XXXVIII. Further Studies on the Energetic Efficiency of Milk Production and the Influence of Live Weight Thereon

Samuel Brody and Richard Cunningham

(Publication Authorized May 2, 1936)
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foreword and Acknowledgments</td>
<td>3</td>
</tr>
<tr>
<td>Abstract</td>
<td>4</td>
</tr>
<tr>
<td><strong>I. Introduction</strong></td>
<td>5</td>
</tr>
<tr>
<td>1. Historical orientation</td>
<td>5</td>
</tr>
<tr>
<td>2. Objects</td>
<td>7</td>
</tr>
<tr>
<td>3. Literature</td>
<td>9</td>
</tr>
<tr>
<td>4. Partition equation used in the preceding report (Res. Bull. 222)</td>
<td>9</td>
</tr>
<tr>
<td>5. Gross energetic efficiency of milk production</td>
<td>10</td>
</tr>
<tr>
<td>6. Net energetic efficiency of milk production</td>
<td>10</td>
</tr>
<tr>
<td>7. Properties of the partition equation and methods of solving it</td>
<td>11</td>
</tr>
<tr>
<td><strong>II. Data</strong></td>
<td>17</td>
</tr>
<tr>
<td>1. Experiment Station data</td>
<td>17</td>
</tr>
<tr>
<td>2. Louisiana Purchase Exposition data</td>
<td>17</td>
</tr>
<tr>
<td>3. Superior A. R. Holstein cows (Dixon Testing Plant data)</td>
<td>20</td>
</tr>
<tr>
<td><strong>III. Tabular summaries with discussions of data</strong></td>
<td>20</td>
</tr>
<tr>
<td>1. Tabular summaries of data and of their equation constants</td>
<td>20</td>
</tr>
<tr>
<td>2. Factors influencing values of equation constants and apparent net efficiency of milk production</td>
<td>27</td>
</tr>
<tr>
<td>3. Comparison of gross efficiency of milk production with gross efficiency of muscular work and gross efficiency of growth</td>
<td>29</td>
</tr>
<tr>
<td><strong>IV. Factors influencing gross and net efficiencies of milk production with special reference to the applicability of the law of diminishing increments</strong></td>
<td>32</td>
</tr>
<tr>
<td>1. Influence of body weight on gross energetic efficiency</td>
<td>32</td>
</tr>
<tr>
<td>2. Influence of milk production level on gross energetic efficiency</td>
<td>42</td>
</tr>
<tr>
<td>3. Influence of milk production level and lactation stage on net energetic efficiency</td>
<td>45</td>
</tr>
<tr>
<td>Summary and conclusions</td>
<td>51</td>
</tr>
</tbody>
</table>
FOREWORD

The special investigation on growth and development is a cooperative enterprise in which the departments of Animal Husbandry, Dairy Husbandry, Agricultural Chemistry, and Poultry Husbandry have each contributed a substantial part. The plans for the investigation in the beginning were inaugurated by a committee including A. C. Ragsdale, E. A. Trowbridge, H. L. Kempster, A. G. Hogan, F. B. Mumford. Samuel Brody served as Chairman of this committee and has been chiefly responsible for the execution of the plans, interpretation of results and the preparation of the publications resulting from this enterprise.

The investigation has been made possible through a grant by the Herman Frasch Foundation, now represented by Dr. F. J. Sievers.

F. B. Mumford
Director Agricultural Experiment Station

ACKNOWLEDGMENTS

The material contained herein was discussed in critical detail before the Dairy Seminar and the senior author's class on "Growth and Development." Grateful acknowledgments are made to the members of these groups, particularly to: Professor Ragsdale for penetrating suggestions concerning the practical implications of the results; to Professor C. W. Turner for criticisms, and for use of data on 42 superior Holstein cows tested at the Dixon, Illinois Testing Plant (for description of these Dixon data see C. W. Turner, J. Dairy Sc., 7, 535, 1924); to Dr. W. R. Graham, Jr. for suggesting the ideas and collaboration in preparing section IV, 3, on the application of the law of diminishing returns to net efficiency of milk production, and for critical reading of the entire MS; to Messrs. Harry Herman, Ralph P. Reece, John H. Kruger, C. E. Murphy, L. E. Washburn, E. T. Gomez and A. S. Foot for analyzing the older literature (e. g., Jordan, Woll) and indicating their bearing on the theories here proposed. We are particularly indebted to Miss Margaret Sappington for painstaking computations, checking, typing and many valuable suggestions.
ABSTRACT

This bulletin is a continuation of Missouri Research Bulletin 222 having for its aims determination of: energetic efficiency of milk production of lactating dairy cattle; influence of live weight of cows and of milk production level on energetic efficiency; partitioning of TDN (total digestible nutrients) consumed between its several uses in the lactating cows' body. The present analysis of 368 cow records confirms the conclusion of Research Bulletin 222 that gross energetic efficiency (not monetary profit) tends to be independent of live weight. The specially featured data in this bulletin were obtained on 120-day tests of Brown-Swiss, Holstein, Jersey and Shorthorn cattle conducted at the St. Louis "World's Fair." Defining gross energetic efficiency by the percentage ratio of energy in milk produced to energy in digestible feed (TDN) consumed, the "World's Fair" Jersey and Holsteins produced their milk at practically the same gross energetic efficiency, namely 34% as compared to: 30% of 243 average experiment-station cows; 34% of a very superior group of Holstein cows in Illinois; 43.5% of the 1700-pound champion Holstein cow Carnation Ormsby Butter King "Daisy" which produced 36,476 lbs. FCM (4% milk); 47.5% of the 700-pound champion Jersey cow Stonehurst Patrician's Lily which produced 25,946 pounds FCM per year. (The efficiencies of these two champion cows were not observed, but computed by the chart in Missouri Station Bulletin 351.)

Gross energetic efficiency of milk production of "good" cows is of the same order as of early postnatal growth on "good" rations. The efficiency of both processes (with respect to TDN) is of the order of 30%; the gross efficiency of both processes appears to be independent of live weight (small Jerseys and large Holsteins seem to produce milk with the same gross energetic efficiency; small and large animals, including rats, chicks and cattle seem to grow in early postnatal life with the same gross energetic efficiency). The "law of diminishing returns" appears to apply to gross energetic efficiency of milk production as to growth. Net energetic efficiency, that is efficiency of the lactation process aside from the overhead cost of maintenance, is of the order of 60%, and it appears that the law of diminishing increments is also operative for net energetic efficiency of milk production.

It is emphasized that monetary profit of milk production depends on many factors other than energetic efficiency. The relation between efficiency and profit is a complex problem which will be discussed in a following research bulletin (239).
INTRODUCTION

1. Historical Orientation.—One of the fascinating problems in biology is concerned with the “work” of transforming non-living matter into living organisms. Bricks are the same before and after they are made into a house but their arrangement in the form of a house requires work; it involves considerable energy expenditure. Likewise, the building units in the egg are probably the same before and after they are made into a chick, but their rearrangement from positions in the egg to those in the chick—the transformation from non-living to living—must involve an energy cost. What is the price—what is the energy cost—of becoming alive, of becoming organized into a living being, of crossing from the realm of non-living egg into living chick? We do not know, in spite of the romantic quest of a brilliant array of investigators beginning in 1903 with Tangl in Budapest and Bohr in Copenhagen.

Tangl was optimistic about his ability to solve this problem because he oversimplified it: he thought all he would have to do to determine the “work,” the energy cost of “organizing” the chick embryo from the egg, is to burn in a bomb calorimeter eggs at the beginning and end of incubation; the difference in energy content would be the energy cost of producing a chick from an egg.

One fallacy in Tangl’s reasoning is that the energy disappearance from the egg as thus measured includes not only the cost of organizing the chick from the egg, but also the cost of maintaining the formed embryo. He failed to differentiate growth cost from maintenance cost. It is interesting to note that Eckles, in Missouri, likewise oversimplified a similar problem, but in opposite direction. Eckles assumed that the energy content of the new-born calf represents the energy expended by its mother in producing it, thereby ignoring the energy cost of maintaining as well as of growing the young.

