GENETIC ASPECTS OF THE EFFICIENCY OF NUTRIENT UTILIZATION FOR MILK PRODUCTION 1, 2

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CONSIDERING the importance of feed efficiency to the dairy industry, little effort has been devoted to studying its genetic aspects. Perhaps the small amount of published work on this problem is not surprising because of the cost of collecting data on the large number of individual cows required to make valid genetic inferences. The genetic control of nutrient utilization will be discussed under four headings: (1) direct measurement of efficiency, (2) genotype by environmental interactions regarding sources and levels of energy intake, (3) inherent differences in forage or nutrient consumption and (4) economic efficiency. The latter brings into consideration many managerial and resource utilization alternatives which should be considered jointly with physiological efficiency, which is directly an animal problem, but cannot now be considered jointly because of the lack of research information. The discussion of economic efficiency will be superficial, but this should not be connoted to mean it is of minor importance.

Many measures of physiological efficiency have been proposed and are useful. It seems, however, that if any genetic use on a population basis is to be made of efficiency \textit{per se}, the measure should be as simple as possible. The one most used has been gross energetic efficiency or some ratio of the energy produced in milk to the total energy consumed by the animal.

\textit{Direct Measurement of Efficiency}

O. Venge (1956) used two measures of efficiency to study data from the Danish progeny testing stations. He included 3083 cows in 174 progeny groups. The first measure was the total feed units that each cow received divided by the kilograms of butterfat she produced. In the second, called production feed units, the requirements for maintenance and growth were calculated and subtracted from the intake so that production feed units attempted to measure only the feed used for production. There seemed some advantage, at least in this situation, in using production feed units rather than total feed units. There was more variation from station to station in total feed units than in production feed units. This could have been caused by differences in weights of the animals at different stations, a curvilinear relation between feed utilization and level of production or a curvilinear relation between feed utilization and progeny group averages. Other contributing factors could have been differences in length of time milked for progeny groups from one station to the next, or the combining of between farm environmental differences previous to coming to the testing station with progeny groups.

From these data, Venge (1956) estimated the heritability of butterfat production to be 0.54, of total feed units per kilogram of butterfat to be 0.40 and of production feed units per kilogram of butterfat to be 0.23. The heritability values were reduced to 0.10 for butterfat production but only to 0.21 for production feed units per kilogram of butterfat, when the data were corrected for age and length of time milked. As is now well known from the work of Robertson and Mason (1956) and Touchberry \textit{et al.} (1960), the variation between sires in the progeny testing stations was greater than the variation between sires in field data. This led to the conclusion that there was some additional nongenetic variation confounded with sire progeny groups in the stations for yields of milk and fat. Although this is not known to be true for the measures of efficiency, it indicates the heritability estimates could be inflated.

Another genetic study based on sizable amounts of data was reported by Mason \textit{et al.} (1957). They used data collected from 1946 through 1951 from Red Danish cattle in the testing stations in Denmark. These data included records on about 1,300 heifers from 152 sire progeny groups kept under field con-
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Nutrient utilization for milk production is a complex process influenced by various factors. Heritabilities were estimated as follows: milk production 0.57, percent fat 0.84, and efficiency of milk production 0.48. The efficiency was defined as the ratio of total FCM (fat corrected milk) to the feed units consumed by the animal. The phenotypic correlation between milk production and efficiency was 0.84 with the corresponding genetic correlation 0.95. For fat percent and efficiency, the phenotypic correlation was 0.13 and the genetic correlation was 0.21. As mentioned previously, the confounding of some non-genetic differences with sire progeny groups complicates the interpretation of these data. The heritability estimates, particularly of the yield traits, are higher than those estimated throughout most of the world, but the heritabilities of efficiency and weights and the genetic and phenotypic correlations agree reasonably well with other work. Even allowing for some inflation of the computed values, there is little doubt that the genetic correlation between the efficiency of milk production and lactation yield is high. It is partly automatic that the phenotypic correlation between milk production and efficiency is high, since this is a part-whole relation. As McGilliard (1959) pointed out, the amount of milk produced by cows will vary much more than the amount of feed they consume, under normal conditions, and will force efficiency to be dependent upon the production of the cow. As yield and feed level increase, the proportion of feed attributable to maintenance requirements becomes less. This is perhaps another way of stating the automaticity between the correlation for milk yield and feed efficiency. These data certainly indicate that, under a given system of feeding, selection for milk production will automatically lead to an increase in gross efficiency.

