

## New Zealand Society of Animal Production online archive

This paper is from the New Zealand Society for Animal Production online archive. NZSAP holds a regular annual conference in June or July each year for the presentation of technical and applied topics in animal production. NZSAP plays an important role as a forum fostering research in all areas of animal production including production systems, nutrition, meat science, animal welfare, wool science, animal breeding and genetics.

An invitation is extended to all those involved in the field of animal production to apply for membership of the New Zealand Society of Animal Production at our website [www.nzsap.org.nz](http://www.nzsap.org.nz)

[View All Proceedings](#)

[Next Conference](#)

[Join NZSAP](#)

The New Zealand Society of Animal Production in publishing the conference proceedings is engaged in disseminating information, not rendering professional advice or services. The views expressed herein do not necessarily represent the views of the New Zealand Society of Animal Production and the New Zealand Society of Animal Production expressly disclaims any form of liability with respect to anything done or omitted to be done in reliance upon the contents of these proceedings.

This work is licensed under a [Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License](http://creativecommons.org/licenses/by-nc-nd/4.0/).



You are free to:

**Share**— copy and redistribute the material in any medium or format

Under the following terms:

**Attribution** — You must give [appropriate credit](#), provide a link to the license, and [indicate if changes were made](#). You may do so in any reasonable manner, but not in any way that suggests the licensor endorses you or your use.

**NonCommercial** — You may not use the material for [commercial purposes](#).

**NoDerivatives** — If you [remix, transform, or build upon](#) the material, you may not distribute the modified material.

<http://creativecommons.org.nz/licences/licences-explained/>

# THE ROLE OF MATERNAL EFFECTS ON THE EFFICIENCY OF SELECTION IN BEEF CATTLE — A REVIEW

R. L. BAKER

*Ruakura Animal Research Station, Hamilton*

## SUMMARY

In beef cattle a negative *environmental* covariance exists between maternal effects in adjacent generations. High levels of feeding either pre-weaning (mainly from milk production of the dam) or post-weaning (particularly high energy levels) reduce the amount of secretory tissue in the udder of daughters and consequently reduce the milk production in daughters. Some management policies which might help circumvent this environmental effect are discussed.

The *genetic* correlation between direct genetic and maternal effects is negative for birth and weaning weight. When estimating this genetic correlation it is important to avoid using dam-offspring relationships, since these can be biased by the environmental covariance mentioned above. When selecting for weaning weight, a large negative genetic correlation between direct genetic and maternal effects would result in considerable reduction in expected response compared with when the genetic correlation is close to zero. One possible solution to this problem is to select males for direct genetic and females for maternal genetic value.

## DEFINITION OF TERMS

A sire influences his offspring only through genes he transmits in his sperm. A dam may influence her offspring through the maternal environment she provides as well as the sample of genes passed on in the eggs she sheds. The factors which may be responsible for this maternal effect include the cytoplasm of the egg, the uterine environment, and the post-natal environment (*e.g.* milk production and/or mothering ability). This review will only consider maternal effects acting through the pre- or post-natal environment.

Sometimes reference is made to *maternal traits*. These traits are sex-limited and can only be expressed in the female — *e.g.*, fertility (number of young born or weaned), calving ability, milk production, mothering ability (as expressed in weaning weight). These maternal traits can be determined by paternal contributions (direct genetic effects from the cow's sire) and/or maternal contributions (direct genetic and maternal effects).

## EVIDENCE FOR MATERNAL EFFECTS

Koch (1972), in reviewing maternal effects in beef cattle, states that evidence on the existence and size of maternal effects generally comes from experiments which:

- (1) measure known components of maternal effects such as milk production from cows suckling their young;
- (2) compare reciprocal crosses or cross-fostered animals among genetic types (*i.e.*, interbreed studies); and
- (3) compare observed correlations in terms of their causal components for various kinds of relatives (*i.e.*, intrabreed studies).

This review will concentrate on (3), but some brief comments on (1) and (2) are necessary.

## MILK PRODUCTION

Numerous studies relating milk production of beef cows to gain of calves have reported significant correlations in the range of 0.3 to 0.8 depending on the age of the calf or length of the period measured (Koch, 1972). The behaviour of the dam while suckling her calf, which could be partly genetic, is another potentially important component of maternal ability, but this appears to have received little attention in beef cows. Robison (1972) has suggested that it may be important in pigs. Mother-young behavioural relationships in cattle, goats and sheep have recently been reviewed by Poindron and Le Neindre (1979).

## CROSSBREEDING STUDIES

Cross-fostering and egg-transfer experiments to separate the dam's genetic and post-natal environmental contributions to her young have been successfully used in pigs (Robison, 1972), mice (Legates, 1972) and sheep (Bradford, 1972) to obtain evidence on uterine (pre-natal) effects and to separate direct genetic effects and pre-natal maternal effects for birth weight and subsequent growth. Such studies have not been reported in beef cattle.

Evidence for maternal effects in cattle comes from differences among reciprocal crosses in crossbreeding experiments. In crosses among Angus, Hereford and Shorthorn cattle, significant differences between reciprocals were found for gain from birth to weaning, largely reflecting differences in milk production but no significant effects for birth weights (Koch, 1972).

Reciprocal crosses among breeds differing more in mature size, such as Friesian, Jersey and Ayrshire crosses (Donald *et al.*,

1962), did show significant differences among birth weights of reciprocals. Koch (1972) states that, while reciprocal crosses provide evidence that maternal effects on birth and weaning weights can be real, they are not too helpful in quantifying relative variation attributable to maternal effects.

