steps predict proportions of 0, 1, 2, 3, 4, or 5 fetuses given a mean liability for ovulation rate. Additionally, mean litter size, proportion of all births that are multiples, and proportion of all matings resulting in multiple births could be calculated. In all cases, there is a unique mean liability for ovulation rate associated with each value of mean litter size or proportion of multiple births. This one-to-one correspondence of mean liability for ovulation rate to mean litter size or proportion of multiple births allows the mean liability to be determined from observed values for mean litter size or proportion of multiple births by numerical methods.

Validation. Data from the twinning experiment conducted at the U.S. Meat Animal Research Center from 1989 through 1995 were used to test the predictions (Gregory et al., 1997). Two groups of females, first-calf heifers and older cows, were used for each year because the means of the two groups could differ. The mean of observed litter size was used to numerically solve for η , the mean liability for ovulation rate, so that observed and predicted average litter sizes were identical. However, the distribution among singles, twins, and triplets was constrained only for total number of litters and average litter size, leaving 1 df for a χ^2 test for each of the 14 birth year by cow ages tested.

Results and Discussion

Predicted litter size, percentage of triplets, and percentage of quadruplets are shown in Table 1 for

Table 1. Average litter size and percentage of triplet and quadruplet births predicted from percentage of multiple births

Multiples, %	Mean litter size	Triplets, %	Quadruplets, %
5	1.050	.0	.0
10	1.101	.1	.0
15	1.152	.2	.0
20	1.203	.3	.0
25	1.256	.6	.0
30	1.309	.9	.0
35	1.364	1.4	.0
40	1.421	2.1	.0
45	1.482	3.1	.0
50	1.546	4.6	.0
55	1.617	6.6	.1
60	1.696	9.4	.1
65	1.787	13.2	.2
70	1.894	18.3	.5
75	2.020	24.6	1.2

frequencies of multiple births ranging from 5 to 75%. Predicted mean litter size exceeded 2.0 calves when multiple births were 75%. Predicted quadruplets did not exceed 1.2% and were less than .5% when multiple births were 50% or fewer. Predicted triplets were fewer than 5% when multiple births equaled 50% but predicted triplets increased rapidly above 50% multiple births. Increases in predicted triplets and quadruplets accounted for most of the increase from 60 to 65% multiple births and all of the increase from 65 to 75% multiple births. In fact, predicted frequency of twins actually decreased from 51.2 to 49.2% as multiple births increased from 70 to 75%.

Numbers of heifers and older cows by litter birth year and litter size at birth are shown in Table 2. No quadruplets were observed in these data. Mean litter size ranged from 1.14 to 1.36. The total χ^2 was 16.85 with 14 df ($P = .26$), which indicates a good fit between observed and predicted distribution of litter size when the mean litter size is known and is not greater than 1.36.

Unlike statistical models that are fitted to data, this model is a combination of empirical and mechanistic approaches that was parameterized outside the data, with the exception that Romanov data were used instead of Lacaune data. It is impossible to validate the model at genetic levels of 60% multiple births because herds at this level have not been documented. However, it is appropriate to put more confidence in predictions based on a valid mechanistic model than in those based on an empirical model with parameters that were obtained solely from fitting data when predicting responses outside the data range (France and Thornley, 1984; Black, 1995).

The model of litter size in cattle also has implications for conception and pregnancy rates. Having more embryos at ovulation is more likely to result in the survival of at least one embryo during the first phase,

Table 2. Observed and predicted number of singles, twins, and triplet births by year and cow age

Year and cow age	Observed litter size			Predicted litter size			χ^2
	1	2	3	1	2	3	
1989							
Heifer	102	20	1	101.3	21.4	.3	1.59
Cow	436	66	3	433.3	71.0	.7	6.53
1990							
Heifer	114	35	0	114.7	33.6	.7	.78
Cow	459	99	0	460.1	96.5	1.3	1.48
1991							
Heifer	151	41	0	151.7	39.6	.7	.79
Cow	461	137	4	459.9	139.2	2.9	.31
1992							
Heifer	159	24	1	158.1	25.6	.3	1.95
Cow	454	160	4	454.0	159.9	4.1	.02
1993							
Heifer	150	55	3	148.7	57.7	1.7	1.06
Cow	388	142	3	388.7	140.6	3.7	.22
1994							
Heifer	132	56	1	132.7	54.6	1.7	.38
Cow	364	183	8	363.3	184.1	7.5	.01
1995							
Heifer	173	50	1	173.0	50.0	1.0	.00
Cow	337	161	4	338.5	157.8	5.8	.75
Total	3,880	1,229	33	3,877.8	1,231.6	32.4	16.85