Mason et al. (1957) further looked at the effect of "size" on the efficiency of milk production with the data on wither height, heart girth, and weight of the heifers in the Danish progeny testing stations. Heritability estimates concerning size were: weight upon reception at the station, 0.41; weight in March, 0.37; heart girth in March, 0.41, which agreed well with the field data; and height in March, 0.51. They also computed the partial correlation of efficiency on yield independent of height to be 0.91. The partial correlation of efficiency on height independent of yield was 0.33. Quoting from the authors, "For a given milk yield the taller animal is less efficient. But overall, the taller animal is more efficient because the increase in yield outweighs the increase in maintenance requirements. On this evidence, then, selection for yield or for efficiency would result in a slight increase in body size. In the absence of efficiency measurements, the best way would be to select on yield, making some allowance for height. In fact, it can be demonstrated mathematically from the above correlation that the ratio of yield over height would correspond closely to the best index." Also, Wallace (1956) and, later, Mason et al. (1957) in New Zealand suggested a similar index as a simple measure of efficiency. Here the index was yield divided by heart girth squared. Both indexes are highly correlated with milk yield because of the higher coefficient of variation for milk than measurements. Selection on either will reduce the correlated response of body size that selection on yield alone might cause. Mason et al. (1957) calculated that the variance between progeny groups in feed requirements for bodyweight gain is about twice that for maintenance. This suggests that gross efficiency is mostly determined by the partition of food for growth and milk production during lactation. This, of course, assumes the calculated maintenance requirements are correct.

One of the most comprehensive genetic studies in the United States has been conducted at Beltsville (R. D. Plowman, personal communication). They obtained feed intake on the experimental herd for over 10 years. They had information on 684 lactations of 332 Holstein cows by 27 sires. The efficiency of production was computed as the lactation yield of fat corrected milk over the total therms of net energy consumed. Least squares analyses showed differences between years, seasons, years by seasons, lactations, barns and pregnancy effects to be significant. In general, therms of intake and gross efficiency increased with advancing lactation number. The latter probably reflects the decreasing need for energy to increase body size. The phenotypic correlations between milk, fat, FCM, therms intake and gross efficiency were all over 0.7 except the
TABLE 1. HERITABILITY ESTIMATES OF THE EFFICIENCY OF FEED UTILIZATION FOR MILK PRODUCTION

<table>
<thead>
<tr>
<th>Measure of efficiency</th>
<th>Estimate</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>FCM/PU consumed</td>
<td>0.48 ± 0.07</td>
<td>Mason et al. (1957)</td>
</tr>
<tr>
<td>FU/kg butterfat</td>
<td>0.40</td>
<td>Venge (1956)</td>
</tr>
<tr>
<td>Prod. FU/kg butterfat</td>
<td>0.23</td>
<td>Venge (1956)</td>
</tr>
<tr>
<td>FCM/Therm NE consumed</td>
<td>0.45</td>
<td>Plowman a</td>
</tr>
<tr>
<td>TDN/45.4 kg. FCM</td>
<td>0.20 ± 0.41</td>
<td>Gray b</td>
</tr>
<tr>
<td>TDN/45.4 kg. FCM</td>
<td>0.36</td>
<td>Gray b</td>
</tr>
</tbody>
</table>

*a R. D. Plowman, personal communication.  
*b H. G. Gray, personal communication.

one between gross efficiency and therms intake. This was 0.31 for all lactations of all cows. This lower correlation is not surprising because of the variation in feed utilization associated with bodyweight. Heritability of therms intake and gross efficiency was estimated to be 0.21 and 0.43, respectively, from 170 first lactation daughter-dam pairs and 0.43 and 0.52 from all lactations of 255 daughter-dam pairs. The genetic correlations between gross efficiency and the following 4 variables were: milk, 0.84; fat, 0.93; FCM, 0.92; and therms intake, 0.52. The estimated genetic correlations between therms intake and the first three of these variables were: 0.86, 0.77 and 0.82.

Using data collected over 7 years in the Cornell University McDonald Farms herd, studies have been conducted (H. T. Gray, personal communication) on the heritability and repeatability of forage dry matter intake and efficiency of feed utilization in Guernseys. Sampling forage intake 4 consecutive days each month in 3 sequential lots provided a suitable estimate of forage dry matter intake for the 6-mo. barn feeding period. Efficiency was calculated for 140 day periods as the TDN required for the maintenance and production of 45.4 kg. of FCM with adjustments made for changes in bodyweight. Efficiency values were adjusted for age and stage of lactation, and the adjusted data were used to calculate heritability and repeatability estimates. Repeatability of this measure of feed efficiency was estimated to be 0.26 using 219 records of 127 cows. Heritability estimates were 0.20 ± 0.41 from daughter-dam regression and 0.36 from paternal half sibs (189 records from 18 sire groups).

