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# CATTLE TWINS : THE MATERNAL ENVIRONMENT AND ANIMAL PRODUCTION

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## Summary

Using data derived from field records, estimates of the contribution of the maternal environment ( $m^2$ ) to the variation in lactation records indicated that approximately 10 per cent. of the total within-herd variation in milk and butterfat yield could be attributed to this source of variation.

The low environmental variance encountered in monozygous twin records is discussed in relation to this result. It is pointed out that even with the variance, ( $m^2$ ), added to the variance within monozygous pairs, the total is still markedly less than that derived from half-sib data.

It is postulated that the low within set variance in monozygous pairs originates because the genotype will, in part, determine the environmental variance associated with it.

The contribution of the maternal environment to growth is noted and illustrated by reference to mice growth data.

The nature of the possible differences in the maternal environment is noted and results quoted indicating a possible cytoplasmic influence on growth in mice.

The importance of the variation found in the maternal environment is discussed in relation to selection experiments, and the value of the technique of ova transplantation in interpreting genetic problems is stressed.

THE USE of monozygous and dizygous twins in animal breeding studies has focused increasing attention on the influence of the maternal environment on quantitative characters in domestic animals, in particular on growth and lactation performance. In such circumstances it seems appropriate to place on record some facets of data concerning the role of the maternal environment in influencing animal production.

Consider first the influence of the pre-natal environment on lactational performance.

Some years ago an attempt was made to assess the likely importance of a common pre-natal environment in contributing to the similarity of the lactation records of monozygous cattle twins (Brumby and Hancock, 1956). This was done by comparing the within-set variance of the milk yield and butterfat test

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of monozygous twins with that of dizygous twins, for the difference between the two variances provides an estimate of the genetic variation free of any bias imposed by the maternal environment. By comparing this estimate with those obtained in such a manner as to contain the variation due to the maternal environment, an indication of the magnitude of this latter source of variation was obtained. Suffice to say here that this particular trial indicated that the maternal environment appeared to be of no great importance in influencing an animal's subsequent lactation performance. As this conclusion was based on limited data, it was decided to pursue the problem further by examining the lactation records of dizygous twins as identified by Herd Book records. The rationale underlying this approach rested on the following argument.

The approximate composition of the variation within dizygous pairs may be represented by the environmental variance  $e^2$  and by half the genetic variation,  $\frac{1}{2}g^2$ , while that of non-related cows in one herd may be represented by  $e^2 + g^2 + m^2$  where  $m^2$  is the additional variation due to different maternal environments. Subtracting one from the other leaves a figure which approximates  $m^2 + \frac{1}{2}g^2$ . The likely value of  $m^2$  can then be assessed for various assumed values of  $g^2$ .

The data obtained were derived from two sources. In the first, the within-pair variance of milk yield in 140 sets of British Friesian twins was estimated. In the second, the data refer to the within-pair variance of butterfat yield for 52 sets of New Zealand Jersey twins. In each case the Breed Society Herd Books were examined for the occurrence of twin registrations. Subsequent production records for twin animals reared and milked in one herd were then obtained by courtesy of the Milk Marketing Board of England and Wales and the New Zealand Dairy Board.

The first problem in interpreting the within pair variances derived from these data involved a correction to allow for the expectation that about 10 per cent. of the twins recorded in the herd books would be monozygotic rather than dizygotic (Hancock, 1954). This correction was made by simply estimating the expected variance within dizygous pairs from the following formula:

$$\text{Observed Variance} = \frac{9 \times \text{Variance within dizygous pairs} + \text{Variance within monozygous pairs}}{10}$$

Details of the estimation of  $m^2$  are shown in Table 2.

The estimates of the total variance and the variance within monozygous pairs used in the calculation of  $m^2$  are listed in Table 1.

The results shown in Table 2 suggest that the importance of the maternal effect as a source of variation in milk yield and fat test is relatively small; the maternal effect appears to account for about 10 per cent. of the total variation in milk and butterfat yield encountered within herds; its influence on fat test appears negligible.

TABLE 1: ESTIMATES OF THE TOTAL VARIANCE WITHIN MONOZYGOUS PAIRS USED IN CALCULATING  $m^2$ .

