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SELECTION FOR INCREASED COW FECUNDITY: A REVIEW*

L. R. PIPER and B. M. BINDON
CSIRO, Division of Animal Production, Armidale, N.S.W., Australia

SUMMARY

Efficiency in the beef industry is directly related to reproduction rate. Increases in fertility, calf survival or fecundity will increase reproduction rate, but major changes are possible only through changes in fecundity.

Rapid initial increases in twinning rate may be achieved by intense selection of foundation stock, and performance records from several recently established herds confirm the expected phenotypic consequences of such selection. Within the line, continued selection based on dam's twinning record should lead to annual rates of improvement of about 0.8%.

The advent of strains of cattle with increased fecundity would allow proper assessment of the value of increased twinning and would provide the means of rapidly augmenting reproduction rate in those sections of the national herd where appropriate environmental conditions already exist or can be economically provided.

INTRODUCTION

Unlike animals in the wool, sheep-meat, or dairy industries, the beef cow produces no marketable product other than her calf crop. Furthermore, since the average calf crop (number of calves weaned per cow exposed to the bull per year) almost never exceeds one and is usually less than 0.9 (*e.g.*, Bichard and Özkütük, 1977), there are likely to be substantial benefits in economic efficiency associated with increased reproduction rate (Moav, 1966; Dickerson, 1970, 1978).

Increases in reproduction rate may be achieved by increases in fertility (proportion of cows pregnant), fecundity or litter size (number of offspring/pregnancy), or calf survival (proportion of calves weaned of those born), but the total increase that is ultimately possible depends on the component that is being manipulated. Thus, with maximum fertility and calf survival, reproduction rate will only equal the current average litter size,

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which is of the order of 1.005 to 1.045 (Johansson *et al.*, 1974; Rutledge, 1975). Since the cow has four functional mammary glands and often has a high level of milk production, it seems well equipped to cope with two or more offspring.

This paper reviews the theoretical aspects of increasing litter size in cattle by genetic means and brings together some of the early results from several recently established herds in which selection for increased litter size is being practised.

EXPECTED RESPONSE TO SELECTION

Single-record estimates of the heritability of twinning considered as an *all or none* trait and excluding heifer calvings range from 1.8 to 11%, with an average of around 3%. Equivalent estimates for repeatability range from 2.9 to 12.7%, with an approximate mean of 6% (Maijala and Syväjävi, 1977).

With these parameters and an unselected foundation population having a mean twinning incidence in adult cows of around 3%, the expected annual response to conventional mass selection will be extremely small. Land and Hill (1975) derived expected annual responses of the order of 0.1 to 0.15% when replacements were chosen on dam's twinning record. These expectations would be little altered if in addition some selection among dams on their own records was allowed. As an alternative to this basic design, Land and Hill (1975) examined the effects of using laparoscopy to measure the natural ovulation rate of animals over several oestrous cycles followed by super-ovulation and egg transfer from selected females. The rate of progress in ovulation rate (and by implication in litter size) was dependent on the base population twin ovulation incidence, and was found to be unlikely to exceed 0.6% per year unless that incidence exceeds 8%.

The key to increasing litter size by genetic means is to raise the initial incidence of twinning by intense selection of foundation animals. Johansson *et al.* (1974) examined a programme in which cows which had previously had at least two sets of twins were joined with the best 20% of progeny tested bulls (1000 daughter litter size records/bull), and calculated that the twinning rate in the progeny should increase by about 3%. Qualitatively similar schemes were suggested by Land and Hill (1975) and Maijala and Syväjävi (1977), but no estimates of expected progress were provided. Piper and Bindon (1979) investigated a design where foundation females had previously had at least two sets of twins and where foundation bulls were chosen as the sons of cows with very extreme twinning records (3 to 8 sets of twins plus higher order births in some cases). The expected twinning rate in the progeny of foundation animals was estimated in two ways. In the first approach, selection response was calculated in the conventional manner from the *all or none* scale heritability and selection differentials. Estimated initial gain was 2.5%, but for traits such as twinning with *all or none* expression and low incidence this method of calculating responses is likely to yield estimates that are substantially biased downwards (Dempster and Lerner, 1950). In the alternative approach (Falconer, 1965) which should be free of this bias, the estimates of response were derived in terms of an assumed underlying normally distributed scale of twinning tendency. Using this method, the predicted initial gain increased to 5%, giving an estimated twinning frequency in adult first generation progeny of 8%. Subsequent increases in twinning frequency resulting from continued within-line selection based on dam's litter size record were predicted to be of the order of 0.8%/year.

This rate of genetic improvement is not much less than usually considered satisfactory for continuously distributed traits such as milk yield, wool weight or body weight. However, it would clearly be desirable to increase the rate of improvement still further, and criteria that could be used to select the young animals directly, such as testis size in males (Land, 1974), ovulation rate in females (Bradford, 1972), or hormone levels in both (Land, 1974), are being investigated.

