The Interplay of Feeding and Genetics on Heifer Rearing and First Lactation Milk Yield: A Review

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ABSTRACT: Weight gain of young dairy replacement heifers, even over several months, is highly variable, lowly heritable, and a poor indicator of either weight at calving or first lactation milk yield. Voluntary forage consumption is much less variable, more heritable, and a better predictor of weight at calving and milk yield. Weight at calving is highly heritable but not correlated genetically with milk yield. Heavier weight at first calving due to feeding and management does increase milk yield. When grain is fed according to milk yield, weight loss during the first month or two after calving and milk yield are under strong genetic control and tightly genetically correlated to each other and to energy intake. The feed to milk ratio is managementally determined. Better-grown heifers eat more forage and can tolerate more grain consumption without digestive or metabolic disorders. Good body condition at calving seems essential for high milk yield. Genetic ability to mobilize body condition to increase milk yield justifies more grain and results in greater total efficiency up to the point of causing digestive disorders. Good heifer rearing is essential to high milk yield and feed efficiency. Realizing genetic potential for high yield demands excellence of feeding and management during lactation.

Key Words: Dairy, Genetics, Growth, Lactation, Feeding

Introduction

Genetics determine the inherent potential for an embryo to grow into a highly profitable adult cow. Feeding and management determine the extent to which that potential will be realized. Feeding is systematically adjusted to the estimated genetic potential and nutrient requirements of the individual or group to maximize profits, particularly during lactation. Observed growth, body condition and milk yield form the basis of adjustment. To the extent that such traits are heritable, this becomes genetic. Hence, any biologically based interaction of genetics with feeding is masked by adjustments of feeding. Even ad libitum feeding of a single total mixed diet masks biology because, if it meets the requirements of the very highest producers, it will generally overfeed the poorest producers. The choice of nutrient density and type of feeds used is a management decision limiting genetic response. This review of research on feeding, growth, and lactation is based primarily on results of the Canadian National Cooperative Dairy Cattle Breeding Project (NCDCBP) and related research from the literature, particularly a recent study in The Netherlands. The overall objective is to consolidate our understanding of the genetics of feed efficiency in growth and lactation and their interrelationships. A brief description of the NCDCBP is followed by consideration of heifer growth, first lactation, and finally their interrelationships.

Experimental Procedures

The NCDCBP experimental data used to study feed efficiency came from a long-term breeding project involving selection for protein yield in Holstein and Ayrshire cattle and their crosses. Crossbred females were mated to F₁ crossbred bulls from elite parents. The population involved 800 milking cows at five research stations (Charlottetown, Prince Edward Island; Normandin, Quebec; Lennoxville, Quebec; Ottawa, Ontario; Lethbridge, Alberta). Approximately 1,300 Holstein females, progeny of 74 sires, born at Ottawa, Lennoxville, and Lethbridge between 1972
Table 1. Heritabilities (h²), and genetic (G) and phenotypic (P) correlations

<table>
<thead>
<tr>
<th>Heifer trait</th>
<th>Energy consumption, 26–34 wk (h² = .23)</th>
<th>Weight gain, 26–34 wk (h² = .17)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weight, 26 wk (h² = .14)</td>
<td>G = .54</td>
<td>G = .44</td>
</tr>
<tr>
<td>P = .01</td>
<td>G = .44</td>
<td>P = .27</td>
</tr>
<tr>
<td>Weight gain, 26–34 wk (h² = .17)</td>
<td>G = .44</td>
<td>P = .52</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Cow trait</th>
<th>Weight gain, 0–8 wk (h² = .29)</th>
<th>Weight gain, 8–16 wk (h² = .13)</th>
<th>Milk energy, 8–16 wk (h² = .37)</th>
<th>Energy intake, 8–16 wk (h² = .27)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weight at calving (h² = .37)</td>
<td>G − .15</td>
<td>G − .37</td>
<td>G = .05</td>
<td>G = .23</td>
</tr>
<tr>
<td>P − .39</td>
<td>P − .10</td>
<td>P − .34</td>
<td>P = .19</td>
<td>P = .28</td>
</tr>
<tr>
<td>Weight gain, 0–8 wk (h² = .29)</td>
<td>G = .17</td>
<td>G − .32</td>
<td>G − .63</td>
<td>G = .26</td>
</tr>
<tr>
<td>P − .06</td>
<td>P − .34</td>
<td>P = .34</td>
<td>P − .08</td>
<td>P = .26</td>
</tr>
<tr>
<td>Weight gain, 8–16 wk (h² = .13)</td>
<td>G − .69</td>
<td>G − .63</td>
<td>G = .94</td>
<td>G = .78</td>
</tr>
<tr>
<td>P − .13</td>
<td>P = .08</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*From Lee et al. (1992).*