For comparison, table 1 gives the estimates of heritability of feed efficiency and the measure of efficiency that was used. The estimates range from about 0.20 to about 0.50. This range is not surprising, considering the different definitions of efficiency and the amount of data from which they were computed. The genetic and phenotypic correlations given in table 2 are uniformly high (≥0.80) for efficiency and yield traits. They are somewhat lower for efficiency and intake.

It seems clear that we should attempt to increase the efficiency of feed utilization for milk production in the cattle population. The two essential conditions for making genetic gain seem to exist. The trait must be heritable and there must be appreciable variation present in the population. The estimates of heritability are certainly positive; and it seems reasonably sure that genetic gain in efficiency could be realized, although this has not been demonstrated experimentally. A practical limitation is also clear. It would be expensive and difficult to obtain accurate feed intake on individual cows over a large sample of the cow population. In fact, considerable economic incentive would probably have to exist before such measurement would be routinely taken by commercial dairymen.

The evidence to date certainly indicates that milk production is highly correlated, both phenotypically and genetically, with efficiency. That is, any genetic gain in milk production will automatically be accompanied by genetic gain in feed efficiency. The mechanics for making genetic gain in milk production are in use and are effective, so it seems worth estimating the effectiveness of indirect selection for efficiency. Table 3 has been prepared, using the method outlined by Falconer (1960), to indicate the relative rate of genetic change in feed efficiency by selecting for milk production as opposed to direct selection for efficiency. The values were computed assuming equal selection differentials for the two traits. The table is constructed using approximately the range of parameters found in the literature for the heritability of feed efficiency.
and the genetic correlation between efficiency and milk production.

If the heritabilities and selection intensities of the two traits are equal, the magnitude of the genetic correlation specifies the effectiveness of indirect selection. Current evidence indicates that selection for milk production would make between 70 and 95% as much improvement in efficiency as direct selection for efficiency when the selection intensities are equal for the two traits. Because in practice it is much easier to measure production than feed efficiency on large numbers of cows, the effective selection intensity for production will almost surely be larger than for efficiency. This makes indirect selection on milk production more advantageous; and, in practice, indirect selection will probably accomplish more genetic gain in increasing feed efficiency than direct selection.

The work of Lamb and Anderson (1966) is a progress report of a well-designed experiment in Utah investigating the interaction of sire progeny groups with rather widely different rations. They reported results from 200 daughters of 14 sires. One-half of the daughters of each sire were fed an all roughage ration during their first 305 day lactation, and the other half of the daughters received roughage plus 1 kg. of grain per 3.5 kg. of fat corrected milk. All heifers were reared similarly on a standard ration. Two measures of gross feed efficiency were computed. They were kilograms of FCM over kilograms of digestible dry matter and 750 times kilograms of fat corrected milk over the calories of energy consumed. Values of the first measure of efficiency ranged from 1.24 to 1.51 for the sire groups on all forage and from 1.42 to 1.73 for animals on the forage plus grain ration. The average efficiency was slightly higher on the forage plus grain ration. Correlations were almost 1 between the two measures of efficiency for both rations. The phenotypic correlation between production of fat corrected milk and gross efficiency was about 0.8.

An interesting observation on the work of Lamb and Anderson (1966) is that daughters of a New Zealand bull were the most efficient on the all roughage diet and least efficient on the roughage plus grain diet. This is in the expected direction of response, since selections in New Zealand have been among cattle that were mostly fed an all roughage ration. Only one New Zealand bull was included in this group and the differences were not large enough, compared with the variation within sires and rations, to cause the interaction over all sires to be significantly different from 0.

An experiment somewhat similar to the one in Utah is being conducted in Tennessee (D. O. Richardson and co-workers personal communication). Jersey sire progeny groups are split between an all roughage and a roughage plus grain ration. These results corroborate those in Utah because there is no evidence of a sire by ration interaction.