A second fallacy in Tangl’s reasoning is due to his ignoring the fact that before the chick embryo is burned in the calorimeter it is necessarily killed and dried. The killing and drying, of course, not only returns the
living to the non-living state but also destroys the physico-chemical arrangement of molecules constituting normal living chick embryo. The energy cost of becoming alive and of organization disappears in the process of dying and drying before the burning stage is reached. Tangl therefore missed what he was looking for, namely the energy of organization of the embryo and the energy of becoming alive.

The problem of “work” of growth is a part of the more general problem of “work” of other functions such for example as “work” involved in producing milk from its precursors in the blood and from the food. What is the energy cost of transporting and rearranging the ultimate building units from the realm and form of hay and grain into the realm and form first of milk precursors in the blood, then of milk? We do not know. Our ignorance is due to the complexities of the process as indicated by the following outline, discussed in terms of energetic efficiency of transformation of food into milk.

The gross energetic efficiency of a process may be defined by the ratio of output to input or by the ratio

\[
\frac{\text{Energy in the desired product}}{\text{Energy expended to produce the desired product}} \tag{A}
\]

In the case of milk secretion, the gross energetic efficiency might be defined by the ratio

\[
\frac{\text{Energy in milk produced}}{\text{Energy in the feed consumed to produce the milk}} \tag{B}
\]

Since it does not seem fair to charge to milk production the part of the food which is not digested, and since cattle feed stuffs vary tremendously in their digestibilities, it is more appropriate to define the efficiency of milk production by the ratio

\[
\frac{\text{Energy in milk produced}}{\text{Energy in TDN consumed to produce the milk}} \tag{C}
\]

where TDN represents total digestible nutrients.

The above ratio refers to gross, or overall, efficiency of milk production, including the overhead cost of maintaining the cow. It does not indicate specifically the cost of “making” milk from milk precursors aside from overhead expenses of maintaining the cow.

For securing an insight into the detailed energy expenses of milk production the above ratio for gross efficiency may be written in the following, more detailed, form:
Milk Energy Produced

TDN energy equivalent of: (1) milk produced + (2) maintenance of cow (not including the active mammary gland) + (3) maintenance of the active mammary gland + (4) work of milk secretion + (5) increased metabolic level of the cow due to stimulating influence of lactation hormones, etc. + (6) wastes incidental to the transformation of TDN to milk precursors furnished by the blood to the mammary gland. + (7) wastes incidental to the transformation of milk precursors furnished to the mammary gland into milk.

The above ratio indicates that the “work” of milk production constitutes only one of at least seven items in the total cost of milk production.

Dr. W. R. Graham, Jr. is now collecting data, in the University of Missouri Dairy Department, on: (1) blood flow through mammary gland; (2) O₂ decrement of the blood in its passage through the mammary gland; (3) CO₂ increment in this passage; (4) changes in concentration of some milk precursors. We hope that these data will enable Dr. Graham to compute the energy expense of transforming milk precursors into milk (i.e., “work” of milk secretion) together with the maintenance cost of the mammary gland (provided that the O₂ decrement is not greatly complicated by changes in O₂ concentration due to interconversion of fats and carbohydrates in the process of milk secretion).

Dr. Graham’s data on milk production will resemble Tangl’s data on embryo growth in that they will be complicated by a maintenance factor. How shall one differentiate the maintenance cost of the lactating mammary gland from the energy cost of milk formation? The maintenance cost of a non-lactating gland—either of a gland from a naturally dry animal, or a gland the secretion of which is temporarily stopped by not milking—can not be compared to a naturally functioning gland. The maintenance cost of the gland probably varies with its size, blood flow, milk production level, etc. so that indirect gland maintenance computations will probably not be satisfactory. Moreover, the energy content of the milk as determined by bomb-calorimetry is probably too low. Some of the “organization” of the milk is destroyed in the preliminary drying process, with a corresponding energy loss. The above discussion indicates the extreme complexity of the problem.

It occurred to us that while it may not at present be possible to partition the TDN energy consumed by a lactating animal between its uses for each of the 7 purposes indicated in ratio (D), it may be possible to partition the TDN by an indirect mathematical method for fewer purposes.

2. Objects.—One of the objects of the present bulletin is to partition the TDN consumed by lactating cows between three principal
purposes for which TDN is used, namely:

(A) **Milk production** which includes the following items in ratio (D): (1) Energy in milk produced; (3) Energy for maintaining the lactating mammary gland; (4) Energy of "work" of milk production; (6) Energy of wastes incident to transformation of TDN to finished milk-precursors furnished by the blood to the mammary gland; (7) Energy of wastes incident to the transformation of milk precursors furnished to the mammary gland, into milk.

(B) **Maintenance** which includes the following items in ratio (D): (2) Energy for maintenance of cow, not including extra maintenance of actively lactating gland; (5) Energy cost of increased metabolic level of cow due to stimulating influence of lactation hormones etc., or general elevation of metabolic level of body due to act of lactation.

(C) **Weight gain.**

A second object of this bulletin is to determine the average and the range in gross or overall efficiencies of milk production of cows of various types, and how this gross efficiency of milk production varies with milk production level and, particularly, with size of cows. Res. Bul. 222 was concerned with the efficiency of an average experiment-station group of cows; this bulletin is concerned especially with high-producing cows, and the relation between production level and efficiency.

A third object of this bulletin is to evaluate the net efficiency of milk production, defining "net efficiency" of milk production by the ratio

\[
\text{Energy in milk produced} \quad \text{Energy in total TDN consumed less TDN used for maintenance of the lactating cow and for weight gain}
\]

This net efficiency, defined by ratio (E) includes the energy expense of transforming TDN to milk precursors; energy losses of the so-called specific dynamic effect (which may amount to 20% of the consumed TDN) and fermentation losses (which may amount to 10% of the gross energy of the consumed feed). In other words, a 60% net efficiency as defined by ratio (E) might be a 90% efficiency if the TDN in ratio (E) were replaced by Armsby's "net energy," which does not include the energy of the so-called specific dynamic effect and energy of fermentation. If in addition other losses (listed in the denominator of ratio E) incidental to milk production were deducted from the TDN consumed, the efficiency of the mammary gland might be still higher.

A fourth object of this bulletin is to point out the relations between the energetic efficiency of milk production, and the energetic efficiencies of other processes, such as growth and muscular exercises.

Before closing this section we wish to make it clear that this bulletin is concerned with energetic efficiency of milk production, not with monetary profit. Energetic efficiency is a ratio—ratio of output to input;
monetary profit is a *difference*—difference between money expended for feed and money realized for milk. The relation between energetic efficiency and monetary profit is a rather complex one, and we decided to make this relation a subject of a special investigation which will be reported in the next bulletin of this series.

3. Literature.—The newer literature (e.g., the important papers by Gaines, McDowell, and Kleiber) relating to the problem of efficiency of milk production was discussed in Missouri Research Bulletin 222, the first report on this investigation, and also to some extent in Missouri Station Bulletin 351. We shall in this bulletin discuss some of the older literature (Jordan, Woll, Grady, etc.) as occasion may arise.

4. Partition equation used in the preceding report (Res. Bul. 222): In the preceding report it was assumed that: (a) The digestible nutrient (TDN) need for milk production is directly proportional to the milk-energy production (this assumption is now questioned); (b) The TDN need for body-weight gain is directly proportional to body weight gained (this assumption is likewise now questioned); (c) The TDN need for maintenance (this includes extra metabolism due to influence of lactation hormones etc.) is proportional not to simple body weight, but to body weight raised to the 0.73 power; (d) The consumed available TDN energy equals to the algebraic sum of the energy costs of milk secretion (including "work" of secretion and of converting milk precursors into milk, TDN cost of converting TDN to milk precursors and TDN cost of maintaining lactating mammary gland); of maintenance cost; weight-gain.