OBSERVED RESPONSE TO SELECTION

Mechling and Carter (1964) reported an attempt by a private breeder to select for increased twinning in Angus cattle. Foundation females were "twins, daughters of twins, dams of twins or cows that otherwise had twinning in their background", and foundation males were all twin-born purebred Angus. In subsequent generations, selection of both males and females was based on birth type and twinning pedigree, but after some 20 years of selective breeding the twinning frequency was only 1.71% (based on 585 calvings). Analysing this apparent lack of response, Piper and Bindon (1979) showed on theoretical grounds that the initial selection intensity was only moderate, and noted that it failed to produce any appreciable increase in twinning frequency in first-generation females. Consequently, there was little opportunity for selection in later generations and little real hope of any progress.

TABLE 1: SOME DETAILS OF THE DESIGN OF SEVERAL NEW EXPERIMENTS WHERE SELECTION IS FOR INCREASED LITTER SIZE IN CATTLE

Body Responsible and Location	*Breed*	*Method of Selection of Foundation Animals*		*Reference*
		Males	*Females*	
INRA, Jouy en Josas, France	Maine-Anjou	Twinning in pedigree	At least two sets of twins previously	Menissier and Frebling (1974)
	Charolais	Twinning in daughters	,,	,,
CSIRO, Armidale, Australia	Mixed beef and dairy breeds	From dams with extreme twinning records (*e.g.*, 3-8 sets of twins)	,,	Piper and Bindon (1979)
USDA Clay Center, U.S.A.	Mostly Holstein	Twinning in pedigree	,,	Echternkamp and Cundiff (unpublished)

In recent years a number of fresh attempts to alter litter size in cattle by selection have begun. For each experiment, some details of the breeds involved, method of choice of foundation animals and geographic location of the herd are given in Table 1.

The information in Table 1 indicates that there was fairly intense selection of foundation animals, with some variations in the method of choosing males but with females in all cases having previously had at least two sets of twins.

Data on calving records of daughters of these initial matings are not yet sufficient to give a reliable estimate of the genetic effects of the intense selection of foundation males and females. However, the subsequent calving records of the foundation cows themselves are of interest and these are summarized in Table 2, along with some relevant data from Johansson *et al.* (1974). There is considerable variation in subsequent twinning incidence between the different samples of cows. Apart from chance effects, this will be due to variation between the original populations in mean twinning incidence and possibly repeatability of twinning, and also to variation in the selection differential achieved in the actual sample of cows whose subsequent records appear in Table 2. For example, in the Swedish population samples no cows had previously had greater than two sets of twins, while the French samples included cows with up to six sets of twins.

Precise predictions of subsequent performance depend on knowledge of the relevant parameters for each population, and these

TABLE 2: SUBSEQUENT LITTER SIZE IN COWS PREVIOUSLY TWINNING AT LEAST TWICE, OR IN CONTROL COWS

Breed of cow	*No. Records*	*Twin Births (%)*	*Reference*
Maine-Anjou / Charolais	60	32	Menissier and Frebling (1974)
Swedish Red and White	186	11	Johansson *et al.* (1974)
Swedish Friesian	183	15	
Mostly Holstein	49	20	Eckternkamp and Cundiff (unpublished)
Mixed beef and dairy			
(1) Selected	87	15.5	Bindon and Piper
(2) Control	177	0.6	(unpublished)

are not all available for any of the populations listed in Table 2. Assuming the same parameters used by Piper and Bindon (1979) —repeatability 6%, incidence 3%—the expected incidence of twins in cows previously twinning at least twice is 16.7% when the calculations are based on the underlying scale.

CORRELATED RESPONSES TO SELECTION

There are no estimates of realized genetic correlations from selection experiments. However, there are a number of estimates of genetic correlations between twinning and other traits derived from several dairy cattle populations, and these have been summarized in Table 3.

TABLE 3: PATERNAL HALF SIB ESTIMATES OF GENETIC CORRELATIONS BETWEEN TWINNING FREQUENCY AND OTHER TRAITS IN SEVERAL DAIRY CATTLE POPULATIONS

Trait	*Estimates*	*References*
Inter-calving interval	0.079 ± 0.10, 0.19, 0.29*	Bar-Anan and Bowman (1974), Maijala and Syväjävi (1977)
Number of services per calving	0.035 ± 0.035	Maijala and Syväjävi (1977)
Milk production	0.100 ± 0.052, 0.19, 0.21, 0.32*	Bar-Anan and Bowman (1974), Syrstad (1974), Maijala and Syväjävi (1977)
Fat percentage	-0.049 ± 0.053	Maijala and Syväjävi (1977)
Growth	0.13	Bar-Anan and Bowman (1974)
Liveweight	0.058 ± 0.053	Maijala and Syväjävi (1977)

* $P < 0.05$.