In another experiment still in progress at Iowa State University, identical and fraternal twins have been used to investigate the interaction of genotypes with two feeding regimes. All animals were offered hay free.
choice with the amount of grain differing. After 9 mo. of age, the high ration group received 2.72 kg. of grain per day and the low ration group no grain until calving. After calving, the high ration animal received 1 kg. of grain per 2 kg. of milk on all milk over 4.54 kg. daily. The low ration group received 1 kg. of grain per 6 kg. of milk on all over 4.54 kg. daily. The pairs were allocated to rations so that both members of one pair received a high ration, the next two pairs were split with one member of each pair on the high ration and on the other on the low one, and both members of the fourth pair were on a low ration. The same sequence of assigning pairs to rations was continued for additional replications. The twins were not individually fed, so direct measurement of efficiency of food utilization could not be made. The data were analyzed using an iterative weighted least squares analysis described by Hayman (1960). First lactation production is available from 21 monozygotic split ration pairs and 22 monozygotic uniformly treated pairs, 11 pairs each on the high and low rations. The ration difference was about 850 kg. of milk on a mature equivalent basis. The ration (R) by additively genetic (A) interaction was estimated as 0 for percent fat and mature equivalent milk and fat. These results are given in Table 4. Using the same type analysis, an additional 18 split ration and 13 uniformly treated pairs were included, which allowed separation of the contemporaneity effects (C) that are common to a pair of twins but lacking in single born animals that are randomly drawn from the cattle population. The interaction of rations with A and with C (not shown in the table) were jointly estimated to be near zero. Table 4 also demonstrates that when the effects of contemporaneity are removed, the heritability (ratio of A to the sum of all components of variance) estimates of these traits are reduced. In this sample of data, the heritability estimates are of about the same magnitude as in field data. Using monozygotic twins Bonnier et al. (1948) conducted two experiments using a total of 14 twin pairs. In one experiment, ration differences were maintained within twin pairs up to calving, and then each animal was fed according to its production, allowing for growth. In the second experiment, the ration difference was maintained throughout life. The interaction of pairs and rations, for production traits, was significantly different from zero, but the rank order of twins across rations was nearly unchanged. Because of this, the genotype by environmental interaction was practically unimportant.

In another monozygotic twin experiment, Hancock (1955) used 15 pairs in a balanced incomplete block design where the twins were allocated to 3 ration comparisons. He found no evidence of any important genotype by environment interaction in spite of rather large differences in milk yield from ration to ration. Heritability estimates from these twin studies were high, but contemporaneity effects were not removed from the between pair variances.

Although sources and levels of energy intake are not available from farmer owned herds and many other environmental differences exist between such herds, if there is a large interaction between sire progeny groups and ration differences, it should be detectable from such data. These rather extensive investigations are typified by those of Hichman and Henderson (1955) and Van Vleck et al. (1961) in New York; Legates et al. (1956) using data from all over the United States; Wadell and McGilliard (1959) and Specht and McGilliard (1960) using Michigan data; and Bereskin (1963) and Kelleher (1964) using Iowa data.

In these studies, the size of the sire by herd or sire by herd-year-season interaction estimates varied from negative ones to one that accounted for 7% of the total variation. They would average about 2 to 3% of the total variation. All these estimated components of variance were derived from highly non-orthogonal data. Kelleher (1964) selected balanced two sire by n herd-year-season sets of data and estimated the sire by herd-year-season interaction to account for 2% of the total variation. He further showed that the influence of sire by herd-year-season interaction is a small source of error in sire selection.

TABLE 4. PARAMETER ESTIMATES FROM FIRST LACTATION PRODUCTION OF CATTLE TWINS (COMPONENTS OF VARIANCE AS % OF TOTAL)*

<table>
<thead>
<tr>
<th>Trait</th>
<th>Estimated from</th>
<th>R</th>
<th>C</th>
<th>A</th>
<th>RA</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>M.E. Milk</td>
<td>MZ</td>
<td>25</td>
<td>.</td>
<td>54</td>
<td>0</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>MZ + DZ</td>
<td>31</td>
<td>16</td>
<td>31</td>
<td>.</td>
<td>21</td>
</tr>
<tr>
<td>M.E. Fat</td>
<td>MZ</td>
<td>22</td>
<td>.</td>
<td>55</td>
<td>0</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>MZ + DZ</td>
<td>30</td>
<td>24</td>
<td>24</td>
<td>.</td>
<td>21</td>
</tr>
<tr>
<td>% Fat</td>
<td>MZ</td>
<td>2</td>
<td>6</td>
<td>85</td>
<td>.</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>MZ + DZ</td>
<td>4</td>
<td>36</td>
<td>50</td>
<td>.</td>
<td>13</td>
</tr>
</tbody>
</table>

* R—variance due to rations;
C—variance due to the effects of contemporaneity;
A—additive genetic variance;
RA—variance due to the interaction of rations with additive effects;
E—residual variance.
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relative to all other sources when sire's progeny are distributed over several herds. However, when sires are progeny tested in very limited numbers of herd-year-seasons, the interaction can be an appreciable source of error in sire evaluation.

There is little evidence, for production traits, of an appreciable interaction of genotypes with environments over the range of conditions tested. The results from field data are reasonably conclusive, but only a limited number of designed experiments have been conducted. Certainly, if sufficiently diverse environments and genotypes are chosen, such an interaction exists. However, within the confines of the usual selection procedures, genotype by environmental interactions appear to cause only very slight, if any, errors in selection.