The above assumptions were summarized by the equation:

\[ \text{TDN} = B(FCM) + C(M)^{0.73} + D \Delta M \]  

In equation 1a, TDN represents total digestible nutrients; FCM, milk containing 4% fat (method of Gaines); M, live weight; \( \Delta M \), gain in live weight; B, units TDN required for producing unit FCM; D, units TDN required for gaining unit live weight; C, is the maintenance coefficient. C may be said to represent units TDN required to maintain unit "active mass" (weight raised to the 0.73 power). It was shown in Missouri Research Bulletin 220 that basal energy metabolism and endogenous nitrogen excretion tend to be proportional not to simple weight but to weight raised to the 0.73 power. Equation 1a was fitted, by the method of least squares, to the data of the 243 average experiment-station cows with the following results:

\[ \text{TDN} = 0.305FCM + 0.053M^{0.73} + 2.1 \Delta M \]  

Equation 1b indicates that on the average, 0.305 pounds TDN was expended for producing one pound FCM; 2.1 pounds TDN was expended for gaining 1 pound live weight. 0.053 is the maintenance coefficient for live weight M as explained above.
5. **Gross energetic efficiency of milk production.**—This efficiency indicated by ratio C, includes the overhead maintenance cost. It is defined by equation:

\[
\text{Gross Efficiency} = \frac{\text{Energy in milk produced}}{\text{Energy in digestible nutrients consumed}} \tag{2a}
\]

Since 1 pound 4\% milk, designated by FCM, is assumed to have an energy value of 340 Calories (Gaines), and 1 pound digestible nutrients, designated by TDN, 1814 Calories, therefore for 4\% milk, equation 1 is written:

\[
\text{Gross Efficiency} = \frac{340 \times \text{FCM} \text{ (lbs.)}}{1814 \times \text{TDN} \text{ (lbs.)}} \tag{2b}
\]

The denominator in equation 2b includes the TDN expense for maintenance \((0.053\times1.73)\) and for gain in weight \((2.1\times\triangle M)\). On substituting these values from equation 1b into equation 2b we obtain:

\[
\text{Gross Efficiency} = \frac{340 \times \text{FCM}}{1814 (0.305\times\text{FCM} + 0.053\times 1.73 + 2.1\times\triangle M)} \tag{2c}
\]

\[
= \frac{340 \times \text{FCM}}{553\times\text{FCM} + 96.1\times 1.73 + 3700\times\triangle M} \tag{2d}
\]

6. **Net energetic efficiency of milk production.**—From equations 1b and 2d it is clear that if the overhead maintenance cost is not included, only 0.305 pounds TDN, or 553 Calories \((0.305 \times 1814 = 553)\), are on the average needed to produce 1 pound, or 340 Calories, FCM. The ratio of 340, the Calories in 1 pound FCM, to 553, the Calories in the TDN required to produce 1 pound FCM, that is 0.61 or 61\% is the net efficiency of milk production as defined by ratio E; in this sense it is the efficiency of the cow as converter of TDN into milk apart from the maintenance cost. Dividing the numerator and denominator in equation 2d by 553, presents net efficiency, 0.61, as a separate term

\[
\text{Gross Efficiency} = 0.61 \times \frac{\text{FCM}}{\text{FCM} + 0.173\times 1.73 + 6.64\times\triangle M} \tag{2e}
\]

Net efficiency, the ratio of energy in the milk produced to energy in the TDN consumed above that used for maintenance and gain in weight, may likewise be written in equation form:

\[
\text{Net Efficiency} = \frac{\text{Energy in milk}}{\text{Energy in TDN consumed less TDN expended for maintenance and for live weight gain}} \tag{3a}
\]

By substituting the values of equation 1b into 3a we obtain:

\[
\text{Net Efficiency} = \frac{340 \times \text{FCM}}{1814 \, \{\text{TDN} - (0.053\times 1.73 + 2.1\times\triangle M)\}} \tag{3b}
\]
The 61% net-efficiency level (indicated in equation 2e) is, of course, only a statistical average, for the given conditions, computed by the given method, and not applicable to an individual cow.

7. Properties of partition equation 1a and method of solving it.—Partition equation 1a is a statement of an energy balance between TDN consumption on the left side, and milk production, maintenance, and weight-gain on the right side. The significance of its parameters (B, C, D) depends on the accuracy of the basic data (TDN, milk, live weight, live-weight gains) the size and homogeneity of population, range of data, goodness of equation, and method fitting equation to data.

We solve the equation by the method of least squares which determines the values of B, C, and D so that the sum of the squares of the differences between observed TDN and TDN computed from equation 1a is a minimum. The solution consists, as explained below, in substituting in three “normal equations,” simultaneously weighting the trends of TDN with the other three variables (FCM, M, ΔM) in equation 1a in such manner as to give at once a minimum value for the sum of the squares of the differences. The same result may be obtained by the following step-by-step procedure: Plot TDN successively against each of the independent variables, FCM, M^{0.73} and ΔM; correct observed TDN values for the influence of one variable by approximating TDN cost per unit of that variable; subtract computed TDN required for the one variable from the observed TDN for each datum; correlate corrected TDN with another variable and determine a second correction. Thus are obtained the first approximations of the parameters. By continuing this process of approximation, the three trends (TDN vs FCM, TDN vs M^{0.73}; TDN vs ΔM) approach more and more closely to the ideal fit when the sum of the squares of the differences between observed TDN and computed TDN is a minimum. The use of the “normal equations” in the least squares method merely eliminates the laborious successive approximations.

For simplicity of discussion 1a was fitted to the small but excellent Pennsylvania group of data described in Section II, 4, with the following results:

\[
\text{TDN} = 0.292 \text{FCM} + 0.053M^{0.73} + 1.52\Delta M
\]

It will be instructive to show that this equation made a reasonable distribution of the consumed TDN between its three principal uses: maintenance, milk production, weight gain.

If we plot (see Fig. 1) TDN consumed by each cow against FCM produced, the resulting distribution of data points is within a rather broad band.
Fig. 1.—The left chart shows plots of total TDN consumed (light circles), total TDN less TDN used for weight gains (light squares), and total TDN less TDN used for milk production (crosses) all plotted against milk (FCM) production. Note that the distributions of the data in successive plots become increasingly orderly indicating that equation 1a partitions satisfactorily the TDN between its various uses in the body. The other two quadrants in the chart show similar plots against (weight)\(^{0.73}\) and weight gains. See text for further details.

If we plot TDN - 1.52 \(\Delta M\) against FCM, the distribution is but slightly improved thereby, because the weight gain, \(\Delta M\), constitutes but a slight factor in the use of TDN.

If, finally, we plot TDN - 1.52 M - 0.053M\(^{0.73}\) against FCM, the resulting distribution is within a narrow band, quite orderly linear, thus demonstrating that the method did bring out an orderly relation from an initially disorderly distribution of data. The deviations of the individual data points from the average curve are within the limits of expectation. Cows 1, 6 and 12 were farrow, the other seven were in various stages of gestation. One would therefore expect individual differences in maintenance and weight-gain costs, which would be reflected in deviations of data points from the average line.

A similar orderly relation may be derived, as shown in Fig. 1, between TDN and the maintenance factor, M\(^{0.73}\); by first plotting TDN against M\(^{-0.73}\); then TDN - 1.52 \(\Delta M\) against M\(^{0.73}\); and finally TDN - 1.52 \(\Delta M\) - .292 FCM against M\(^{0.73}\). Only the last plot gives an orderly linear distribution.

A similar orderliness is demonstrated in Fig. 1 between TDN and weight gain, \(\Delta M\).
The curve in Fig. 1 indicates that equation 1a partitions satisfactorily the consumed TDN among its 3 major uses, but it does not demonstrate that it is the best possible equation for the purpose. Other, perhaps better, functional relations may be conceived, and it is easy to advance objections against equations 1a.