On the other hand, estimates of maternal effects for genetic groups, such as breeds or lines, are useful to a breeder to allow him to decide how best to utilize these groups in a breeding programme. Crossing is carried out not only to utilize heterosis, but equally, or more importantly, to combine desirable characteristics of different breeds into either the marketable product (*e.g.*, the carcass) and/or the breeding cow (Robertson, 1977).

Experimental approaches in utilizing breed resources, with emphasis on estimation of genetic and maternal parameters, have been most extensively presented by Dickerson (1969, 1973, 1974). In addition, several excellent international symposia on this subject have been published recently (Minkema, 1974; McGloughlin, 1976; Mason and Pabst, 1977; Vissac, 1979).

#### BIOMETRICAL MODELS FOR MATERNAL EFFECTS

The fact that heritability estimates could be biased by maternal effects was recognized by Lush (1940), who suggested that this source of correlation among relatives could be eliminated by randomly fostering newborn young. Biometrical aspects of maternal effects were developed by Dickerson (1942, 1947), working with pigs. Dickerson (1947) drew a path diagram (Fig. 1) showing how a phenotypic value could be influenced by direct genetic effects, genetic maternal effects originating from the dam, and the possibility of a genetic correlation between these effects.

Koch and Clark (1955) presented the first attempt in beef cattle to partition maternal effects from direct genetic effects. They found that the maternal environment had a considerable influence on birth weight and on gain from birth to weaning, but little on gain from weaning to 1 year of age. They also found evidence for a negative genetic correlation among direct genetic effects and maternal effects for birth to weaning gain and weaning conformation score.

The theoretical expectations of correlations or covariances among different types of relatives when both a direct genetic and a maternal effect are considered are developed further by Willham (1963, 1972), Eisen (1967), Koch (1972), and Thompson

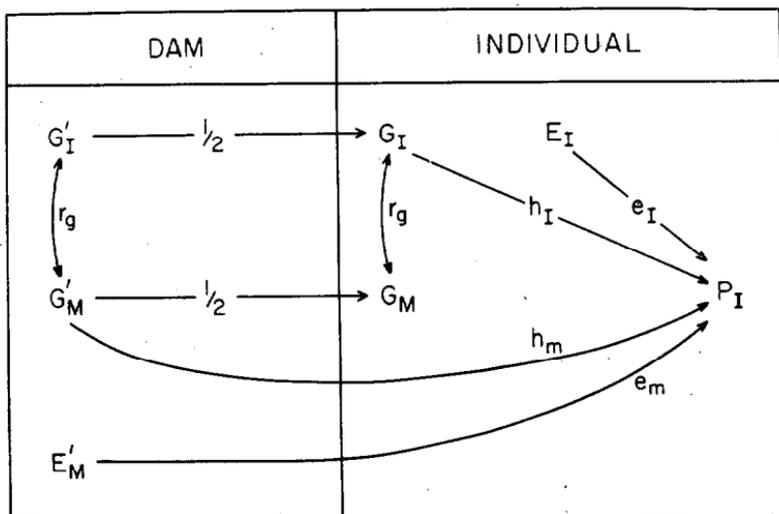


FIG. 1: A path coefficient diagram describing a phenotypic value influenced by a maternal effect (after Dickerson, 1947). See Fig. 2 and text for definition of terms.

(1976), and reviewed by Foulley and Lefort (1978) and Willham (1979). Both Koch (1972) and Willham (1972) include grand maternal effects in their discussion. They show that the real possibility of a direct negative influence of dam's maternal ability on the maternal ability of daughters (*i.e.*, a good milking dam hurts the milking ability of her daughters) will lead to larger negative estimates of the genetic correlation between direct genetic and maternal effects. Thus the negative bias associated with the dam-offspring correlation must be taken into account when interpreting these genetic parameters. The relationships most commonly compared to estimate genetic and maternal parameters have been paternal and maternal half-sibs, offspring-sire and offspring-dam.

The offspring-dam and the offspring-granddam relationships can be quite complex functions if all influences considered by Koch (1972) are included. A simplified path diagram of these relationships, ignoring dominance effects, adapted from Koch (1972) and Foulley and Lefort (1978) is presented in Fig. 2. This is a more detailed breakdown of the dam-offspring relationship first presented by Dickerson (1947) and shown in Fig. 1. In both Figs. 1 and 2 we see the phenotype of an individual ( $P_I$ ) being influenced by two component characters, its own additive genotypic

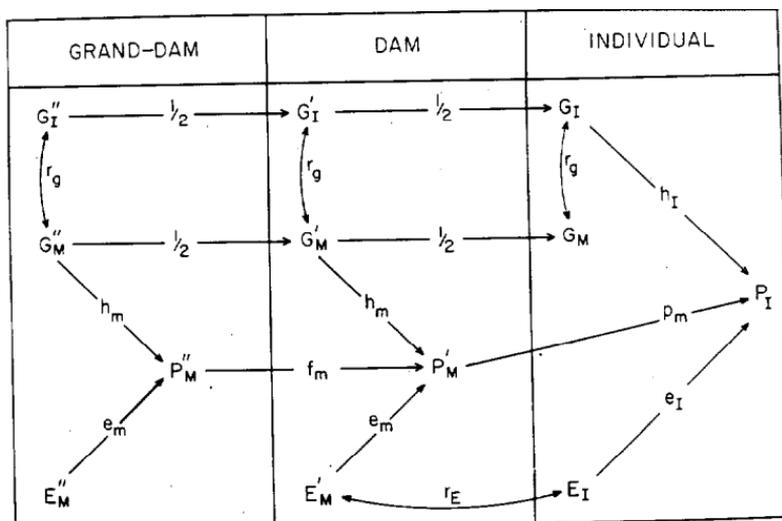


FIG. 2: A path coefficient diagram describing direct, maternal and grand maternal influences on a trait (after Koch, 1972).  $P_I$  is phenotypic,  $G_I$  additive genetic, and  $E_M$  environmental value for traits expressed by individuals. ( $1/2$ ,  $e$ ,  $h$ ,  $f$ ,  $p$ ) are corresponding maternal effects. Path coefficients between symbols ( $1/2$ ,  $e$ ,  $h$ ,  $f$ ,  $p$ ) are standard partial regression coefficients. Double-headed arrows represent residual correlations between traits.