<i>British Friesians</i>		
	Within monozygous pairs ( $e^2$ )	Total ( $e^2 + g^2 + m^2$ )
Milk.....	5,000 gal <sup>o</sup>	31,700 gal†
Butterfat test.....	0.010%	0.090%
<i>New Zealand Jerseys</i>		
	Within monozygous pairs‡	Total‡
Milk.....	2,000 gal	12,000 gal
Butterfat test.....	0.020%	0.250%
Butterfat.....	500 lb	3,300 lb

<sup>o</sup>Based on an assumed twin  $h^2 \cong 85\%$  for milk and 90% for test.

†Robertson and Khishin, 1958.

‡Unpublished data.

TABLE 2: ESTIMATION OF  $m^2$ .

	<i>British Friesian</i>		<i>New Zealand Jersey</i>		
	<i>Milk</i>	<i>Butterfat test</i>	<i>Milk</i>	<i>Butterfat test</i>	<i>Butterfat</i>
Total ( $e^2 + g^2 + m^2$ ).....	31,700	0.0900	12,000	0.2500	3,300
Calculated M.S. within pairs.....	22,363	0.0622	7,919	0.1684	2,300
Corrected M.S.					
( $e^2 + \frac{1}{2} g^2$ ).....	24,292	0.0680	8,575	0.1849	2,500
Difference ( $\frac{1}{2} g^2 + m^2$ )....	7,408	0.0220	3,425	0.0651	800
$\frac{1}{2} g^2$ ( $h^2=30\%$ Milk and Fat; $h^2=50\%$ Test)....	4,755	0.0220	1,800	0.0625	500
$m^2$ .....	2,653	0.0000	1,625	0.0026	300
$m^2$ /Total $\times 100/1$ .....	8%	0%	14%	1%	9%

Having concluded that a common maternal environment does not contribute in any great degree to the similarity of monozygous twins there still remains the questions: "Why are monozygous twins so much more alike than one would predict from their genetic relationship?" The explanation is probably associated with lack of precision in definition, for one normally imagines the environmental variation associated with non-related and half-sib animals to be identical with that associated with that observed within pairs of monozygous twins, whereas comparison of reasonable estimates of environmental variance in the two cases shows a marked difference between the two.

Table 3 illustrates typical values of  $e^2$  obtained from monozygous twin trials and from the analysis of records associated with the herds in the "feeding-breeding" experiment at Ruakura.

TABLE 3: COMPARISON OF ENVIRONMENTAL VARIATION IN MONOZYGOUS TWIN AND HALF-SIB DATA FOR BUTTERFAT YIELD.

	<i>Environmental M.S.</i>
Monozygous twins .....	500
Half-sib .....	2,000

Hancock (1953) has suggested that greater environmental control associated with experimental twin herds might explain the greater than expected similarity of twins but more recent experience suggests that this is not really the case. Rather the problem probably arises through endeavouring to consider the environmental variation independently of the genotype.

The environmental variation may be partitioned into three distinct portions:

- (a) A residual or true  $e^2$ .
- (b) An  $e^2$  dependent on the genetically determined buffering or homeostatic mechanisms controlling development in individual animals.
- (c) An  $e^2$  due to an interaction of the particular phenotype with the environment it happens to meet.

The within pair variance of monozygous twins will contain (a) plus perhaps a fraction of (b), where the environmental variance measured in half-sib data contains (a) (b) and (c). That the two estimates of  $e^2$  differ is not really surprising, and in retrospect it seems unwise ever to have considered them interchangeable. If this partitioning of the environmental variation is considered reasonable the problem of the similarity of the

monozygous twins falls apart. They are similar in performance simply because their genotype largely determines the environmental variation common to both.

Before leaving this topic of the lactation records of twins and their maternal environment it is of interest to pose the question: "Although the maternal environment may not markedly influence the lactation performance of dairy cattle, does the lactation performance of an animal influence the maternal environment that that animal provides?"

One might imagine such an effect manifesting itself in terms of fertility, gestation length, birth weight and/or post-natal growth of the young.