An obvious objection is that equation 1a was formulated on the assumption that the milk secretion, maintenance, and weight-gain factors are independent. This is by no means certain. Moreover, since the coefficients in equation 1a are computed by the method of least squares, it is clear that if the value of one coefficient is too high due to some experimental or biological situation, the values of the other coefficients will be influenced thereby. Each of the 4 terms represented in equation 1a has its separate set of experimental errors and biological variations. When combined into one interrelated system, each of these terms influences the value of every other term. There consequently results a very complex system of interinfluencing relationship.

A large population compensates and smoothes out individual experimental errors and biological variations so that there result dependable average values for the equation constants B, C, and D in equation 1a. But if a small population is combined with large errors and variations, the equation constants are no longer dependable, often absurd, as illustrated by the following numerical examples.

The aforementioned three "normal equations" for equation 1a are:

\[ \sum (TDN) (FCM) = B \sum (FCM)^2 + C \sum (FCM)(M^{0.73}) + D \sum (FCM)(\Delta M) \]
\[ \sum (TDN) (M^{0.73}) = B \sum (FCM)(M^{0.73}) + C \sum (M^{0.73})^2 + D \sum (M^{0.73})(\Delta M) \]
\[ \sum (TDN) (\Delta M) = B \sum (FCM)(\Delta M) + C \sum (M^{0.73})(\Delta M) + D \sum (\Delta M)^2 \]

Taking, by way of illustration, the data for the 15 World's Fair Holsteins described in Section II, 2, and which will be listed in detail in the forthcoming bulletin we obtain the following summations:

\[ \sum (TDN) (FCM) = 19525.1508 \quad \sum (FCM) (\Delta M) = 593.90690 \]
\[ \sum (TDN) (M^{0.73}) = 74486.866 \quad \sum (M^{0.73})^2 = 522017.86 \]
\[ \sum (TDN) (\Delta M) = 327.95458 \quad \sum (M^{0.73})(\Delta M) = 2303.8917 \]
\[ \sum (FCM)^2 = 36129.7151 \quad \sum (\Delta M)^2 = 11.251476 \]
\[ \sum (FCM) (M^{0.73}) = 136482.688 \quad \sum (TDN)^2 = 10642.4553 \]

Substituting in the "normal equations" we have:

\[ 19525.1508 = B \times 36129.7151 + C \times 136482.688 + D \times 593.90690 \]
\[ 74486.866 = B \times 136482.688 + C \times 522017.86 + D \times 2303.8917 \]
\[ 327.95458 = B \times 593.90690 + C \times 2303.8917 + D \times 11.251476 \]

Solving these equations we obtain B = .11642, C = .11146, and D = .18040, i.e., TDN = 0.116FCM + 0.11M^{0.73} + 0.180 \Delta M. Illustrating
the solution by Doolittle’s method (Mills p. 577, Ezekiel Chap. 12) we have:

<table>
<thead>
<tr>
<th>Line</th>
<th>Reciprocals</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td></td>
<td>36129.7151</td>
<td>136482.688</td>
<td>593.90690</td>
<td>-19525.1508</td>
</tr>
<tr>
<td>II</td>
<td></td>
<td>522017.86</td>
<td>2303.8917</td>
<td>-74486.866</td>
<td>586317.5737</td>
</tr>
<tr>
<td>III</td>
<td></td>
<td>11.251476</td>
<td>-327.95458</td>
<td>2581.09549</td>
<td>-4.253594542</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Line</th>
<th>Reciprocals</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td></td>
<td>522017.86</td>
<td>2303.8917</td>
<td>-74486.866</td>
<td>586317.5737</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>-0.000276780483</td>
<td>-1.00000000</td>
<td>-3.77757443</td>
<td>-0.016438184</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>11.251476</td>
<td>-327.95458</td>
<td>2581.095496</td>
<td>-0.540418067</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>-9.762751</td>
<td>320.95802</td>
<td>-2526.239169</td>
<td>-54.099620</td>
</tr>
<tr>
<td>5</td>
<td></td>
<td>-513573.51</td>
<td>-2243.5275</td>
<td>73757.710</td>
<td>-580542.0166</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>60.3642</td>
<td>-729.156</td>
<td>5775.3571</td>
<td>-896220265</td>
</tr>
<tr>
<td>7</td>
<td></td>
<td>-0.00155174687</td>
<td>-1.00000000</td>
<td>-0.009366996</td>
<td>-54.099620</td>
</tr>
<tr>
<td>8</td>
<td></td>
<td>11.251476</td>
<td>-327.95458</td>
<td>2581.095496</td>
<td>-0.540418067</td>
</tr>
<tr>
<td>9</td>
<td></td>
<td>-565431</td>
<td>6.830000</td>
<td>-54.099620</td>
<td>-54.099620</td>
</tr>
<tr>
<td>10</td>
<td></td>
<td>-9.762751</td>
<td>320.95802</td>
<td>-2526.239169</td>
<td>-54.099620</td>
</tr>
<tr>
<td>11</td>
<td></td>
<td>11.251476</td>
<td>-327.95458</td>
<td>2581.095496</td>
<td>-0.540418067</td>
</tr>
</tbody>
</table>

\[ D = .180397576 \]
\[ C = .111366711 \]
\[ B = .116416411 \]

The standard error of estimate for equation 1a is

\[ S_r^2 = \frac{\sum(TDN)^2 - B \sum(TDN)(FCM) - C \sum(TDN)(M^{0.72}) - D \sum(TDN)(\Delta M)}{N} \]

Where \( N \) is the “degree of freedom” (see Mills, p. 567). The “degrees of freedom” is the number of data points less the number of arbitrary constants in the equation fitted, thus \( N = 15 - 3 = 12 \).

Substituting:

\[ S_r^2 = \frac{10642.4553 - (.11642 \times 19525.1508) - (.11146 \times 74486.866) - (.18040 \times 327.95458)}{12} \]
\[ S_r^2 = \frac{10642.4553 - 2273.1181 - 8302.3061 - 59.1630}{12} = 7.8681 \]
\[ S_r^2 = 0.655675 \]
\[ S_r = 0.810 \]

The standard error of estimate, \( S_r = 0.81 \), means that two-thirds of the time the TDN computed from this equation will agree with the observed TDN consumption within \( \pm 0.81 \) pounds.

This small value of \( S_r \) leads one to think that the numerical values of \( B, C, \) and \( D \) are significant and reliable. As a matter of fact these values are so far out of line that they must be considered as meaningless. Thus the maintenance of a 1000-pound cow is according to this equation \( 0.1115 \times 1000^{0.72} = 17 \) pounds, which is over twice the Morrison allowance of 7.9 pounds and therefore absurd. The net efficiency is according to this equation \( \frac{340 \times 100}{.1164 \times 1814} = 164\% \), which is of course impossible.

In other words, of the available TDN, far too much is apportioned by this equation to maintenance, and far too little for milk production (and for weight gain).
Does this mean that equation 1a is wrong? Not necessarily. It means that the number of animals in the population is too small in comparison to the variability. The data points are too irregular and too few to give the equation a lead, so to speak, to the real situation. The three sets of sign posts involved in showing the road (TDN trends for FCM production, maintenance, weight gain) are so few, and distributed so erratically, that they are blurred and therefore useless as guides for reaching the desired goal.

It is not the fewness of the data that is alone responsible for the erratic results as the combination of fewness, limited range, and erratic distribution of data. The erratic distribution of the data is probably due to their experimental errors. Better (even if fewer) data give better results. Thus equation 1a fitted to only 10 of the Pennsylvania Animal Nutrition Institute (Forbes) data gave entirely satisfactory results. In this case the value of C for equation 1a was found to be 0.053, so that the maintenance for a 1000-pound cow is 8.2 pounds (which is the average of the value found for the 243 Experiment Station cows reported in Research Bulletin 222); the value of B was found to be 0.292, indicating net efficiency of 64% (in comparison to 61% found for the 243 experiment Station cows reported in Research Bulletin 222). This brings us back to the statement made at the outset that reliability of the equation parameters is conditioned on accuracy of the data. To summarize, equation 1a gives dependable average values separately, for FCM production, maintenance, weight-gain but only provided that the population is reasonably large and the data are reliable. The resulting fitted equation can not be used for evaluating net efficiency of milk production of an individual cow because an individual cow's maintenance or weight-gain cost is likely to differ from the average, depending on her muscular activity, fatness, composition of the weight gains, etc. These properties of equation 1a must be kept in mind when interpreting its constants and net-efficiency values listed in Tables 3a and 3b.