$h^2_I$  = heritability of the direct genetic effect

$h^2_m p^2_m$  = heritability of the maternal effect ( $h^2_m$  in Fig. 1).

$f_m$  = path coefficient relating the maternal ability of a dam to future maternal ability of female offspring

value ( $G_I$ ) and the additive genotypic values for maternal ability of its dam ( $G_M$ ). If the character was weaning weight, for example, then  $G_I$  would be the calf's own genes for growth while  $G_M$  would be the genes for milk production.

#### EVIDENCE FOR A DIRECT INFLUENCE OF DAM'S MATERNAL ABILITY ON DAUGHTER'S MATERNAL ABILITY

The situation is probably best summarized by quoting from Koch's (1972) review:

It is significant to note that with one exception (Hohenboken and Brinks, 1971) workers evaluating maternal effects have assumed environmental correlations in the offspring-dam covariance were zero to solve for genetic components. Many years ago Dr H. H. Stonaker suggested the negative genetic correlation involving maternal ability hypothesized by Koch and Clark (1955) could have been due to

direct negative influence of dams on maternal ability of her female offspring through overfeeding. At this time I dismissed this hypothesis as unlikely because our data were from a sparse range environment. It did not seem that milk production was abundant enough to affect future development. I now believe I was wrong. Studies of dairy calves indicate that overfeeding heifers during rearing resulted in lower average milk production than from heifers fed normal standards. Underfeeding heifers was detrimental in some cases to the first lactation, but in later lactations subnormally reared heifers equalled or exceeded milk production from normally reared heifers.

Koch (1972) then reviewed the limited amount of data from beef herds relating levels of rearing to milk production of cows. This evidence (e.g. Totusek, 1968; Mangus and Brinks, 1971) indicated that early-weaned heifers (160 days) or heifers out of young dams subsequently produced heavier calves at weaning than heifers weaned at normal ages (240 days) or out of mature cows. Koch (1972) sought additional evidence on this question by analysing 4060 Hereford calves from the Fort Robinson Beef Cattle Research Station, Nebraska. He classified heifer calves from the same birth year according to their dam's age, and found that those from older dams subsequently had calves with poorer birth weights and gains from birth to weaning. This confirms the detrimental effect of the high level of milk production from older dams.

Further evidence on environmental covariance through maternal ability was obtained by Koch by comparing offspring-dam and offspring-granddam regressions. This again suggested for gain from birth to weaning, but not in this case for birth weight, negative direct effects between maternal values or large negative dominance covariance.

Kress and Burfening (1972), from data on 3342 Hereford calves in Montana, obtained similar results to Mangus and Brinks (1971). The relationships between various measures of early growth rate in heifers (both pre-weaning and post-weaning to the yearling stage) and their subsequent maternal ability as cows expressed as the most probable producing ability (MPPA) for weaning weight at 180 days of age were negative.

Recently, Sejrsen (1978) has reviewed the literature on mammary development and milk yield in relation to growth rate in dairy and dual-purpose heifers. He presents a possible negative relationship between growth rate (feeding intensity plus genetic growth potential) and mammary development. A high feeding intensity, particularly high energy intake, leads to lower growth

hormone and prolactin concentration in the blood. Since these hormones stimulate mammary development, the mammary growth, and thereby the milk yield is inhibited. This inhibition takes place mainly in the period before and around the onset of puberty, when the development of the udder is rapid. But Sejrson suggests that animals with high genetic growth capacity, both between or within breeds, seem to have higher growth hormone concentrations in the blood and consequently better mammary growth and higher milk yield. If this hypothesis is true, then there is some cause for optimism that improvement of growth through performance selection may not necessarily lead to a decline in milk yield. But if it is not true, there could be problems in improving milk production in self-replacing beef herds, and there might be a need for development of specific maternal lines which would be mated to terminal sire breeds with all male and female offspring being marketed. These findings could also indicate that effective selection for milk yield in dairy cattle has been enhanced by separating heifers from their dams at a young age (Cundiff, 1972).

Clearly there is need for more research on this question. Lawson (1977) in Canada reported on the initiation of a selection study, with both Angus and Hereford cattle, for high 168-day post-weaning gain on two levels of nutrition—high plane (HP) and low plane (LP). Preliminary milking tests indicated that cows from the LP lines tended to produce more milk than cows from the HP lines. It is planned after about 10 years of selection that half the heifer calves of each line will be fed the HP and half the LP ration. The subsequent response of these heifers to milking should therefore indicate the extent to which either the long-term selection or the management system has affected the milk yield and its constituents.

#### ESTIMATES OF DIRECT AND MATERNAL EFFECTS IN BEEF CATTLE

Most of the published data on this subject to date have concentrated on pre-weaning growth traits, *i.e.*, birth weight, daily gain from birth to weaning, and weaning weight. Table 1 summarizes published data presently available for these traits. Barlow (1978) produced a similar summary when reviewing selection for pre-weaning growth in beef cattle.