and 1983, had complete data through first lactation. These data were the basis of the genetic correlation study by Lee et al. (1992). Newborn calves in the project received colostrum within 24 h of birth and were milk fed to 8 wk with access to calf starter. From 9 to 34 wk, calves received 2.5 kg starter grower and ad libitum forage. After a 2-wk adjustment period, heifers were individually fed from 26 to 34 wk using Calan gates (American Calan Inc., Northwood, NH). From 34 to 50 wk, heifers received ad libitum forage and 1.8 kg/d grower ration. All heifers were bred at first heat after 50 wk of age, regardless of size, and calved for the first time at 22 ± 2 mo. From 50 wk to 2 wk pre-calving, only forage was provided. After calving, cows received forage ad libitum plus 1 kg of concentrate for each 3 kg of milk over 7 kg milk/d with a 5 kg concentrate per day minimum during the first 8 wk of lactation. Concentrate feed was approximately 83% TDN and 21% CP with a Ca:P ratio of 1:1 plus trace minerals. During the feeding trial from 8 to 16 wk of first lactation, feed offered and weigh backs were recorded individually. Cattle were fed stored feeds year-round. Milk weights were taken at an evening milking and a morning milking each week, and samples for composition were obtained at 8, 16, 24, 32, and 40 wk of lactation. Body weights and measurements were recorded at 26, 34, 50, 66, and 82 wk, at calving, and at 8 and 16 wk of first lactation. Breeding of cows during first lactation began at 8 wk post-partum. A detailed description is in McAllister et al. (1978). Restricted maximum likelihood estimates of sire and residual variance and covariance components for all heifer and first lactation traits were obtained simultaneously under a multiple trait model with random sire effects (Lee et al., 1992). A canonical transformation was used because the same model was used for all traits, and data were restricted to those for animals with all traits recorded.

Heifer Growth. There are substantial additive genetic differences between dairy breeds and sire groups within breed for size and growth rate of replacement heifers (Lee et al., 1988). Heterosis or non-additive genetic differences have limited effects in heifers (Batra et al., 1986), but more substantial effects on growth rate and fatness of males raised for beef on high-energy diets (Lee and Drevjany, 1984). Feed intake of a total mixed diet or of the forage component fed ad libitum is closely correlated with body weight (Table 1), as expected. Adjustment of feed intake for body weight and growth rate during the feeding trial eliminates most if not all of the variation (Lee et al., 1988; Korver et al., 1991). This indicates that feeding standards based on body weight and growth rate are reasonably accurate. Differences in gross efficiency are primarily related to metabolizable energy density of an otherwise balanced diet and rates of voluntary consumption of the diet. No evidence exists for substantial real differences between genetic groups or individual heifers in biological feed efficiency. Somewhat facetiously, if an Ayrshire cow was as big as a Holstein cow and grew as fast as a Holstein, it would eat just as much feed as a Holstein and have similar feed efficiency. In fact it would be a Holstein not an Ayrshire. Hence, I would argue that residual feed intake adjusted for body weight and growth rate is essentially meaningless. Feed intake is
being adjusted for differences in size and growth rate that are genetic in origin and that are genetically correlated with feed intake. This is an inappropriate use of covariates. Adjustment for non-genetic differences using regressions free of genetic covariance might be appropriate. An equivalent and much more direct evaluation is possible using multiple trait mixed model analysis (e.g., Lee et al., 1992). There are a few very interesting aspects of heifer growth and feed consumption. Growth rates, even over several months, are notoriously variable (coefficient of variation 20% or more) and only moderately heritable (Table 2). Feed consumption is much more stable (10% CV) and more highly heritable (.25 to .56) (Korver et al., 1991; Lee et al., 1992). Hence, nutrient composition of feed and voluntary intake rates provide much more reliable and timely bases of monitoring the feeding system than cattle weights.