As regards the relative significance and definiteness of gross and net efficiencies, gross efficiency, as indicated by ratio C and equation 2, is unambiguous, indeed clear cut. It is simply the ratio of energy in milk produced to energy in TDN consumed (assuming 1 gm TDN has an energy content of 4 Calories). No theoretical assumptions are involved in estimating gross efficiency.

The meaning of net-efficiency is, on the contrary, quite involved, as indicated by ratio D, section 1, and equation 3, section 6. The numerical value of net-efficiency is dependent not only on the reliability of the basic data (milk energy produced, TDN energy consumed, gain or loss in live weight or more accurately gain or loss of energy in the body), but also on: goodness of partition equation, 1a, employed; number of ani-
mals included in the computations, range in live weight and milk production; homogeneity with regards to relative inherited capacities for milk production, fattening, maintenance-need levels, etc.

Moreover, as indicated by ratio D, section 1, the numerical value of net efficiency will depend on fine shades of definition. The statement that net efficiency represents the efficiency of the mammary gland as a machine apart from the rest of the body is true but not precise. Thus if the feed energy is expressed in terms of TDN, then the net efficiency term includes the 20 to 30 per cent of energy loss incident to transforming TDN energy into Armsby’s net energy.

It is moreover possible that the metabolic level of lactating cows is higher than of dry cows due to stimulating influence of lactation, lactation hormones, etc. This extra expense should perhaps not be charged to the mammary gland, yet equation 1a charges it to the expense of milk secretion. This expense, if it exists, would not be found by Dr. Graham’s method. Graham’s experimental determination of the energy expenses of the mammary gland (by measuring blood-flow rate, oxygen decrement, carbon dioxide increment, milk precursors decrements in passing through the gland) includes the energy expenses of (see ratio D, section 1): (b) maintenance of the active mammary gland and (c) energy equivalent of work of milk secretion. It does not include the expenses of: (d) energy wastes incident to the transformation of TDN to milk precursors, and (e) increased metabolic level of the cow due to stimulating influence of lactation, lactation hormones, etc.

This discussion is intended to make it clear that the term net efficiency of milk secretion as given in Table 3a has a special connotation. It is possible that if the TDN term in equation 1a were replaced by Armsby’s net energy, the net efficiency would reach 90 or 95% instead of 60%; if other wastes incident to the transformation of nutrients as they enter the blood stream, into “finished” milk precursors were deducted, then the net efficiency might reach still higher levels.

“Practical” dairy-production investigators may suggest that instead of evaluating TDN cost of maintenance from equation 1a, one should determine TDN cost of maintenance by direct feeding trials on dry cows of various weights; then TDN cost of milk production by the TDN consumed during lactation above the determined maintenance TDN: in other words, evaluate TDN needs, separately, for maintenance, milk production and weight-gain by the customary feeding-trial method instead of the present mathematical partition method. The answer to this suggestion is that our theoretical method is more practical than the suggested method for the following reason: (1) The mathematical method is infinitely less expensive than the feeding-trial method. Indeed it would be economically prohibitive to secure a sufficiently large,
statistically significant, group of cows of various live weights on a maintenance feeding trial as we used for mathematical analysis (368 cows). As previously emphasized, we think it necessary to have many animals in order to compensate for variability in maintenance costs (some are "hard" keepers, others "light" keepers; some are fat, others thin; some have a high water percentage in their body, others low as will be presently explained in detail) and to furnish a wide range of live weights. (2) Moreover, as indicated above, the maintenance cost of a lactating cow is probably higher than of a dry cow of the same weight not only on account of stimulating action of hormones etc. (see item 5 in the denominator of ratio D), but also because the utilization of the TDN may be different at the higher nutritional level associated with lactation. (3) Finally the compactness and elegance of partition equation 1a, its generalizing properties and its usefulness for neat computation of gross and net energetic efficiency, monetary, efficiency and profitableness (as will be explained in Research Bulletin 239), influence of live weight and of milk-production level on efficiency, are important arguments in favor of using equation 1a in preference to direct feeding trial methods.

II. DATA

This bulletin presents results of analyses and comparisons on four sets of data. One set of the numerical data was presented in Missouri Research Bulletin 222; the other three sets will be presented in Research Bulletin 239.

1. Experiment station data.—The data on the 243 experiment station cows, discussed in detail in Research Bulletin 222, were re-investigated and the results compared with three new sets of data: (2) Data obtained at the Louisiana-Purchase Exposition; (3) Data on a superior group of Holstein cows from the Illinois Testing Plant. (4) Data from the Pennsylvania Institute of Nutrition.

2. The Louisiana Purchase Exposition (St. Louis "World's Fair") Data.—These data were secured on the Exposition grounds in St. Louis, in 1904. The detailed data and their descriptions were presented by Professor Farrington in a publication (copyrighted in 1905 by W. D. Hoard Co.) entitled "Dairy Cow Demonstration of the Louisiana Purchase Exposition." Grateful acknowledgments are made to Mrs. E. H. Farrington for sending us this publication, to Dr. L. W. Gaines for calling our attention to these data and suggesting the need for their analysis in connection with our efficiency project.

The animals representing the several breeds were chosen, fed, managed, by interested breed associations and individuals, but the records of milk production, feed consumption, body weight, were kept by disinterested officials under Professor Farrington's direction. This arrangement was designed to combine maximum economy of production with maximum reliability of records.
<table>
<thead>
<tr>
<th>Feed</th>
<th>Brown Swiss</th>
<th>Holsteins</th>
<th>Jerseys</th>
<th>Shorthorns</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alfalfa Hay</td>
<td>7</td>
<td>15</td>
<td>18</td>
<td>9</td>
</tr>
<tr>
<td>Cut Alfalfa Hay</td>
<td>15</td>
<td>15</td>
<td>16</td>
<td>24</td>
</tr>
<tr>
<td>Corn Silage</td>
<td>40</td>
<td>15</td>
<td>16</td>
<td>24</td>
</tr>
<tr>
<td>Green Cut Corn</td>
<td>15</td>
<td>35</td>
<td>15</td>
<td>24</td>
</tr>
<tr>
<td>Wheat bran</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Linseed</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Ground Oats</td>
<td>6</td>
<td>5</td>
<td>2.5</td>
<td>2</td>
</tr>
<tr>
<td>Hominy Feed</td>
<td>2</td>
<td>5</td>
<td>2.5</td>
<td>2</td>
</tr>
<tr>
<td>Gluten Feed</td>
<td>1</td>
<td>5.0</td>
<td>2.5</td>
<td>2</td>
</tr>
<tr>
<td>Corn Meal</td>
<td>5</td>
<td>4.0</td>
<td>2.5</td>
<td>2</td>
</tr>
<tr>
<td>Corn Hearts</td>
<td>1</td>
<td>1.5</td>
<td>1.5</td>
<td>2</td>
</tr>
<tr>
<td>Cottonseed Meal</td>
<td>0.75</td>
<td>1</td>
<td>2.5</td>
<td>2</td>
</tr>
<tr>
<td>Distiller's Grain</td>
<td>8.1</td>
<td>7.65</td>
<td>2.5</td>
<td>2</td>
</tr>
<tr>
<td>Union Grain</td>
<td>15</td>
<td>14</td>
<td>5.65</td>
<td>4</td>
</tr>
<tr>
<td>Totals</td>
<td>71</td>
<td>87</td>
<td>59.0</td>
<td>54</td>
</tr>
</tbody>
</table>

Ratio of lbs. DCP to lbs. TDN: 15, 18, 20, 17

1TDN = Total digestible nutrients.
2DCP = Digestible crude protein.
One regulation, however, might have introduced considerable error in the feed-consumption data. This reads as follows: "Feed will not be weighed back, but after it is once weighed out for a given cow, this amount will be charged to her as stated in the records." This regulation might have resulted in charging cows with feed that they left over. Since, however, the cows were rated on the "excess of milk value over feed value," the feeders undoubtedly tried not to take more feed than the cows would consume. On the other hand this regulation introduced personal factors due to differences in judging ability of the several feeders as to the maximum amount of feeds the cows would consume.