So far as dairy cattle is concerned there is relatively little information available. The fact that the number of matings per conception is of the order of 1.25 for yearling cattle and 1.5 for two-year-old cattle (Brumby, unpublished data) suggests that lactation may detrimentally affect fertility. This seems to be an all or none effect, however, for the study made by Miss Currie of the New Zealand Dairy Board indicated no relationship between level of lactation yield and conception rate (Currie, 1956). In mice the detrimental influence of lactation upon fertility is well established (Bruce and East, 1956) and the phenomenon of delayed implantation appears to be an evolutionary development designed to mitigate the stressing effect of lactation superimposed on pregnancy. Delayed implantation apparently does not exist in cattle or pigs for the gestation period of young carried by lactating animals of these two species appears identical with that of young carried by non-lactating animals (Brumby and Smith, unpublished data).

For nutritional reasons, one might reasonably expect a small positive phenotypic correlation between the birth weight of calves from maiden cattle and the subsequent yield of the heifers that bore them; likewise one might expect a negative phenotypic relationship between the two-year-old lactation record and birth weight of the second calf. Whether or not any fundamental genetic relationship exists between the characters of lactation, fertility and growth, whereby an animal with a genotype for high milk yield or growth leaves progeny lower than normal in fertility, remains to be seen. The importance of such relationships is illustrated by the recent interim report concerning selection for lactational performance in mice (Bateman, 1955). Bateman has observed that, while considerable genetic variation in lactation performance (as measured by 12-day weight) exists in his

mice, departure from an intermediate level of lactation performance is strongly opposed by natural selection. The detailed nature and general validity of this result yet remains to be clarified, even so, it provides grounds for closely examining the premises upon which one assesses the potential improvement one hopes to make in animal production through enlightened breeding methods.

The marked influence of the maternal environment on the birth weight and subsequent growth of an animal is well known. An example of the magnitude of this effect is provided by recent work in mice using the egg transplantation technique (Brumby, 1959). The growth curves for the mice shown in Fig. 1 each represent the average growth of approximately 50 mice of uniform genotype and litter size reared in three ways. Line (1) had the maternal environment of Strain U females both pre-natally and post-natally; Line (3) had the maternal environment of Strain S pre-natally and post-natally, while Line (2) had the pre-natal

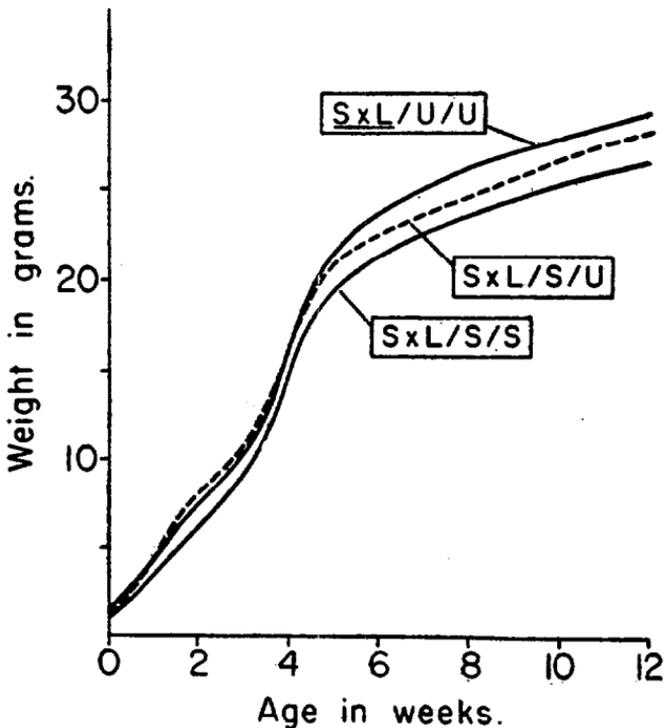


Fig. 1: Growth curves of mice in three maternal environments.

environment of Strain S and the post-natal environment of Strain U and was, in consequence, intermediate in size.

