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Partial failure of multiple ovulations - a question of uterine efficiency or embryo quality?

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ABSTRACT

Amongst individuals that produce multiple ovulations, and conceive, a variable proportion fail to deliver all potential offspring at term. This source of reproductive inefficiency has been termed partial failure of multiple ovulation (PFMO). In the case of twin ovulators, PFMO is manifest as single births. Most reports in the literature have attributed PFMO to uterine capacity or efficiency factors. An alternative model is proposed, in which it is assumed that a given reproductive outcome is determined by independent binomial effects of embryos and uterine/maternal factors. Using this model, it can be demonstrated that PFMO in twin ovulators can only occur because one of the two embryos is not competent to survive - that is, the uterine/maternal component plays no role in determining variation in PFMO. It follows that in pregnant farm animals with twin ovulations 100% twin births is possible, but is only constrained by low embryo quality. All published data examined to date in sheep cattle and goats are consistent with this alter–native model.

Keywords: partial failure of multiple ovulation, uterine efficiency, embryo quality, embryo survival

INTRODUCTION

Reproductive efficiency is an important component of biological as well as economic efficiency of many animal production systems. Since the incidence of monozygotic twins is low, a high incidence of multiple ovulations is a prerequisite for high levels of reproductive performance. Under field conditions in sheep and cattle, this requirement can be met by a higher incidence of twin (or possibly triplet) ovulating females. Alternatively, multiple embryos could be transferred to single ovulating females to increase reproductive efficiency.

It is well documented that reproductive efficiency is not absolute and that some reproductive wastage occurs. Under New Zealand conditions, this has been studied extensively in sheep. For example, it has been demonstrated in commercial flocks that a mean of 26 potential lambs are lost between mating and lambing (Kelly, 1982). Importantly, 19 of this 26 potential lambs were lost because multiple ovulating ewes which lambed produced fewer lambs than indicated by their ovulation rate at conception time. This source of loss has been termed partial failure of multiple ovulation (PFMO) (Kelly, 1982). In the context of this paper, the term is restricted to only those females which have twin ovulations.

Definitions

PFMO is defined as the percentage of all twin ovulating females which deliver a single offspring at term rather than twins (% twin ovulating and single offspring/twin ovulating and single + twin offspring). The term embryo is used in its broadest sense to include the conceptus through to term. The PFMO concept can equally be applied to recipient females which receive twin embryos as a result of embryo transfer.

Aims

The aims of this paper are to:
- briefly review factors affecting PFMO, and
- describe 3 models that may explain variation in PFMO

Brief review of factors affecting PFMO

PFMO varies considerably between flocks. For example, amongst 61 commercial flocks the proportion of ewes undergoing PFMO varied from 11-56% with a mean of about 30% (Kelly, 1980). Furthermore, there was no evidence in that study to suggest that the incidence of PFMO changed during the joining season. In another study, the incidence of PFMO ranged from 12-54% amongst mobs of research ewes with an average of 31% (Meyer *et al.*, 1983). PFMO appears to be lower in ewes which have had 2 rather than 1 or 0 ovulations (25 vs 35 vs 39%) in the previous cycle (Kelly and Smith, 1980). The incidence of PFMO appears to be similar in ewes with bilateral (one on each ovary) and unilateral (both on one ovary) ovulations (28 vs 25%, Meyer *et al.*, 1983).

MODELS FOR PFMO

Partial failure of fertilisation (PFF)

PFF may be defined as the proportion of twin ovulating females which have only one fertilised egg instead of two when examined within a few days of mating. Fertilisation rates are high in New Zealand sheep flocks (90-100%) (Quinlivan *et al.*, 1966). The incidence of PFF is low in sheep (2-8%, Moore, 1981). This has lead to the concept that fertilisation failure is apparently an all-or-none phenomenon in multiple ovulating ewes (Restall *et al.*, 1976). PFF is thus an unlikely contributor to PFMO, at least in sheep.