Of the 73 cows on test, 25 were Jerseys, 15 Holsteins, 28 Shorthorns, 5 Brown-Swiss. In addition to breed groups, these 73 cows were also grouped into three production classes: Class A, so-called butter-test cows, for "economical production of butter"; Class B so-called milk-test cows, for "economical production of milk for all purposes"; Class C, dual purpose cows, for "economical production of milk and beef, together with the calves which shall be judged for their beef merits."

The cows were fed and milked three times a day. Daily milk composites were tested by two analysts working independently. Some of the cows were fed two or three different grain constituents, others eight, as illustrated in Table 1.

Differences in kinds of feeds and protein percentages fed to the several groups, shown in Table 1, may have influenced appreciably the milk production and gross efficiency levels. The Brown-Swiss received (see Table 1) only 4 different feed stuffs of relatively low (and probably of relatively inferior) protein content (15% of the calories in the form of protein) as compared to the Jerseys that received 10 different feed stuffs of relatively high (and probably relatively superior) protein content (20% of the calories as protein). These qualitative feed differences may, perhaps, account in part for the relatively poor gross efficiency of the Brown-Swiss (28%) as compared to the Jerseys (33.6%) and Holsteins (34.3%).

<table>
<thead>
<tr>
<th>Feed</th>
<th>TDN per 100 lbs.</th>
<th>Feed</th>
<th>TDN per 100 lbs.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Green Cut Corn</td>
<td>14.3</td>
<td>Wheat Middlings</td>
<td>69.3</td>
</tr>
<tr>
<td>Green Oats and Peas</td>
<td>14.4</td>
<td>Malt Sprouts</td>
<td>70.6</td>
</tr>
<tr>
<td>Corn Silage</td>
<td>15.0</td>
<td>Cottonseed Meal</td>
<td>74.8</td>
</tr>
<tr>
<td>Green Cut Clover</td>
<td>17.1</td>
<td>Linseed Oil Meal</td>
<td>77.9</td>
</tr>
<tr>
<td>Clover Hay</td>
<td>50.9</td>
<td>Gluten Feed</td>
<td>80.7</td>
</tr>
<tr>
<td>Ground Oats</td>
<td>51.1</td>
<td>Rolled Oats</td>
<td>83.2</td>
</tr>
<tr>
<td>Alfalfa Hay</td>
<td>51.6</td>
<td>Corn Meal</td>
<td>84.0</td>
</tr>
<tr>
<td>Distiller’s Grain</td>
<td>54.7</td>
<td>Hominy Feed</td>
<td>84.6</td>
</tr>
<tr>
<td>Union Grains</td>
<td>54.7</td>
<td>Corn Hearts</td>
<td>84.6</td>
</tr>
<tr>
<td>Wheat Bran</td>
<td>60.9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Values taken from "Feeds and Feeding," Table III, Pages 728-43, Henry and Morrison, 1923.
The test at the Exposition lasted 120 days. In the present report, however, the results of the test are given in the form of daily averages. To save space, the feed-consumption data are here presented in the form of TDN (total digestible nutrients) only. The conversion factors we used for computing TDN from the original data, are presented in Table 2.

3. Superior Illinois A. R. Holstein cows.—We are indebted to Dr. C. W. Turner of this Department for these data. They were described by Dr. Turner in the Journal of Dairy Science Vol. 7, p. 535, 1924. These records were secured under the management of C. M. Long, Secretary of the Illinois Holstein-Friesian Association and W. H. Dressel in charge of the Illinois Testing Plant at Dixon, Illinois. The cows were kept under the best possible conditions and every effort was made to secure maximum milk production from each cow. Unlike other data discussed in this bulletin, the live weights of these Holsteins were not obtained by direct weighing but by estimating, which involved a possible live-weight error of about 50 pounds. Since the weight gains were less than 50 pounds, the third (weight-gain) term in equation 1a as fitted to these data is without significance. Moreover, since the TDN distribution between maintenance (C) and milk production (B) depends on live weight, the numerical values of B and C, and consequently the numerical values of the net cost and net efficiency of milk production are greatly influenced by errors in live weight, and are consequently without significance. However, these data are interesting because of their gross-efficiency values.

4. Pennsylvania Nutrition Institute Data.—These most excellent data were taken by us from the interesting monograph entitled “The Mineral Requirements of Milk Production” (Pennsylvania Station Technical Bul. 319, 1935) by E. B. Forbes and associates. There is of course no question about the meticulous accuracy of these data collected under the rigorous metabolism-stall conditions of the Pennsylvania Institute of Animal Nutrition.

This monograph reports data for 12 cows by 28-day periods. However, we confined our analysis to 10 cows (1, 3, 5, 6, 7, 8, 9, 10, 11, 12), for 8 periods (2nd to 9th lactation periods inclusive).

III. TABULAR SUMMARIES WITH DISCUSSIONS OF DATA

1. Tabular summaries of the data and of their equation constants.

—Before proceeding with detailed analyses it will be convenient to have before us the pertinent data in tabular form. These are presented in Table 3 (3a, 3b, 3c, and pictorially, in Fig. 2.)

Table 3a shows that in the case of the 243 experiment-station cows, the average (observed) weight was 1087 pounds; the average daily FCM
Table 3A.—Summary of the Data Discussed in the Present Bulletin

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>B</td>
</tr>
<tr>
<td>Experiment Sta. (Res. Bull. 222)</td>
<td>243</td>
<td>1087</td>
<td>0.117</td>
<td>28.26</td>
<td>17.64</td>
<td>30.1</td>
<td>62.2</td>
<td>0.305</td>
</tr>
<tr>
<td>La.-Purchase Exposition:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All breeds</td>
<td>73</td>
<td>1161</td>
<td>0.773</td>
<td>49.97</td>
<td>23.90</td>
<td>31.8</td>
<td>51.5</td>
<td>0.367</td>
</tr>
<tr>
<td>Brown Swiss</td>
<td>3</td>
<td>1208</td>
<td>0.675</td>
<td>41.49</td>
<td>27.78</td>
<td>28.0</td>
<td>42.8*</td>
<td>0.274</td>
</tr>
<tr>
<td>Holstein</td>
<td>15</td>
<td>1290</td>
<td>0.823</td>
<td>48.81</td>
<td>26.63</td>
<td>34.3</td>
<td>53.6*</td>
<td>0.116</td>
</tr>
<tr>
<td>Jersey</td>
<td>25</td>
<td>948</td>
<td>0.599</td>
<td>45.59</td>
<td>25.09</td>
<td>33.6</td>
<td>48.7*</td>
<td>0.217</td>
</tr>
<tr>
<td>Shorthorns</td>
<td>28</td>
<td>1252</td>
<td>0.920</td>
<td>32.56</td>
<td>20.69</td>
<td>29.6</td>
<td>54.3*</td>
<td>0.205</td>
</tr>
<tr>
<td>Class A</td>
<td>45</td>
<td>1104</td>
<td>0.682</td>
<td>46.21</td>
<td>25.90</td>
<td>33.2</td>
<td>49.7*</td>
<td>0.263</td>
</tr>
<tr>
<td>Class B</td>
<td>65</td>
<td>1158</td>
<td>0.736</td>
<td>41.93</td>
<td>24.16</td>
<td>32.3</td>
<td>53.2*</td>
<td>0.373</td>
</tr>
<tr>
<td>Class C</td>
<td>34</td>
<td>1280</td>
<td>0.859</td>
<td>35.69</td>
<td>22.60</td>
<td>29.6</td>
<td>51.9*</td>
<td>0.347</td>
</tr>
<tr>
<td>Ill. Testing Plant Sup. Holsteins</td>
<td>42</td>
<td>1322</td>
<td>0.058</td>
<td>51.15</td>
<td>27.83</td>
<td>34.3</td>
<td>82.4</td>
<td>0.229</td>
</tr>
<tr>
<td>Forbes' Pa. Holsteins</td>
<td>10</td>
<td>1131</td>
<td>0.215</td>
<td>36.20</td>
<td>19.75</td>
<td>34.4</td>
<td>64.3</td>
<td>0.292</td>
</tr>
<tr>
<td>All of above</td>
<td>368</td>
<td>1130</td>
<td>0.243</td>
<td>33.64</td>
<td>19.96</td>
<td>31.0</td>
<td>53.6</td>
<td>0.350</td>
</tr>
</tbody>
</table>
TABLE 3B.—The data in Table 3A are here presented in a different form