Inherent Differences in Forage or Nutrient Consumption

A large number of studies have been conducted that relate to appetite or nutrient consumption. The majority of these have been designed to compare different feeds. Only a few have attempted to make genetic inferences from their work.

Mather (1960) prepared an excellent review and discussion of the literature relative to the question: "Can dairy cattle be bred for increased forage consumption and efficiency of utilization?" The details of his review will not be repeated, but the conclusions drawn here are substantially the same as his. The data that are available indicate that the repeatability of roughage consumption from month to month within a year, from month to month across years or of yearly averages is greater than 0. The results are difficult to pool because of such things as differences in sampling periods from one study to the next, in bodyweight of the cows and in stage of lactation.

Since Mather's paper, additional evidence has become available. Stone et al. (1960), pooling the data from 12 forage experiments, have estimated the repeatability of weekly forage intake at about 0.70 when their data were adjusted by covariance techniques for bodyweight and milk production. A multiple regression equation that included 4% FCM, bodyweight and daily weight change gave a multiple correlation of 0.50 indicating that 25% of the differences among cows in forage intake was associated with these three variables. Perhaps of more interest here is that a rank correlation between the consumption of different forages for the same cow over 60 different pairs of treatments was 0.63. In other words, three out of four cows in the top half for consumption of one forage were also in the top half when another forage was fed.

In the work at Cornell, (H. G. Gray, personal communication), age of cow, year of observation and month of lactation had highly significant effects on forage intake. The repeatability of forage dry matter intake, adjusted for these effects, was estimated as 0.32 from 520 records of 221 cows. Heritability of forage dry matter intake was estimated as 0.23 from 167 records of daughters of 22 sires and as 0.09 ± 0.17 from parent-offspring regression.

The Beltsville workers (R. D. Plowman, personal communication) have supplied genetic information on feed intake. They estimated the heritability of therms intake to be 0.21 from first lactations and 0.43 from all lactations. The repeatability of therms intake on a lactation basis was estimated as 0.45. They also estimated the genetic correlation between total therms intake and milk production as 0.86. More research is needed before definite conclusions can be drawn. If these estimates are close to the real parameters in the cow population when many practical feeding regimes are included, the situation seems to be similar to that of efficiency and milk production. That is, selection for milk production might be expected to automatically select for increased forage consumption.

The question might logically be asked—should we select for forage consumption per se? From a philosophical view, we might say, "yes." As world population and that in the United States increases, grain is in demand for human food in most of the world and may become more so in the United States. Grain may become too expensive as a feed stuff for cattle. Then, we should have cattle that can convert roughage into milk as efficiently as possible. Can we predict if this will happen or when it will happen? Regardless of this, don't we have the responsibility to have the knowledge available as to what alternatives might logically and efficiently be pursued when the course to follow becomes clear?

Economic Efficiency

Detailed consideration of the economics of efficient milk production is beyond the scope of this discussion, but a few remarks seem justified. Absolute maximum production for
increased feed efficiency. This indirect selection is expected to be between 70 and 95% as effective as would be direct selection for the two traits. Since, in practice, indirect selection could be more intense, indirect selection may actually achieve more progress in increasing feed efficiency.

Genotype by environmental interactions for sources and levels of energy intake have not been important enough, in the limited number of experiments conducted, to be an important source of error in making selections among cattle for increased production of milk or fat. The same conclusion can be made for the selection of sires when the progeny are tested in many herds. The latter is much more clearly documented. A great deal more research is needed to clarify the genetic relations among size of cow, forage intake and total nutrient intake.

Summary

The evidence to date indicates that selection for increased feed efficiency (gross energetic efficiency) for the production of milk would be effective. But, because of the high genetic correlation between milk production and efficiency and because the ratio of the heritabilities of these traits appears to be approximately equal, selection for milk production alone will automatically select for increased feed efficiency. This indirect selection is expected to be between 70 and 95% as effective as would be direct selection for efficiency if the selection intensity is equal for the two traits. Since, in practice, indirect selection could be more intense, indirect selection may actually achieve more progress in increasing feed efficiency.

Genotype by environmental interactions for sources and levels of energy intake have not been important enough, in the limited number of experiments conducted, to be an important source of error in making selections among cattle for increased production of milk or fat. The same conclusion can be made for the selection of sires when the progeny are tested in many herds. The latter is much more clearly documented. A great deal more research is needed to clarify the genetic relations among size of cow, forage intake and total nutrient intake.

Literature Cited