Binomial Model

A possible model to explain PFMO is that embryo survival is occurring in an independent binomial manner. A sheep example will be used to illustrate the model. If embryo survival resulting from each of a pair of ovulations within a ewe are considered to be independent binomial events, then the expected distribution of ewes within a mob with 0, 1 or 2 lambs at term can be calculated depending on the actual embryo survival rate for the given mob of ewes. Thus, if embryo survival for a mob of twin ovulating ewes is 0.60 (60%), then 16, 48 and 36% would be expected to produce 0, 1 or 2 lambs. These values are derived through the binomial expansion of $(p + q)^2$ where p is embryo survival rate and $(p + q) = 1$. If this model holds, we would expect p to equal 0.82 for a flock with a 30% incidence of ewes with PFMO (since PFMO = $2q/(2q + p)$). Furthermore, according to the model, only 3% (q^2 or 0.18 x 0.18) of ewes would fail to lamb to mating at the twin ovulation when PFMO is 30%. Since this is not consistent with field and research results (e.g., 30% Restall *et al.*, 1976; 23% Kelly and Knight, 1979), it is assumed that this simple binomial model of embryo survival cannot adequately explain PFMO in sheep. Echternkamp *et al.*, 1990 reported that the binomial model could not adequately explain observed calving outcomes in twin ovulating cows. Collectively, the binomial model of embryo survival does not appear to adequately explain PFMO.

Embryo and maternal model

According to this conceptual model, embryo survival can be partitioned into embryo and maternal contributions. Furthermore each contribution is considered to be an independent binomial event. Thus, the proportion of competent embryos in a population could be designated as e (not competent proportion is thus 1-e) and the proportion of females competent at becoming pregnant could be designated as r (not competent proportion is thus l-r). Furthermore, it is assumed that a common r applies whether single or twin embryos are present. It is useful to think of e as the potential survival rate of the embryos - that is, the survival rate of embryos if all females were capable of sustaining a pregnancy to term (i.e., r = l for all such females). However, because the maternal competency is usually less than unity, actual embryo survival rate is less than potential embryo survival rate, e. Similarly, r can be viewed as potential pregnancy rate given e values of unity.

Estimating e and r

With single ovulating females, the expected proportion of surviving embryos is thus e.r. (the proportion of competent embryos and competent recipients of these embryos). It follows that the proportion of failed pregnancies is 1-e.r. It follows that the expected proportion of females with twin pregnancies is e^2r. This estimates the proportion of females in a mob that are inherently capable of becoming pregnant that also have two inherently viable embryos present. The expected proportion of females with single pregnancies after a twin ovulation is 2.e.(1-e).r. It can be seen that these females must be inherently capable of becoming pregnant and must have one competent and one incompetent embryo present. For the sake of completeness, the proportion of females which fail to become pregnant is the composite of the remaining 5 subgroups of varying combinations of competent/incompetent embryos and females, represented by the term l-2.e.r + e^2r. Values for e and r for any given data set are derived by simultaneously solving the five equations (single ovulating and 0 or 1 offspring; twin ovulating and 0, 1 or 2 offspring) so as to provide estimates that are as close as possible to the observed data. In practice, a goodness of fit test such as a minimised chi square statistic could be used to determine appropriate values for e and r.

Conceptually, it may help to imagine embryos being sampled at random from a population (in singles or pairs) containing some 'good' embryos (e represents this proportion) and 'bad' embryos (l-e represents this proportion). These embryos are then matched with a sample of females from another independent population containing some 'good' (r represents this proportion) and 'bad' (l-r represents this proportion) females which act as recipients of the embryos and provide the 'maternal' component.

The above equations for twin ovulating ewes can be rearranged to represent the expected proportion of twin ovulating and pregnant females which have only one rather than two offspring at term, i.e., the proportion of females exhibiting PFMO. Thus, the expected incidence of PFMO in a given group of females is represented by the term [2.e.(1-e).r]/[2.e.(1-e).r + e^2r] which reduces to l-{e/(2-e)}. It is clear from this relationship that their is no r term and therefore no uterine/maternal contribution to PFMO. It follows that the only source of variation in PFMO is variation in e. This is not surprising since all pregnant females, by definition, must have an r value of unity and thus any variation in PFMO can only arise from differences in e.

Information on the incidence of PFMO can be used to estimate e. The relationship between these two parameters is plotted in Figure 1 and allows e values to be estimated by inspection if the incidence of PFMO is known. This model can now be tested using published data sets where, for example, lambing outcomes of single and twin ovulating ewes are known.

How well does the 'e and r' model predict actual PFMO?