because losses are independent. Having more embryos at the beginning of the second phase is less likely to maintain pregnancy, because embryo losses are dependent. Therefore, higher-ovulating cows are expected to have higher initial conception but also higher late-gestation pregnancy failures than would cows that ovulate one ovum. Cows with early pregnancy failure may have an opportunity to rebreed, but those with late pregnancy failure would not have an opportunity to rebreed in the same season.

Table 3 shows the predicted early and late embryo losses for a single mating and full-term pregnancy rates for one, two, and three mating cycles; we assume that early embryo loss in the first cycle allows for two more mating opportunities and early embryo loss in

the second cycle results in one more opportunity. Single-cycle pregnancy rate increases up to 60% multiple births, but pregnancy rate following two or three cycles is predicted to decline slightly. At high ovulation rates there is little difference in pregnancy rate between one- and three-cycle breeding seasons.

Rutledge et al. (1993) have proposed a model for evaluating the survival of embryos based on a combination of ova or embryo competency and uterine (recipient) competency. McMillan (1996) has made a similar analysis of embryo transfer studies. In this model, the survival of each embryo is independent of the survival of other embryos, but the uterus may be incompetent, which results in pregnancy failure. Table 4 shows the probabilities of transition from number of

Table 3. Pregnancy rates predicted from proportion of births that are multiples

Multiples	Single-cycle embryo losses		Pregnancy rate by number of breeding cycles		
	Early	Late	1	2	3
			%		
1	20.7	9.9	69.4	83.8	86.7
10	18.5	11.1	70.4	83.4	85.8
20	16.0	12.5	71.5	83.0	84.8
30	13.4	13.9	72.7	82.4	83.7
40	10.8	15.5	73.7	81.7	82.5
50	8.3	17.2	74.5	80.7	81.2
60	5.8	19.2	75.0	79.3	79.6
70	3.6	21.8	74.6	77.3	77.4

Table 4. Comparison of transition probabilities from ovulation rate to calves at birth using an embryo-uterine competency model^a or an embryo dependence model

No. of calves born	Embryo-uterine model ^a ovulation rate				Embryo dependence model ovulation rate			
	1	2	3	4	1	2	3	4
0	.375	.230	.197	.189	.307	.230	.275	.376
1	.625	.290	.101	.031	.693	.290	.091	.025
2		.480	.334	.155		.480	.301	.126
3			.369	.342			.333	.278
4				.283				.195

^aBased on Rutledge et al. (1993).

ova to calves at birth for the embryo-uterine competency model and the embryo dependence model proposed in this research. Both models were parameterized so that the transition probabilities for two ova were identical. The primary difference between the models is the probability of no calves at birth. The embryo-uterine competency model predicts decreasing pregnancy failure with increasing number of ova. The embryo dependence model predicts the lowest rate of pregnancy failure when ovulation rate is two. Data sufficient to test these different predictions were not identified. There is little difference in the relative proportions of singles, twins, and triplet births between the models. The embryo-uterine competency model fit to the data in Table 2 ($\chi^2 = 17.01$, $P = .26$) was similar to the embryo dependence model. The implications of the embryo-uterine competency model on conception and pregnancy following more than one mating cycle are not clear. Neither the timing of embryo loss nor the persistence of uterine incompetency is directly specified.

Conclusion. The distribution of singles, twins, and triplets in cattle can be accurately predicted from mean litter size within the range of data available. Accuracy beyond this range depends on the appropriateness of the combination of empirical and mechanistic elements of the model. The proposed model has implications for conception rates as well as litter size distribution. The main difference between the proposed model and an alternative model of embryo survival is pregnancy rate and not the distribution of litter size among those that calve.

Implications

A proposed model of litter size distribution in cattle accurately predicts the proportion of triplets found in cattle with genetically high-twinning rates. Predicted

triplets are fewer than 5% when twins and triplets represent 50% of births. This model can be used in projecting efficiency changes resulting from genetically increasing the twinning rate in cattle.

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