Only three reports to date have published estimates of these genetic parameters excluding the offspring-dam relationship but including other relationships such as maternal-grandsire sibs and maternal-grandsire's progeny and grand offspring to obtain solu-

TABLE 1: ESTIMATES OF DIRECT AND MATERNAL EFFECTS ON PRE-WEANING GROWTH  
(after Menissier, 1976)<sup>1</sup>

Trait	Heritability (%)				Reference		
	Total $h_T^2$	Direct $h_1^2$	Maternal $h_m^2$	Genetic Correlation $r_g$	Number	Breed	Authors
Birth weight	42	35	—	$\geq 0$	4553	Hereford	Koch and Clark (1955)
	2	22	4-15	-0.93	1064	Holstein	Everett and Magee (1965)
	36	56	30	-0.58	789	Hereford	
	17	14	25	-0.39	932	Angus	Brown and Galvez (1969)
	48	72	—	-0.56 to -0.89	1962	Hereford	Vesely and Robison (1971)
	56	44	10	0.14	4060	Hereford	Koch (1972)
	49	45	9	0.0 <sup>2</sup>			
Average <sup>2</sup>	34	40	19	-0.42			
Daily gain: Birth to weaning	12	21	—	-0.65	4553	Hereford	Koch and Clark (1955)
	25	18	15	0.0	725	Brahman	Deese and Koger (1967)
	17	40	46	-0.73	466	Brahman	
	12	26	11	-0.41	4060	× Shorthorn Hereford	Koch (1972)
	32	20	28	-0.05 <sup>2</sup>			
Average <sup>2</sup>	17	26	24	-0.45			
Weaning weight	32	44	40	-0.32			
	42	32	51	-0.46	717	Hereford	Hill (1965)
	17	37	—	-0.73 to 1.07	1692	Hereford	Vesely and Robison (1971)
	8	23	54	-0.79			
	28	23	34	-0.28 <sup>2</sup>	2618	Hereford	Hohenboken and Brinks (1971)
	—	14	64	-1.14			
32	14	34	-0.07 <sup>2</sup>	228	Charolais	Foulley and Menissier (1974)	
Average <sup>2</sup>	25	30	52	0.72			

<sup>1</sup>  $h_T^2 = (\text{Var. } G_I + 3/2 \text{ Cov}(G_I G_M) + 1/2 \text{ Var. } G_m) / \text{Var. } P.$

<sup>2</sup> Estimates excluding the offspring-dam relationship.

tions to equations (Hohenboken and Brinks, 1971; Koch, 1972; Foulley and Menissier, 1974). It immediately becomes apparent that very different estimates of  $r_g$ , and in some cases  $h_m^2$ , are obtained when excluding the offspring-dam relationship. The following conclusions can be drawn from Table 1:

1. The average estimates of heritability of total influences ( $h_T^2$ ) for birth weight, daily gain from birth to weaning, or weaning weight are all of reasonable magnitude. Therefore response to selection for any of these traits is expected to be effective even when the unfavourable association between direct and maternal effects is ignored (Barlow, 1978). However, response to selection will not be as effective as it would be if the genetic correlation ( $r_g$ ) between these effects were zero. More efficient breeding plans can be developed to take this factor into account.
2. For birth weight,  $h_l^2$  is about double  $h_m^2$ . An average estimate of  $-0.42$  for  $r_g$  is obtained from six estimates including the offspring-dam relationship, but when it is excluded (Koch, 1972) the estimate is close to zero.
3. For both daily gain from birth to weaning and weaning weight it appears that maternal effects ( $h_m^2$ ) are at least as heritable as direct effects ( $h_l^2$ ) and possibly a little more heritable for weaning weight. As for birth weight, the average genetic correlation estimate when including offspring-dam relationships is quite highly negative ( $-0.45$  or  $-0.72$ ). But from the three studies excluding offspring-dam relationships the average  $r_g$  estimate is  $-0.13$ .
4. Koch (1972) speculates that the negative direct influence between the maternal ability of dam and daughter which is biasing the dam-offspring relationship for weaning weight could have a value of  $-0.1$  to  $-0.2$ . Such values for this direct path (*i.e.*,  $f_m$  in Fig. 2) lead to estimates of environmental covariance which satisfy observed correlations and regressions.

Whether the relatively weak genetic antagonism between direct and maternal effects estimated after allowing for  $f_m$  (*i.e.*,  $-0.05$  to  $-0.28$ ) is important enough to consider in breeding plans is still a matter of some debate but will be considered further in the next section.

It has usually been found that maternal influences decline after weaning (*e.g.*, Koch and Clark, 1955), but there appears to be

TABLE 2: ESTIMATES OF DIRECT AND MATERNAL EFFECTS FOR SOME REPRODUCTIVE TRAITS

Trait	Heritability (%)			Reference	
	$h_i^2$	$h_m^2$	$r_g$	Number and Breed	Authors
Calving score (easy, normal, difficult)	10	11	-0.19	6724 Swedish Friesian (heifers)	Philipsson (1976)
Stillbirth (alive, born dead)	4	1	0.07		
Birth weight	19	8	-0.53		
Gestation length	50	17	-0.56		
Failure to conceive	0-7	7-9	-	1249 Angus, Hereford, Shorthorn Dearborn <i>et al.</i> (1973) and crosses (315 heifers)	
Foetal mortality	0	0	-		
Stillbirths	0	0	-		
Early post-natal death less	0	12	-		
Death — 2 weeks to weaning	0	4	-		
First service conception	0-18	18-22	-		
Conceptions per oestrous cycle exposed	0-22	22-27	-		
Calving difficulty	5	15-20	-	- Charolais	Menissier (1976)

only one report (Mavrogenis *et al.*, 1978) which has partitioned the covariance between direct genetic and maternal effects for post-weaning feedlot traits in beef cattle. This study just examined the paternal half-sib correlation and the sire-offspring regression which yields estimates of  $h_1^2$ , and the covariance of direct and maternal effects, but not  $h_m^2$ . The results of this study strongly suggest that the negative antagonism between direct and maternal effects apparent for pre-weaning traits may also be important post-weaning, at least up to the yearling stage.