There is good agreement between data sets and it seems reasonable to conclude that if twinning frequency were to be increased by selection there would at least be no undesirable genetic changes in milk yield or growth rate, though there may be a small reduction in fertility.

It should be stressed that these predictions are really only valid for dairy cattle populations managed in the traditional way where food supply may be geared to individual milk production but will not be influenced by individual fecundity since each cow is assumed to be carrying a single foetus. In cattle with lower average milk yield (and therefore reduced lactation stress) and improved nutrition in late pregnancy (see below), the small negative genetic correlation between fecundity and fertility may be substantially reduced or even eliminated.

MULTIPLE BIRTHS AND HERD PRODUCTIVITY

The literature on the effects of multiple births on cow and calf performance was comprehensively reviewed by Hendy and Bowman (1970). Documented effects on the cow included shorter gestation length, increased incidence of problems associated with parturition (principally increased incidence of retained placenta), and increased inter-calving interval. There was some evidence of increased death rate of cows but no overall consensus on the effects of twin pregnancy on milk production. A recent study by Chupin *et al.* (1976) on hormone-induced twins in French Friesians (FFNP) confirms the increased incidence of retained placentas in twinning cows (30% vs. 11% for singles), but finds no reduction in subsequent fertility or in milk production either during or following the multifoetal pregnancy. Thus, with current management practices, it is clear that there are some problems associated with parturition in twinning dairy cows. However, there is some evidence (Gordon *et al.*, 1962; Chupin *et al.*, 1976), though not from well-controlled nutritional experiments, that many of these effects may be overcome or much reduced by increased feeding in late pregnancy.

Effects on calves (Hendy and Bowman, 1970) included increased perinatal mortality, reduced birth weight, and a high proportion of freemartins among females born as co-twins to males. There was no evidence of birth type effects on subsequent milk production or on growth, but some recent evidence (Russell, 1976) indicates that twins may be subject to a small degree (1 to 2%) of permanent stunting if reared on the same regime as singles. Freemartins aside, the principal effect seems to be on perinatal mortality, and Hendy and Bowman (1970) also suggested that this might be largely overcome by improved nutrition of the dam during pregnancy.

Two additional points are worth making. First, the increase in numbers of freemartins that accompanies an increase in twinning frequency is usually regarded as one of the disadvantages of raising average litter size in cattle. In fact not all females with a male co-twin are sterile, but even if they were all to be regarded as such, their numbers are balanced by like-sex twin females at birth. The small reduction in the number of fertile heifer replacements that accompanies increased twinning (Cady and Van Vleck, 1978) is simply a consequence of the increased perinatal mortality of twin-born calves. The freemartins, rather than being a disadvantage, are part of the bonus of extra salable cattle and have normal or better than average growth rates. Second, the data reviewed by Hendy and Bowman (1970) arise from sporadically occurring cases of twinning in a vast array of herds and management systems. Because of the nature of such data, the twin vs. single comparisons may rarely be free of the confounding effects of other factors (*e.g.*, age of cow, previous calving history) known to influence performance. The advent of herds with substantially increased twinning frequencies will greatly improve the precision of these analyses and also facilitate the husbandry research required for the development of management strategies to overcome any problems associated with twinning.

THE FUTURE

During the past decade there has been an awakening of interest in increasing fecundity in cattle, and a number of herds practising genetic selection for increased twinning have been established in various countries. Environmental manipulation of existing genotypes, principally by the use of exogenous hormone treatments, has received a great deal of attention, but it is fair to say that as yet no reliable method of producing a moderate controlled increase in litter size has been developed.

Egg transfer techniques with two eggs transferred surgically to the non-pregnant female and follow-up mating (Wilmut, 1978) or a single egg transferred non-surgically to the pregnant female (Gordon and Boland, 1978) appear much more promising, but their economics have yet to be evaluated under Australasian conditions.

From a genetic standpoint there are some important gaps in knowledge. The first is whether the threshold model is adequate as a description of the relationship between genotype and phenotype, and it will be several years before enough data are available to evaluate the accuracy of predictions based on that model. A second and related need is for analyses of existing bodies of data to obtain estimates of the relative frequencies and, if possible, breeding values of animals with different combinations of litter size records. Such estimates would provide a rational basis for selection of foundation animals for a twin selection herd and would also improve understanding of the underlying genetic model. Perhaps the most important remaining genetic tasks are investigations of alternative or additional selection criteria and the continued monitoring of correlated responses to selection. The recently developed technique for repeated observation of ovulation rate in cattle (Holland *et al.*, 1979) is especially important in this regard.

In developing appropriate management systems for highly fecund cattle it will be essential to be able to identify cows carrying twins or larger litters, and the results of Terqui *et al.* (1975) and Sreenan *et al.* (1978), using circulating total oestrogens at around day 200 of pregnancy, are very encouraging. Clearly the most immediate management requirement is to document the nature and extent of any cow and calf performance problems associated with twinning and to establish the degree to which they can be overcome by improved management in late pregnancy.

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