The appreciable influence of the maternal environment on the growth of mice appears to be of equal validity in terms of cattle growth, for when the growth data of the monozygous and dizygous twins described earlier were considered, the maternal contribution to growth was found to be marked (Brumby and Hancock, 1956). A similar conclusion was reached by King and Donald (1955).

Having demonstrated the magnitude of the maternal influence on growth two basic questions may be asked: What is the nature of the differences in the maternal environment provided by mammals? Of what importance is the variation encountered in maternal performance?

Consider first the possible nature of potential differences in the maternal environment provided by animals under uniform environmental conditions. One might imagine that both the size and transfer efficiency of the maternal and foetal placentae might vary, leading in consequence to differing nutritional levels of embryos within and between mothers. One might also imagine that varying endocrine levels cause differences in embryo growth rates, and, finally, one might imagine that cytoplasmic factors play a role.

In the first place it does seem clear that a variation in placental weight of the foetus occurs which appears to be related to foetal weight (Hammond, 1935). A between-species difference in the functional efficiency of placental transfer is also known (Mossman, 1937, Flexner and Gellhorn, 1942) and it seems reasonable to extrapolate this between species difference to a within-species one of lesser magnitude. Variation in the size and transfer efficiency of the placental barrier seems, therefore, a likely cause of varying maternal performance.

Growth hormone may possibly act as a growth factor during foetal development (Cotes, 1954) while deficiencies of progesterone have been shown to be associated with embryonic mortality (Hall, 1957). The free-martin condition in cattle is a further example of a probable pre-natal endocrine influence on growth and conformation. This latter example raises the possibility that the ratio of males to females in mixed litters of multiparous animals might conceivably influence growth. The writer is indebted to Dr D. S. Falconer for providing records of mice weights in order to examine this possibility. Table 4 summarizes the results of this investigation.

TABLE 4: SIX-WEEK BODY WEIGHTS OF MIXED SEX LITTERS OF EIGHT MICE.  
(Per cent. females in litter)

	75%	62.5%	50%	32.5%	25%
<i>First Litter:</i>					
Females	24.73(66)	25.14(90)	24.96(100)	24.81(57)	24.37(20)
Males	29.21(22)	29.98(54)	29.43(100)	28.86(95)	28.80(60)
Difference	4.48	4.48	4.47	4.05	4.43
<i>Second Litter:</i>					
Females	24.00(36)	25.17(90)	25.25(132)	24.58(52)	24.50 (6)
Males	29.33(12)	30.80(54)	30.68(132)	29.54(70)	30.88(18)
Difference	5.33	5.63	5.43	5.07	6.38

The sex composition of the litter did not appear to influence the weight of individual males and females, nor the difference between them. Surprisingly, however, the sex difference was increased in the second litter, owing to an increase in weight of second litter males. This sex by parity interaction presents a puzzling query to which the writer can see no clear-cut answer. One might speculate that it is a phenomenon similar to the enhancement effect described by Beatty (1956), who observed that the differences in birth weight of genetically diverse embryos were magnified by rearing such embryos in a common uterine environment. He suggested competition for a growth factor to be the cause. Such an explanation is not an altogether happy bed-fellow with the sex weight differences in these mice for the difference is greater in second rather than first litters, and it is the second litters that have the greater average body weight and the better maternal environment.

Whatever the explanation of this situation, it is of interest to take the problem a little further and inquire into the permanence or otherwise of the influence of the maternal environment. The growth curves shown in Fig. 1 suggest that the size differences apparent in the birth weight are maintained as a relatively constant percentage deviation from the mean up to body weights recorded at 12 weeks of age. Similar data from other experiments of this nature confirm this (Brumby, 1960).

Another way of examining this aspect of the problem is to observe the growth of monozygous twins whose birth weights differed slightly. In Table 5 data are presented on the live-weights of 10 pairs of monozygous twins whose birth-weights differed by 5 lb or more. The average difference of 10 per cent. in birth weight has been maintained through to 15 months.