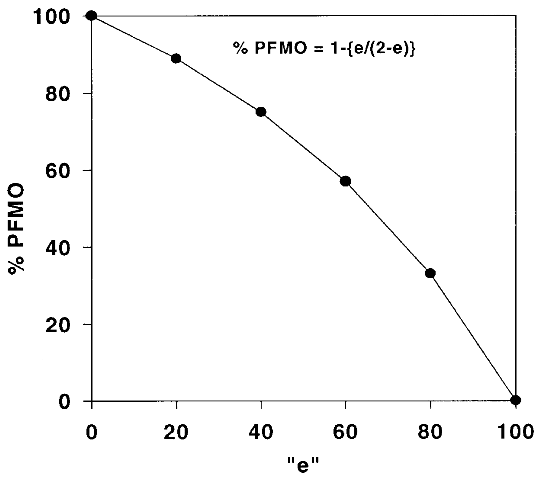
The model was tested using published data on sheep, cattle and goat reproductive performance (Table 1). This was achieved by estimating e and r as described above and then e was used to estimate expected PFMO (as per Figure 1). This expected value for PFMO was compared with the actual PFMO value based on the published data used in the estimations. In the case of sheep, lambing data in single and twin ovulating ewes were used to estimate e. For cattle, single and twin ovulating cattle as well as single and twin embryo transfer recipient data was used. Only single and twin embryo transfer recipient data from goats was available. In the case of the cattle and goat twin transferred recipients, PFMO can be interpreted as the ratio of recipients which produce a single offspring to recipients which produce single and twin offspring.

There is little difference between the 9 expected PFMO estimates and the 9 corresponding actual estimates

TABLE 1: Comparison of e, actual PFMO and expected PFMO in sheep, cattle and goats

Source	Description	e	Actual PFMO	Expected PFMO
Kelly & Johnstone, 1983 (Sheep)	Single and twin left ovulators (N = 1961)	0.87	0.25	0.23
	Single and twin right ovulators (N = 2541)	0.86	0.25	0.25
	All single and bilateral twin ovulators (N = 4445)	0.86	0.27	0.25
	All ewes (N= 6517)	0.86	0.25	0.25
Smith and McGowan, 1986 (Sheep)	Single and twin ovulating 1984 Control ewes (N = 77)	0.78	0.35	0.36
Kelly and Allison, 1976 (Sheep)	Single and twin ovulating ewes (N = 509)	0.82	0.33	0.31
Echternkamp et al., 1990 (Cattle)	Single and twin ovulating cows (N = 474)	0.79	0.38	0.35
McMillan, W.H. 1995 (Cattle)	Single and twin in vitro embryo recipient cows (N = 604)	0.63	0.56	0.54
Armstrong et al., 1983	Single and twin embryo recipient goats (N = 380)	0.77	0.36	0.37

FIGURE 1: Relationship between e and PFMO (PFMO = 1-{e/2-e)})



(Table 1). In fact, the maximum difference was 0.03 units. Collectively, these data indicate that the 'e and r' model of PFMO adequately explains all published data examined. One way of experimentally testing the model is to transfer embryos of known and contrasting e (i.e., known and contrasting PFMO) into a common pool of recipients. According to the model, the incidence of PFMO would differ between the two groups of embryos. Published data in sheep are consistent with this proposition (e.g., Larsen and McDonald, 197l).

SUMMARY AND CONCLUSIONS

The most appropriate of the three models examined was the 'e and r' model of embryo survival which partitions embryos survival into independent embryo and maternal components. According to this model, variation in PFMO arises exclusively from variation in e (interpreted broadly as embryo quality) and not r (or uterine/maternal quality). Thus, embryo quality rather than uterine efficiency is more likely to involved in explaining variation in PFMO. Research efforts aimed at improving embryo quality would thus be expected to yield improvements in reproductive wastage from PFMO. With bovine *in vitro*-produced embryos, the converse has been demonstrated in that PFMO in recipients has been higher with the transfer of freeze-thawed rather than fresh embryos (McMillan, unpublished).

One of the implications of the model is that a mob or flock with a 100% twinning rate (or conversely a 0% incidence of PFMO) at term is possible. The only limitation on achieving this is the competency of the embryos in the pregnant females.

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