<table>
<thead>
<tr>
<th>Description of Data</th>
<th>No. of Cows</th>
<th>Live Weight Pounds</th>
<th>Absolute FCM Production/day</th>
<th>Ratios of FCM Calories produced to:</th>
<th>Observed Absolute TDN Consumption</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Pounds</td>
<td>Calories</td>
<td>Computed Basal Metabolism Calories</td>
</tr>
<tr>
<td>Experiment Station</td>
<td>243</td>
<td>1087</td>
<td>28.26</td>
<td>9608</td>
<td>1.48</td>
</tr>
<tr>
<td>Exposition</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All Breeds</td>
<td>73</td>
<td>1161</td>
<td>40.97</td>
<td>13910</td>
<td>2.05</td>
</tr>
<tr>
<td>Brown Swiss</td>
<td>5</td>
<td>1208</td>
<td>41.49</td>
<td>14107</td>
<td>1.87</td>
</tr>
<tr>
<td>Holsteins</td>
<td>15</td>
<td>1290</td>
<td>48.81</td>
<td>15695</td>
<td>2.25</td>
</tr>
<tr>
<td>Jerseys</td>
<td>25</td>
<td>948</td>
<td>45.59</td>
<td>15501</td>
<td>2.64</td>
</tr>
<tr>
<td>Shorthorns</td>
<td>28</td>
<td>1252</td>
<td>32.56</td>
<td>11070</td>
<td>1.54</td>
</tr>
<tr>
<td>Class A</td>
<td>45</td>
<td>1104</td>
<td>44.21</td>
<td>15711</td>
<td>2.40</td>
</tr>
<tr>
<td>Class B</td>
<td>65</td>
<td>1158</td>
<td>41.93</td>
<td>14256</td>
<td>2.10</td>
</tr>
<tr>
<td>Class C</td>
<td>34</td>
<td>1280</td>
<td>35.69</td>
<td>12135</td>
<td>1.66</td>
</tr>
<tr>
<td>Illinois Testing Plant</td>
<td>42</td>
<td>1322</td>
<td>51.15</td>
<td>17391</td>
<td>2.32</td>
</tr>
<tr>
<td>Forbes' Pa. Holsteins</td>
<td>10</td>
<td>1131</td>
<td>36.20</td>
<td>12308</td>
<td>1.84</td>
</tr>
<tr>
<td>Ave. of all groups</td>
<td>368</td>
<td>1130</td>
<td>33.64</td>
<td>11438</td>
<td>1.71</td>
</tr>
<tr>
<td>Column number</td>
<td></td>
<td></td>
<td>C1</td>
<td>C2</td>
<td>C3</td>
</tr>
</tbody>
</table>

Footnotes: Column 2, observed; c.3 = c.2 x (340); c.4 = c.5 = c.6 = c.7 = c.8 = observed; 9 = 8 x (1814); 10 = 9; 11 = 9; 12 = 9; 13 = 22 x 2; 14 = c.19 x 15 x (1814); 15 = 23 x M0.74 values of weight M, given in Col. 1; 16 = 15 x (1814); 17 = 8; 18 = 19; 19 = computed from Basal metabolism (Cal) = 39.5M0.74 where M is live weight in pounds given in Col. 1; 20 = 16; 21 = 14; 22 = 19; 23 = 19; 24 = 19.
TABLE 3B.—THE DATA IN TABLE 3A ARE HERE PRESENTED IN A DIFFERENT FORM—CONTINUED

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment Station</td>
<td></td>
<td></td>
<td>4.9</td>
<td>2.0</td>
<td>3.3</td>
<td>8.6</td>
<td>15637</td>
<td>8.7</td>
<td>15836</td>
<td>48.9</td>
<td>49.5</td>
<td>6475</td>
<td>2.4</td>
<td>2.4</td>
</tr>
<tr>
<td>Exposition All Breeds</td>
<td></td>
<td></td>
<td>6.4</td>
<td>3.0</td>
<td>3.1</td>
<td>15.0</td>
<td>27264</td>
<td>7.9</td>
<td>14403</td>
<td>62.9</td>
<td>33.2</td>
<td>6806</td>
<td>2.1</td>
<td>4.0</td>
</tr>
<tr>
<td>Brown Swiss</td>
<td></td>
<td></td>
<td>6.7</td>
<td>3.2</td>
<td>3.6</td>
<td>15.2</td>
<td>27637</td>
<td>8.8</td>
<td>15927</td>
<td>54.8</td>
<td>31.6</td>
<td>7527</td>
<td>2.1</td>
<td>3.7</td>
</tr>
<tr>
<td>Holsteins</td>
<td></td>
<td></td>
<td>6.6</td>
<td>3.1</td>
<td>2.9</td>
<td>17.9</td>
<td>33489</td>
<td>8.6</td>
<td>15382</td>
<td>67.3</td>
<td>32.3</td>
<td>7363</td>
<td>2.1</td>
<td>4.4</td>
</tr>
<tr>
<td>Jerseys</td>
<td></td>
<td></td>
<td>7.7</td>
<td>3.7</td>
<td>2.9</td>
<td>16.7</td>
<td>30348</td>
<td>6.9</td>
<td>12444</td>
<td>66.7</td>
<td>27.3</td>
<td>5881</td>
<td>2.1</td>
<td>5.2</td>
</tr>
<tr>
<td>Shorthorns</td>
<td></td>
<td></td>
<td>5.2</td>
<td>2.5</td>
<td>3.4</td>
<td>12.0</td>
<td>21677</td>
<td>8.4</td>
<td>15256</td>
<td>57.8</td>
<td>40.7</td>
<td>7204</td>
<td>2.1</td>
<td>3.0</td>
</tr>
<tr>
<td>Class A</td>
<td></td>
<td></td>
<td>7.2</td>
<td>3.4</td>
<td>3.0</td>
<td>17.0</td>
<td>30765</td>
<td>7.7</td>
<td>13877</td>
<td>65.5</td>
<td>29.5</td>
<td>6558</td>
<td>2.1</td>
<td>4.7</td>
</tr>
<tr>
<td>Class B</td>
<td></td>
<td></td>
<td>6.5</td>
<td>3.0</td>
<td>3.1</td>
<td>15.4</td>
<td>27917</td>
<td>7.9</td>
<td>14385</td>
<td>63.7</td>
<td>32.8</td>
<td>6792</td>
<td>2.1</td>
<td>4.1</td>
</tr>
<tr>
<td>Class C</td>
<td></td>
<td></td>
<td>5.6</td>
<td>2.7</td>
<td>3.4</td>
<td>13.1</td>
<td>23763</td>
<td>8.5</td>
<td>15492</td>
<td>58.0</td>
<td>37.8</td>
<td>7321</td>
<td>2.1</td>
<td>3.2</td>
</tr>
<tr>
<td>Illinois Testing</td>
<td></td>
<td></td>
<td>6.8</td>
<td>1.8</td>
<td>3.0</td>
<td>11.7</td>
<td>21242</td>
<td>15.9</td>
<td>28861</td>
<td>42.1</td>
<td>57.2</td>
<td>7484</td>
<td>3.9</td>
<td>2.8</td>
</tr>
<tr>
<td>Plant Holsteins</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forbes’ Pa.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Holsteins</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ave. of all groups</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Column number...</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Column number...</th>
<th>C10</th>
<th>C11</th>
<th>C12</th>
<th>C13</th>
<th>C14</th>
<th>C15</th>
<th>C16</th>
<th>C17</th>
<th>C18</th>
<th>C19</th>
<th>C20</th>
<th>C21</th>
<th>C22</th>
<th>C23</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
(4% milk) production was 28.3 pounds (or 9622 Calories); the average daily TDN consumption was 17.64 pounds (or 32,000 Calories); the average gross energetic efficiency of milk production was 30%. For the 73 "World's-Fair" cows (in this case not yearly but 120-day records), the average (observed) weight was 1161 pounds, but the breed weights ranged from 948 pounds for Jerseys to 1290 pounds for Holsteins; the average daily FCM production ranged from 32.5 pounds (11,050 Calories) for Shorthorns to 48.81 pounds (16,595 Calories) for Holsteins; the daily TDN consumption ranged from 20.69 pounds (37,532 Calories) for Shorthorns, to 26.63 pounds (48,307 Calories) for Holsteins; the gross energetic efficiency ranged from 28% for the Brown-Swiss to 34.3% for Holsteins. For the 42 Illinois superior Holstein cows, the average (estimated) weight was 1322 pounds; the average daily FCM production was 15 pounds (or 5100 Calories); the average daily TDN consumption was 27.83 pounds (or 50,484 Calories); the average gross efficiency was 34%. For Forbes' 10 cows (2nd to 9th lactation periods inclusive) the average live weight was 1131 pounds; the average daily FCM production was 36.20 pounds (or 12,308 Calories); the average daily TDN consumption was 19.75 pounds (or 35,829 Calories); the average gross efficiency was 34.5%.