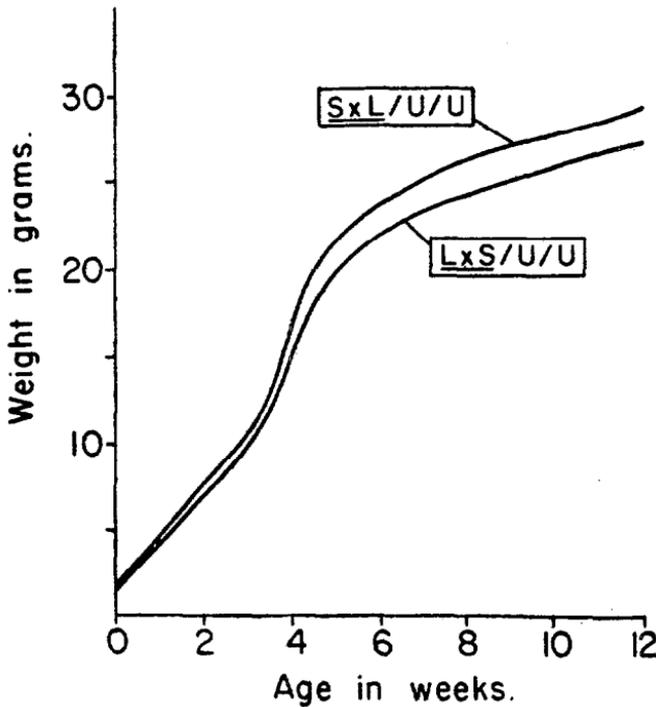


Fig. 2: Comparison of growth of reciprocal crosses in a uniform maternal environment.

Thereafter, because of pregnancy and the imposition of experimental treatments, weight and size differences in these animals are difficult to interpret. Even so it seems reasonable to conclude that any deviation in size apparent at birth is likely to be permanent.

Along with nutrition and endocrine influences, the third possible field of explanation of maternal effects lies in cytoplasmic inheritance. The potential importance of this source of variation in performance records has usually been disregarded for the very sound reason that it could not be measured. With the advent of egg transplantation techniques this objection no longer holds and steps are now being taken to explore this field. The early results obtained in this work are particularly interesting and are worth outlining here.

Reciprocal crosses were made between Falconer's large and small strain mice and the resulting fertilized eggs transplanted in the blastocystic stage to females of non-related strain. In this

manner a common maternal environment was provided for all embryos.

The growth curve for the mice involved is depicted in Fig. 2.

The standard error of each curve is approximately 2 per cent. of its mean value to any point while the difference between the two curves is of the order of 10 per cent. of the mean value at any point. The two growth curves differ significantly. It appears that the cytoplasm of the animals selected for small size enhances body size to a greater degree than does the cytoplasm of the large strain. This observation provides grounds for speculation concerning the origin and development of homeostatic mechanisms, for it is tempting to suggest that selection for size in the nuclear genetic material has been opposed by the development of compensating biochemical systems within the cytoplasm of ovum.

TABLE 5: LIVE-WEIGHT CHANGES IN MONOZYGOUS TWINS  
DIFFERING IN BIRTH WEIGHT.  
(All weights in lb)

<i>Age in Months</i>						
<i>Twin No.</i>	0	3	6	9	12	15
17	69	202	349	394	465	576
22	44	154	268	294	303	421
23	53	183	320	362	381	471
44	43	171	282	308	344	441
116	57	179	249	267	313	450
17	78	228	389	533	653	823
47	56	176	302	374	430	524
168	45	159	284	323	442	536
169	60	177	292	353	438	535
176	61	183	290	283	366	481
	56.6	181	303	349	414	526
<i>Age in Months</i>						
<i>Twin No.</i>	0	3	6	9	12	15
18	62	69	196	343	392	473
21	38	146	254	262	285	331
24	48	175	304	350	361	441
43	36	158	237	308	367	410
115	51	176	247	256	313	419
18	67	208	348	478	553	707
48	48	161	286	370	445	513
167	39	137	241	282	385	506
170	55	166	273	324	405	503
175	56	169	252	213	316	427
	50.0	157	264	319	382	473

This particular experiment appears to be the first case in which cytoplasmic factors have been shown to influence growth. How unique this observation is likely to be is yet unknown, as are the nature and inheritance of the cytoplasmic effect. The point to be made here is that the development of the egg transplantation technique has opened up a large field for investigation. Not only is the technique of major value in studying the general importance and nature of maternal effects, but it promises to be a most valuable tool for the experimental geneticist.