It is well known that reproductive traits are much less heritable than pre- or post-weaning growth traits and therefore require larger data sets for genetic parameters to be estimated with reasonable accuracy. Phillipson (1976), working with Swedish Friesian heifers, provides the only estimates of both direct and maternal effects and the genetic correlation between them for calving performance, stillbirths, birth weight and gestation length, and the results are shown in Table 2. Also shown in Table 2 are some similar results from Dearborn *et al.* (1973), who could not estimate  $r_g$  but did present approximate estimates of  $h_1^2$  and  $h_m^2$ . These authors also obtain evidence for a direct influence of sire's phenotype on conception in addition to the direct influence of the samples of genes transmitted to his female offspring for conception traits. Menissier (1976) reviewed the genetic parameters of maternal performance (calving rate, survival, calving difficulty and mothering ability), with particular emphasis on results from the French Charolais population. He concluded that the results pertaining to genetic variability of all these traits show the necessity of pursuing the analysis of the variation and covariation for direct and maternal effects in order to optimize selection and breeding systems. Menissier (1979) reviewed in some detail the joint action of direct and maternal effects on calving difficulties in cattle.

#### POSSIBLE STRATEGIES TO INCORPORATE MATERNAL EFFECTS INTO SELECTION PROGRAMMES

##### DIRECT INFLUENCE OF DAMS ON MATERNAL ABILITY OF DAUGHTERS

Studies with beef cattle indicate that to maximize the producing ability of cows, their early growth rate may need to be controlled. Feeding for maximum growth rate may be beneficial for bulls, steers, and those heifers not selected as replacements, but could be detrimental to the producing ability of replacement

heifers. Unfortunately, the optimum growth rate for heifers which would maximize producing ability is not known, but it is likely to vary for different breeds, crossbreeds and management systems. In the study of Kress and Burfening (1972), the average 180-day weaning weight was 182 kg and weaning to yearling average daily gain was 0.37 kg. But the heifers exposed to the poorer pre-weaning and post-weaning environments, *i.e.*, having lower levels of early growth performance, were the best producers in the cow herd.

New Zealand data (Nicoll and Rae, 1977, 1978) indicated an average 180-day weaning weight of about 168 kg for heifer calves, and post-weaning gain to 550 days of about 0.75 kg/day for bulls and 0.35 kg/day for heifers. Since these average New Zealand figures are similar to those reported by Kress and Burfening, it seems that productivity of New Zealand beef cows could be adversely affected by early overfeeding.

In the absence of published research results from New Zealand, the following provisional recommendations for feeding and management of replacement Angus and Hereford heifers might be considered. These are based completely on published overseas information, not necessarily from the same feeding systems. Clearly these recommendations must be integrated with feeding policies for beef cows to optimize production in terms of not only the heifer calf's lactational development, but also calving and weaning performance and post-partum intervals of the cows (Scales and Stevenson, 1976; Smeaton *et al.*, 1979).

It is assumed that a breeder is mating heifers as yearlings to calve for the first time as 2-year-olds, rather than adopting the more traditional practice of calving heifers for the first time as 3-year-olds.

1. Feed cows at a moderate level until about 1 month before calving, and then provide more plentiful feeding just prior to calving and during early lactation.
2. Consider weaning earlier than the traditional 6 to 8 months of age. Weaning at 5 to 6 months of age (*i.e.*, 150 to 180 days) is recommended with average daily gains of calves from birth to weaning of no greater than 0.8 kg/day. Brumby *et al.* (1963), who weaned calves at 24 weeks (168 days), clearly showed the declining dependence of the liveweight gain of the growing calf upon its milk consumption after about 12 weeks (84 days) of age.

3. Separate male and female progeny at weaning. This is probably normal practice. Many farmers separate cows with bull calves from cows with heifer calves at marking time to give preferential treatment to bull calves, and this practice could be advantageous. Presuming heifer calves are weaned at weights of about 160 to 170 kg, feed them to gain in body weight at about 0.25 kg/day. This will result in 15-month joining weights of 210 to 250 kg, which have been shown to be adequate for 2-year-old and lifetime calving and weaning performance (Carter and Cox, 1973). Bull or steer calves can be fed at whatever levels can be sustained on a particular farm or in a particular season, and will probably get preferential treatment over heifers.
4. If there is scope for selection of heifers, then a number of strategies are possible within this management regime. Some culling at weaning is probably justified on the basis of adjusted weaning weights and signs of poor thrift. Further culling on *adjusted* yearling weights could then be practised, or, alternatively, all heifers could be joined with final culling on pregnancy diagnosis results (cull empty heifers) or, if carrying capacity is available, on first calving or weaning results. It might be suggested that a not very logical alternative is to cull the heaviest heifers on adjusted weaning or yearling weights. But these are those most likely to have superior breeding values for growth potential. Presuming our objective is to improve growth potential and probably optimize milk production (*i.e.* in a single-suckled beef cow we do not want it either too low or too high), then hopefully any detrimental effects of feeding level on mammary development will be controlled by moderate levels of feeding.
5. When heifers are not joined until 2¼ years of age, then an average daily gain from 15 months to 2¼ years of about 0.2 kg/day resulting in joining weights of 280 to 320 kg is recommended, but not below a threshold value of 230 kg (Carter *et al.*, 1980).