Heifers at 6 mo of age at the Lethbridge research station were larger and heavier than those at Ottawa. By first calving, heifers at Ottawa were the same weight but were still smaller in body scale (Lin et al., 1983). Genetic backgrounds were almost identical. Weaned calves at Lethbridge were fed alfalfa cubes as their forage, whereas Ottawa heifers received chopped alfalfa hay or silage mixtures. Improvement in ruminal function and diet quality at Ottawa after 8 mo could not make up for the deficient nutrient intake earlier. High quality forage of excellent balanced nutrient content that encourages high rates of voluntary consumption is essential for heifers to attain maximum rates of growth in size and scale. Body condition or weight can be improved later by higher-energy forage diets, such as those containing corn silage, but compensatory gains in size and scale cannot be expected.

The Dutch study reported by Korver et al. (1991) was based on yearling heifer growth between 44 and 66 wk on an all-forage diet rather than 26 to 34 wk in the Canadian study. Heritabilities of weight and energy intake were .77 and .56, respectively, and were correlated .94 genetically and .61 phenotypically.

Larger cattle eat more and grow faster than smaller, less hungry cattle. The low phenotypic correlation may be a reflection of the high variability of body weight changes and measurement error. The underlying genetic drives to eat and to grow are almost inseparable. Genetically hungrier heifers will grow larger than genetically less hungry heifers, even though short-term weight changes may not reflect consumption. Energy is not the only feed nutrient. Adequate protein, mineral, and vitamin content must exist to permit effective use of feed energy for growth, not just fattening. Excess energy consumption will cause excess fatness and other problems. An adequate supply of all nutrients in the feeding guides is essential for maximum lean growth and overall scale. Give genetic excellence a chance to be realized.

**Lactation.** Implications of the Dutch study (VanElzakker and VanArendonk, 1993; VanArendonk et al., 1991) are very similar to those of the Canadian study (Lee et al., 1989; 1992). Results are summarized in Tables 1 and 3. Weight loss during early first lactation was highly positively correlated genetically with first lactation milk yield (Lin et al., 1985), indicating that high-producing heifers lose more weight during early first lactation than low-producing heifers. Forage intake was moderately correlated genetically and phenotypically with lactation yield (.30 to .55) in the Dutch study in which concentrate feeding was fixed. These correlations were almost one in the Canadian study in which concentrate feeding was adjusted according to milk yield of the previous week. Later lactation weight changes in both studies were near zero. Heavier cattle at calving yield more milk, but this is due to feeding and management rather than genetics. Heavier cattle at 4, 8, or 16 wk of lactation are poorer producers, presumably because they did not catabolize body fat to support lactation to the same extent as lighter cattle. Fundamentally, genetic body size is independent of genetic potential for milk production. Similar implications from experimental studies were reported by Hickman and Bowden (1971). Wang et al. (1992) took the view that genetic ability to respond to increased grain feeding generates a genetic × environment interaction. Genetic propensity to eat, lose weight, and produce milk in early

Table 2. Variation in feed intake and growth rate in heifers

<table>
<thead>
<tr>
<th>Trait</th>
<th>Average, kg</th>
<th>Standard deviation, kg</th>
<th>Coefficient of variation, %</th>
<th>Heritability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body weight, 6 mo</td>
<td>165</td>
<td>18</td>
<td>11</td>
<td>.14</td>
</tr>
<tr>
<td>Energy intake, 6–8 mo</td>
<td>209</td>
<td>21</td>
<td>10</td>
<td>.23</td>
</tr>
<tr>
<td>Gain, 6–8 mo</td>
<td>54</td>
<td>11</td>
<td>20</td>
<td>.17</td>
</tr>
<tr>
<td>Gain 15 mo to calving, adj. to 22 mo</td>
<td>96</td>
<td>27</td>
<td>28</td>
<td>.13</td>
</tr>
<tr>
<td>Weight at calving adj. to 22 mo</td>
<td>468</td>
<td>35</td>
<td>7.5</td>
<td>.37</td>
</tr>
</tbody>
</table>

*aFrom Lee et al. (1992).