The final point to consider is the importance of the variation encountered in maternal performance in the interpretation of animal breeding studies.

Usually cytoplasmic influences are confounded with maternal effects, and the changes in gene frequency accompanying selection and inbreeding are often confounded with changes in the maternal environment which accompany response to selection.

This latter problem arises in a twofold manner. In the first place, one may have a correlation between the character selected for and maternal performance leading to a marked difference from expectancy in the selection response. Such a relationship has been shown to exist between size and fertility in mice (Falconer, 1955), whereby selection for high fertility actually reduced fertility in the early generations of selection. Because of a positive phenotypic relationship between maternal size and number of eggs shed, the animals selected for high fertility, which came from large litters and were therefore smaller, actually shed fewer eggs and had smaller litters than those selected for poor fertility.

In the second place, the change of the pre- and post-maternal performance accompanying selection may lead to a change in the reproductive fitness of the extremes of the population such that deviation from an optimal point is but short-lived. As described earlier, this problem has already been encountered in selection for 12-day litter weight in mice (Bateman, 1955).

The interpretation of crossbreeding and inbreeding experiments is likewise complicated by the confounding of genetic and maternal effects. One might also speculate that the selection plateaux attained in selected lines in which considerable genetic variation still exists are imposed by the maternal performance of the female, rather than by the exhaustion of genetic variation in the character selected.

In such situations the techniques of egg transplantation appear to offer the most suitable practical approach to disentangling the multitude of confounded variables.

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## DISCUSSION

PROF. A. L. RAE: In a theoretical breakdown of the variation in a population characteristic it has been usual to include a term for the maternal variance. This term is then usually neglected, for one can only estimate the component due to the maternal environment by subtracting variance components. These components have very high sampling errors and subtraction markedly increases these errors; thus most estimates of  $m^2$  are subject to very large errors. It is for this reason I welcome a direct experimental approach to the problem.

In regard to the possible cytoplasmic effect in the reciprocal crosses, has any sex-linkage effect been excluded?

The problem of the maternal environment and its ramifications in terms of interpreting selection response is a profound and difficult one. Does the maternal environment always act to obscure the genetic potentialities of the animal, or is it that the effect is further complicated by the maternal environment of the dam itself having a genetic basis? Coupled with this is the problem of genetic as well as phenotypic relationships amongst the characters selected and the maternal environment.

A.: Sex-linkage effects were negligible in this particular comparison. As Dr. Rae said, the maternal effect is a complex one and it is certainly difficult to generalize about the way it will influence the response to selection. In selecting for increased size, I believe it probably limits the expression of genetic growth potentials, whereas selection for small size is reinforced by a decline in maternal performance. An asymmetrical selection response then results. Other examples of the way the maternal effect influences the response to selection for fertility and 12-day weight in mice have already been quoted.

DR. S. SEARLE: Dr Brumby has shown that notwithstanding the fact that the estimates of variances used have high errors, the maternal effect could account for only a small part of the discrepancy between the heritability figures obtained from monozygous pairs and half-sibs respectively. A further aspect of this problem of the discrepancy between these two heritability estimates is that of the large between-set variance encountered in twin studies. Can Dr Brumby suggest any reasons as to why this estimate

of genetic variation obtained from twin data is greater than that derived from say half-sib data.

A.: There are several reasons why the two estimates may differ:

(1) Contemporary environmental effects will tend to enlarge between-set differences.

(2) The genetic variance estimated from monozygous twin records contains all of the non-additive genetic variance, whereas that derived from half-sib records contains very little.

(3) Because twin animals are collected from farmers' herds the between-set variation includes the between-herd as well as the within-herd genetic variation. Only the latter is estimated in half-sib analyses.

(4) Herd  $\times$  genotype interactions inflate the apparent genetic variation in twins to some degree.

(5) Twin estimates of genetic variations are inevitably based on a limited number of sets and the decision to include or exclude one or more sets whose lactation records differ somewhat from average markedly affects the between-set variance.