#### THE GENETIC CORRELATION BETWEEN DIRECT GENETIC AND MATERNAL EFFECTS

Since there is now ample evidence that the genetic correlation between direct genetic and maternal effects may be unfavourable, at least for pre-weaning growth traits (Table 1), the question arises as to how this should be taken into account in breeding

plans. Taking weaning weight as an example, and presuming the objective is to improve this both by better growth potential and better milk production, then selection index procedures (Hazel, 1943; Henderson, 1963) can be employed. Van Vleck (1970a, b, 1976) has developed selection index procedures to take into account direct genetic and maternal components.

Using these procedures, Van Vleck *et al.* (1977) examined expected phenotypic response in weaning weight of beef calves from selection for both direct genetic and maternal effects. Various combinations of different records for male and female selection were investigated, with selection among males only for direct genetic effects and in females for either direct effects, maternal

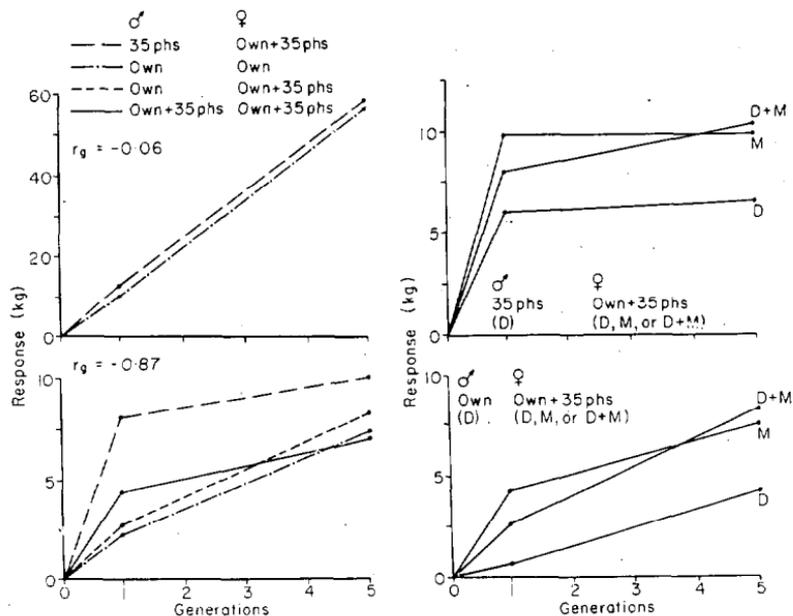


FIG. 3 (left): Expected response to selection for weaning weight (from Van Vleck *et al.*, 1977). Selecting for direct (D) plus maternal (M) effects in females and direct effect only in males with different values for the genetic correlation ( $r_g$ ) between direct and maternal effects.

FIG. 4 (right): Expected response to selection for weaning weight with  $r_g = -0.87$  (from Van Vleck *et al.*, 1977). Relative rates of response when selecting females for direct (D), maternal (M) or direct plus maternal (D + M) effects, and using the individual's own record and the progeny test of the sire of the individual (35 paternal half sibs) as the selection traits.

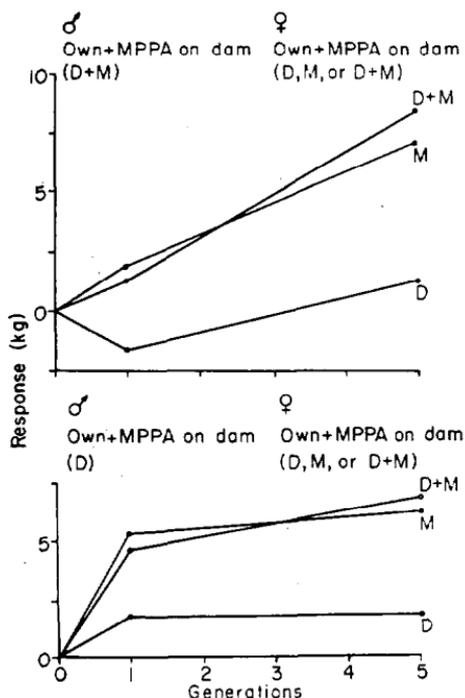


FIG. 5: Expected response to selection for weaning weight (with  $r_g = -0.87$ ) when using an individual's own record and the most probable producing ability (MPPA) of its dam to improve direct, maternal or direct plus maternal effects.

effects, or direct plus maternal effects. Baker (unpublished) investigated selection on the individual's own record for weaning weight plus the most probable producing ability (MPPA) for its dam (based on three weaning weight records). This MPPA measure is similar to the lifetime productivity index (LPI) produced by Beefplan for cows with a weaning weight, although the LPI discounts those cows which do not conceive, or abort or lose their calf before weaning. In developing these additional indices the parameters used were the same as those used by Van Vleck *et al.*, (1977). In particular, the selection intensities assumed were 1.25 for males and 0.6 for females.

Figure 3 illustrates how a large negative covariance term between direct and maternal effect ( $r_g = -0.87$ ) results in a reduction of expected response after five generations of selection by 80 to 90% compared with the situation where the covariance term is close to zero ( $r_g = -0.06$ ). If the genetic covariance is close to zero the expected responses are remarkably similar for all combinations of male and female selection (only two are shown in Fig. 3) and whether or not female selection is for direct value, maternal value or both. On the other hand judicious use of rela-

tives in selection with  $r_g = -0.87$  can result in up to a threefold difference in response after five generations. In Fig. 3 the best strategy shown exceeds the worst by 43%.

With a large negative covariance, selection of males for direct and females for maternal genetic value results in greater expected response in progeny for the first few generations (Fig. 4 illustrates two combinations of records). But for all combinations considered by Van Vleck *et al.* (1977) and for inclusion of MPPA in the selection (Fig. 5) there is advantage in selecting females for direct plus maternal effects for longer-term response — *i.e.*, five generations or more. While Figs. 4 and 5 show little merit in selecting females for direct effect, this is not always the case, particularly when using the female's own record or its own record plus its dam's record (see Table 5 of Van Vleck *et al.*, 1977).