Table 3. Correlations of 105-day fat and protein corrected milk (FPCM) with body weight and feed intake during lactation (h² = heritability)

<table>
<thead>
<tr>
<th>105-day FPCM (h² = .47) correlations</th>
<th>Phenotypic</th>
<th>Genetic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body weight (h² = .31)</td>
<td>-0.3</td>
<td>-0.05</td>
</tr>
<tr>
<td>Weight gain (h² = .27)</td>
<td>-0.42</td>
<td>-0.96</td>
</tr>
<tr>
<td>Energy intake (h² = .31)</td>
<td>0.27</td>
<td>0.61</td>
</tr>
</tbody>
</table>

*aFrom Van Arendonk et al. (1991).
lactation is essentially a single genetic complex independent of size. The challenge in cattle feeding and management during early lactation is to stretch the weight loss and high milk yield as far as possible by heavy feeding of high quality forage and pushing concentrate feeding as close to minimizing negative energy balance as possible without causing ruminal acidosis and metabolic upset. Excess body condition and low grain consumption with genetic propensity for high yield can lead to serious metabolic imbalances. It's a tricky balance.

Implications of these results for feeding of cattle during the latter half of first lactation are important. Continued lean growth to attain mature body size is required (Perotto et al., 1992, 1994). Hence feeding must be adequate to support maintenance, growth, lactation, pregnancy, and recovery of body condition. Cattle in the Canadian project that had low first lactation milk yield often produced very well in second lactation, presumably due to an extended dry period with a good opportunity to grow and calve in good condition. Higher producers in first lactation that bred back quickly often had poor second lactation milk yield. This is an “experimental” interpretation and would balance out to zero in a standard statistical analysis. The practical point is that heifers calving for the first time at 24 to 27 mo are still growing and need to be adequately fed and managed if they are to calve for the second time at 36 to 40 mo, well grown and in good body condition. This is essential to get maximum yield and feed efficiency in second lactation. Genetically elite cattle must be fed and managed to get the most out of them over their whole lifetime.

**Growth and Lactation.** Correlations of milk production traits with heifer traits were very low in the Canadian Study (Table 4). The Dutch study, using weights and intakes at a much older pregnant heifer stage, yielded heritabilities and correlations that were considerably higher (Table 5). Bigger heifers remain larger and eat more feed through first lactation than smaller heifers. In contrast to the Canadian study, genetic correlations of milk yield to heifer weight and feed intake were substantial. Differences in results may be due to different feeding systems and ages at which data were collected. However, the results in Table 4 of Van Arendonk et al. (1991) indicated very weak phenotypic and genetic correlations (−.03 and −.05, respectively) between 105-d FPCM and body weight during lactation. Therefore, no consistent strong associations between heifer rearing traits and first lactation yield traits have been found. Larger cattle are larger throughout life and eat more feed but do not necessarily produce more milk.

**General.** Comparisons across breeds or strains of cattle (Oldenbroek, 1988; Lee et al., 1989; McAllister et al., 1994) provide very similar results. Oldenbroek (1988) writes: “Biological and economic efficiency can be improved by a higher milk yield. Biological efficiency is not affected by differences in dry matter intake or body weight.” Thankfully, feeding standards provide reliable guides of nutrient requirement for growth, lactation, maintenance, etc. What they don't tell you is what determines the growth rate, milk yield, and weight loss.

In the NCDCBP, Holstein cattle at the end of the project were equivalent in yield traits to Holstein progeny of young bulls being progeny tested in artificial insemination (Lee et al., 1994), although project cattle were smaller and lighter than those in

Table 4. Genetic (G) and phenotypic (P) correlation between cow and heifer traits (h^2 heritability)^a

<table>
<thead>
<tr>
<th>Cow trait</th>
<th>Weight 26 wk (h^2 = .10)</th>
<th>Gain 26-34 wk (h^2 = .15)</th>
<th>Feed intake 26-34 wk (h^2 = .19)</th>
<th>Gain 34-66 wk (h^2 = .20)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk energy, 8-16 wk (h^2 = .31)</td>
<td>G = .07</td>
<td>.06</td>
<td>.18</td>
<td>.18</td>
</tr>
<tr>
<td>Energy intake, 8-16 wk (h^2 = .22)</td>
<td>G = .16</td>
<td>.31</td>
<td>.23</td>
<td>.39</td>
</tr>
</tbody>
</table>

^aFrom Lee et al. (1992).