In Fig. 5 the situation is illustrated where males are selected on direct plus maternal effects rather than just direct effects as considered by Van Vleck *et al.* (1977). For this combination of records it never paid to select males for maternal effects, and selecting males for direct effects was always advantageous over direct plus maternal selection in the short term, but not necessarily in the longer term.

#### SOME CONCLUDING COMMENTS

It appears that the relationships between direct and genetic effects reviewed here for beef cattle may be quite general for small animals (*e.g.*, mice and *Tribolium*), pigs, cattle and sheep (Cundiff, 1972; Bondari *et al.*, 1978).

Since maternal effects are a generation behind the direct effects, sex-limited and expressed late in life, pedigree selection by using sets of relatives in which the maternal effect is the primary common element in the group provides one way to increase selection pressure for the maternal effect while keeping the generation interval short (Willham, 1979). In a number of American beef breed associations' performance recording programmes, maternal breeding values are now being calculated for weaned calves by using the weaning weight of the calves of the daughters of the maternal and paternal grandsire plus those of the sire, if available, and the calves of the dam (Willham and Leighton, 1978). It is suggested that such breeding value calculations could be considered for Beefplan in New Zealand. To allow this, it is suggested that future research in New Zealand in this area should consider:

1. Estimation of  $h_d^2$ ,  $h_m^2$  and the genetic correlation between direct and maternal effects for all traits of importance in beef

- cattle, using data both from research herds and where possible from the industry (*e.g.*, Beefplan data).
2. Estimation of the *genetic* correlation between direct and maternal effects for pre- and post-weaning growth traits should take account of possible confounding with the negative environmental correlation between maternal effects in adjacent generations. Special mating designs such as those suggested by Eisen (1967) and Willham (1972) and used by Bondari *et al.* (1978) may need to be considered. In addition, the relatively large sampling variances of these genetic parameter estimates, particularly for  $h_m^2$ , and the genetic correlation between direct and maternal effects (Thompson, 1976; Foulley and Lefort, 1978), mean that large data sets and appropriate statistical and computing techniques are required.
  3. The importance and magnitude of the negative environmental correlation between maternal effects in adjacent generations need elucidating for New Zealand beef production systems. Some work along these lines is under way at Whatawhata and Invermay (D. C. Smeaton; G. W. Montgomery; unpublished).
  4. Further simulation studies of the type reported by Van Vleck *et al.* (1977) seem warranted, particularly allowing for different generation intervals and selection intensities in males and females and for overlapping generations (James, 1979). All index selection procedures developed to date are based on *maximizing* genetic improvement of the traits in the index. In the case of milk production in single suckled beef cows an intermediate optimum is of more concern and restricted selection index procedures would appear to be appropriate in this situation.
  5. It has been shown in laboratory species that it is possible to select against an antagonistic genetic correlation using appropriate index techniques (*e.g.*, Cockrem, 1959; Rutledge *et al.* 1973; Eisen, 1977). While experimental results with laboratory species show some differences between realized and expected responses to antagonistic selection, which may be due to poorly estimated base generation population parameters or to physiological or anatomical incompatibilities (Eisen, 1977), it still appears worth while to attempt to pursue antagonistic selection objectives in beef cattle and other livestock species. However, when pursuing this approach, either

by within-breed selection or between populations and crosses, there will be a need to watch for undesirable interactions. For example, Willham (1974), in a beef-dairy crossbreeding study, while showing the advantage of dairy breeds and dairy-beef crosses for combining growth and milking ability, also demonstrated a poor reproductive performance of the high-milking dairy breeds, which was especially marked under low levels of feeding.

## REFERENCES

- Barlow, R., 1978. *Anim. Breed. Abstr.*, 46: 469.
- Bondari, K.; Willham, R. L.; Freeman, A. E., 1978. *J. Anim. Sci.*, 47: 358.
- Bradford, G. E., 1972. *J. Anim. Sci.*, 35: 1324.
- Brown, J. C.; Galvez, M. V., 1969. *J. Anim. Sci.*, 28: 162.
- Brumby, P. J.; Walker, D. K.; Gallagher, R. M., 1963. *N.Z. J. agric. Res.*, 6: 526.
- Carter, A. H.; Cox, E. H., 1973. *Proc. N.Z. Soc. Anim. Prod.*, 33: 94.
- Carter, A. H.; Baker, R. L.; Hunter, J. C., 1980. *Proc. Ruakura Fmrs' Conf.* (in press).
- Cockrem, F. R. M., 1959. *Nature, London*, 183: 342.
- Cundiff, L. V., 1972. *J. Anim. Sci.*, 35: 1335.
- Dearborn, D. D.; Koch, R. M.; Cundiff, L. V.; Gregory, K. E.; Dickerson, G. E., 1973. *J. Anim. Sci.*, 36: 1032.
- Deese, R. E.; Koger, M., 1967. *J. Anim. Sci.*, 26: 250.
- Dickerson, G. E., 1942. *J. Anim. Sci.*, 1: 326.
- 1947. *Iowa Agric. Exp. Stn. Res. Bull.*, 354: 489.
- 1969. *Anim. Breed. Abstr.*, 37: 191.
- 1973. *Proc. Anim. Breed. Genet. Symp., Blacksburg, Virginia.* Am. Soc. Anim. Sci. and Am. Dairy Sci. Assoc. p. 54.
- 1974. *Proc. Working Symposium on Breed Evaluation and Crossing Experiments.* Zeist, Netherlands. p. 7.
- Donald, H. P.; Russell, W. S.; Taylor, St. C. S., 1962. *J. Agric. Sci.*, 58: 405.
- Eisen, E. J., 1967. *Can. J. Genet. Cytol.*, 9: 13.
- 1977. *Proc. International Conference on Quantitative Genetics.* Iowa State University Press, Ames. p. 117.
- Everett, R. W.; Magee, W. T., 1965. *J. Dairy Sci.*, 48: 957.
- Foulley, J. L.; Lefort, G., 1978. *Ann. Genet. Sel. anim.*, 10: 475.
- Foulley, J. L.; Menissier, F., 1974. Cited by Foulley and Lefort (1978).
- Hazel, L. N., 1943. *Genetics*, 28: 476.
- Henderson, C. R., 1963. In *Statistical Genetics and Plant Breeding.* NAS-NRC, 982: 141.
- Hill, J. R., 1965. Ph.D. thesis, North Carolina State University, Raleigh, NC.
- Hohenboken, W. D.; Brinks, J. S., 1971. *J. Anim. Sci.*, 32: 26.
- James, J. W., 1979. *Livestock Prod. Sci.*, 6: 215.
- Koch, R. M., 1972. *J. Anim. Sci.*, 35: 1316.
- Koch, R. M.; Clark, R. T., 1955. *J. Anim. Sci.*, 14: 979.
- Kress, D. D.; Burfening, P. J., 1972. *J. Anim. Sci.*, 35: 327.
- Lawson, J. E., 1977. *Beef Selection for Gain on Two Rations.* Canada Agriculture Publication.