Table 5. Phenotypic (P) and genetic (G) correlations of pregnant heifer with first lactation traits (h^2 = heritability)^a

<table>
<thead>
<tr>
<th>Pregnant heifers</th>
<th>Body weight (h^2 = .82)</th>
<th>Rougahage intake (h^2 = .25)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body weight (h^2 = .85)</td>
<td>P = .82</td>
<td>G = .92</td>
</tr>
<tr>
<td>Weight gain (h^2 = .26)</td>
<td>P = .05</td>
<td>G = .12</td>
</tr>
<tr>
<td>FPCM (h^2 = .51)</td>
<td>P = .21</td>
<td>G = .32</td>
</tr>
<tr>
<td>Energy intake (h^2 = .33)</td>
<td>P = .13</td>
<td>G = .21</td>
</tr>
</tbody>
</table>

the industry. Industry emphasis on size and conformation, in  
addition to production, had limited genetic  
progress for milk production to the same as that  
attained by geneticists in a closed population of 400  
milking cows.

The other discovery of the Canadian research  
was that udder height is genetically independent of milk  
yield (Lin et al., 1987). Increased milk yield puts  
extra stress on mammary suspension so that the  
phenotypic association is not favorable. You have to  
select for udder suspension if you want the udders up  
off the floor. However, there is no genetic association  
between udder height and milk yield. It would be  
tempting to select for everything. Appropriate  
economic weights and genetic indices are essential if  
serious imbalances in selection are to be avoided. A  
badly balanced breeding program is as disastrous as a  
badly balanced feeding program. Maximum profit  
demands excellence in both simultaneously.

Most of the concepts presented here are supported  
by earlier studies. Reviews by Freeman (1975) and  
Korver (1988) have similar implications, as do results  
of earlier Canadian research (Hickman et al., 1971).  
The difference is that the quantity of well-designed  
data in both the Canadian (Lee et al., 1992) and  
Dutch (Van Elzakker and Van Arendonk, 1993)  
studies is sufficient to permit precise estimation of  
heritabilities and genetic correlations. Thanks to  
collaboration with D. Boichard of France, I was able to  
use multivariate REML successfully to ensure that the  
collection of parameter estimates is consistent and  
admissible for a multivariate normal distribution.  
However, we were restricted to a sire model. The  
Dutch study, as many studies do now, used animal  
model REML but only a series of univariate and  
bivariate analyses. Results need not be consistent  
across all univariate and bivariate analyses, and the  
estimated parameters may not actually be admissible  
in a multivariate normal distribution. Preconversion  
to canonical variates for univariate analysis would be  
appropriate if the parameter values to be estimated  
were known in advance. All this theoretical approach  
aside, my original first estimates in a fixed model by  
Method III of Henderson (1953) using PROC GLM in  
SAS yielded results that were almost identical to the  
final REML analysis. Probably, the well-balanced data  
design of the NCDCBP with approximately 15 daugh-  
ters per sire made this so. In any case, greater  
sophistication of analysis did not alter basic concepts  
and ideas. What we do have in the two studies,  
reviewed in detail, is documented evidence and  
numbers to back up the sound dairy cattle production  
concepts we all “know.” It is not broad simple  
generalities that are needed for excellence but  
attention to specific details. Fine-tuned, well-managed  
interplay of feeding and genetics is essential for  
excellence.

Implications

1. Breed for milk yield and ignore size. Genetics for  
   size is independent of genetics for yield.
2. Feed heifers under 1 yr of age to maximize growth  
   without excess condition. Better feeding of preg- 
   nant heifers can add condition but cannot make up  
   for lack of early real growth in size.
3. Feed pregnant heifers to calve in good condition.  
   Without adequate body reserves of fat it is very  
difficult to get high milk yield in first lactation.
4. Which heifers will use body reserves to maximize  
   milk yield is hard to predict. The big eaters tend  
   to be the higher producers.
5. Give first lactation cows the best chance you can to  
   show what they can do. Balance fat from weight  
   loss and fiber from forage consumption with  
   energy and protein from concentrate feeds to  
   maximize milk yield while maintaining good  
   health.
6. Cull first lactation cows that do not utilize body  
   reserves to push milk yield. They only get fatter  
   and do not pay their keep.
7. After peak yield, feed first lactation cows to  
   support continued growth as well as milk yield.  
   You want them to reach their potential for mature  
   size.
8. Dry off high yielding first lactation cows early  
   enough and feed well enough to calve in good  
   condition the second time. They will need body  
   reserves to support high milk yield in second  
   lactation also.

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