- Legates, J. E., 1972. *J. Anim. Sci.*, 35: 1294.
- Lush, J. L., 1940. *Proc. Am. Soc. Anim. Prod.*: 293.
- McGloughlin, P., 1976. *Symposium on Optimisation of Cattle Breeding Schemes, Ireland*. Commission of European Communities, Luxembourg. EUR 5490e.
- Mangus, W. L.; Brinks, J. S., 1971. *J. Anim. Sci.*, 32: 17.
- Mason, I. L.; Pabst, W., 1977. *Symposium on Crossbreeding Experiments and Strategy of Beef Utilisation to Increase Beef Production, Verden*. Commission of European Communities, Luxembourg. EUR 5492e.
- Mavrogenis, A. P.; Dillard, E. U.; Robison, O. W., 1978. *J. Anim. Sci.*, 47: 1004.
- Menissier, F., 1976. *Ann. Genet. Sel. anim.*, 8: 71.
- 1979. In *Symposium on the Combined Action of Direct and Maternal Effects on Production Characters*. Bull. tech. Dept. Genet. anim., C.N.R.Z., Jouy-en-Josas. Nos. 29-30: p. 132.
- Minkema, D., 1974. *Proc. Working Symposium on Breed Evaluation and Crossing Experiments*. Zeist, Netherlands.
- Nicoll, G. B.; Rae, A. L., 1977. *N.Z. J. agric. Res.*, 20: 269.
- 1978. *N.Z. J. agric. Res.*, 21: 563.
- Philipsson, J., 1976. *Acta Agric. Scand.*, 26: 201.
- Poindron, P.; Le Neindre, P., 1979. In *Symposium on the Combined Action of Direct and Maternal Effects on Production Characters*. Bull. tech. Dept. Genet. anim. C.N.R.Z., Jouy-en-Josas. Nos. 29-30: p. 33.
- Robertson, A., 1977. In *Symposium on Crossbreeding Experiments and Strategy of Beef Utilization to Increase Beef Production, Verden*. Commission of European Communities, Luxembourg. EUR 5492e. p. 4.
- Robison, O. W., 1972. *J. Anim. Sci.*, 35: 1303.
- Rutledge, J. J.; Eisen, E. J.; Legates, J. E., 1973. *Genetics*, 75: 709.
- Scales, G. H.; Stevenson, J. R., 1976. *Proc. Ruakura Fmrs' Conf.*: 45.
- Sejrsen, K., 1978. *Acta Agric. Scand.*, 28: 41.
- Smeaton, D. C.; Nicoll, G. B.; Reardon, T. F.; Welch, R. A. S., 1979. *Proc. Ruakura Fmrs' Conf.*, 30: 26.
- Thompson, R., 1976. *Biometrics*, 32: 903.
- Totusek, R., 1968. *Okla. Agric. Exp. Stn. Misc. Publ. MP-80*. p. 72.
- Van Vleck, L. D., 1970a. *Genetics Lectures*. Oregon State University, Corvallis. Vol. 2: 133.
- 1970b. *Biometrics*, 26: 477.
- 1976. *Biometrics*, 32: 173.
- Van Vleck, L. D.; St Louis, D.; Miller, J. I., 1977. *J. Anim. Sci.*, 44: 360.
- Vesley, J. A.; Robison, O. W., 1971. *J. Anim. Sci.*, 32: 825.
- Vissac, B., 1979. In *Symposium on the Combined Action of Direct and Maternal Effects on Production Characters*. Bull. tech. Dept. Genet. anim., C.N.R.Z., Jouy-en-Josas. Nos. 29-30.
- Willham, R. L., 1963. *Biometrics*, 19: 18.
- 1972. *J. Anim. Sci.*, 35: 1288.
- 1974. *Proc. Working Symposium on Breed Evaluation and Crossing Experiments*. Zeist, Netherlands. p. 245.
- 1979. *Problems in Estimating Maternal Effects*. E.A.A.P., Harrogate, England.
- Willham, R. L.; Leighton, E. A., 1978. *Breeding Value Considerations*. Beef Improvement Federation Annual Report, U.S.A.