The net efficiency column in Table 3a represents the computed efficiency (computed from equation 1a) of milk production from TDN above maintenance cost of the cow. The net efficiency is seen to be of the order of 60%. (The 82% value of the Illinois superior Holstein cows is probably due to the fact that the weights of these cows were estimated without actual weighing.) This means that of 100 Calories TDN consumed above that used for maintenance and for weight-gain, 60 Calories appear in the milk; the remaining 40 Calories are expended for the "work" of secretion, using the term "work" in a broad sense to include all energy wastes associated with the process.

In this connection it is instructive to quote the following paragraph from a report on a famous experiment by W. H. Jordan, C. G. Genter, and F. D. Fuller, N. Y. (Geneva) Agricultural Experiment Station Bulletin 197, 1901: "over 40% of the available energy value of the ration was used for maintenance, over 30% reappeared in the milk solids, leaving a balance of from one-fifth to one-fourth of the ration. The logical conclusion is that this balance, in part at least, sustain the work of milk secretion." We are obviously not the first to use the expression "work" in connection with the milk-secreting process.

While the expression "net energetic efficiency of milk production" was probably not used before, a considerable number of papers quote partial and complete balance experiments with figures on the utilization of metabolizable feed for milk production above maintenance, which
practically means the same thing as our "net efficiency." Thus Jordan (New York, Geneva, A. E. S. Bull. 197, 1901) reported 49% to 64% utilization of metabolizable feed energy for milk production. Kellner (5th Inter. Kongress für Milchwirtschaft, 1911) reported 67 to 73% utilization of metabolizable energy for milk production. Eckles (Mo. E. S. Res. Bull. 7) reported 59 to 67 (av. 62%) utilization for milk production of metabolizable energy. Haecker (Minn. E. S. Bull. 140, 1914) reported 50% to 66% utilization.

Fig. 2a summarizes in graphic form some of the numerical data of Table 3a. These curves will be discussed in greater detail in future sections. It is sufficient to call attention at this time that gross energetic efficiency of milk production does not uniformly increase or decrease with increasing live weight; in other words, that gross energetic efficiency of milk production is probably independent of live weight.

The data of Table 3a are exhibited in different form in Table 3b.

Columns 1 and 2 in Table 3b give the FCM (4% milk) production in pounds and in Calories. The FCM production is seen to range from about 10,000 Calories, or 28 pounds, per day for the 243 experiment-station cows to over 17,000 Calories, or 51 pounds, per day for the Illinois superior A. R. Holstein cows.

In this connection it is interesting to note that the present Holstein champion, Carnation Ormsby Butter King "Daisy" (see the February 22, 1936, number of the "Holstein-Friesian World") produced during some months at the rate of nearly 40,000 Calories of milk per day, as indicated in the following table (Table 3c).

<table>
<thead>
<tr>
<th>Lactation Month</th>
<th>FCM (4% milk) lbs./day</th>
<th>FCM Calories/day</th>
<th>Estimated Gross Energetic Efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>97.38</td>
<td>33109</td>
<td>43.8</td>
</tr>
<tr>
<td>2</td>
<td>103.61</td>
<td>35907</td>
<td>44.6</td>
</tr>
<tr>
<td>3</td>
<td>103.16</td>
<td>35074</td>
<td>44.4</td>
</tr>
<tr>
<td>4</td>
<td>110.51</td>
<td>37573</td>
<td>44.4</td>
</tr>
<tr>
<td>5</td>
<td>107.68</td>
<td>36611</td>
<td>44.9</td>
</tr>
<tr>
<td>6</td>
<td>102.85</td>
<td>34969</td>
<td>44.3</td>
</tr>
<tr>
<td>7</td>
<td>102.94</td>
<td>35000</td>
<td>44.3</td>
</tr>
<tr>
<td>8</td>
<td>97.15</td>
<td>33031</td>
<td>43.7</td>
</tr>
<tr>
<td>9</td>
<td>96.31</td>
<td>32745</td>
<td>43.6</td>
</tr>
<tr>
<td>10</td>
<td>91.89</td>
<td>31243</td>
<td>42.9</td>
</tr>
<tr>
<td>11</td>
<td>90.01</td>
<td>30603</td>
<td>42.7</td>
</tr>
<tr>
<td>12</td>
<td>91.18</td>
<td>31001</td>
<td>42.9</td>
</tr>
</tbody>
</table>

Years Production FCM 36,476 lbs. or 12,401,840 Calories.

In other words, she produced about 4 times as much milk energy as an average good experiment-station cow; about 2½ times as much as the Illinois Testing Plant Holsteins; she produced enough energy to supply the maintenance need of 16 average adult persons.
Fig. 2.—Graphic comparison of body-weight trends of gross energetic efficiency (upper chart) and milk (FCM) production (lower chart) of the several groups of cows discussed in the text. Meaning of symbols: Ex. S., represents the experiment-station group of cows; Pa. Hol., stands for the Pennsylvania Institute of Nutrition (Forbes) Holstein cows; Ill. T. P. Hol., represents the superior Holstein group from the Illinois Testing Plant; Hol., Jer., SH., B. S. represents respectively the "World's Fair", or Exposition, Holstein, Jersey, Shorthorn and Brown-Swiss groups of cows.
Columns 3 to 6, Table 3b, show that the milk calories produced were: from 1½ to 2 times the basal metabolism calories of the cows; about ½ as much as TDN calories consumed (i. e., gross efficiency of milk production about 33%); ½ to ¾ of the calories consumed above maintenance (i. e., net efficiency of milk production is 50 to 66%).

Columns 7 and 8, Table 3b, show that the cows consumed per day from 17 pounds TDN (experiment-station group) to 28 pounds (Superior Holsteins); or in terms of Calories from 32,000 to 50,000 Calories.

Columns 9, 10, and 11, Table 3b, show that the total TDN calories consumed by these cows was: 5 (experiment-station) to 7 (superior Holstein) times their basal metabolism; 2 to 3 times the computed TDN used for maintenance only; about 3 times the milk calories produced.

Columns 16 and 17, Table 3b, show that the higher the milk production the greater the percentage of the consumed TDN used for milk production. The Illinois superior Holstein group is an exception for reasons previously explained.

2. Factors influencing values of equation constants and apparent net efficiency of milk production.—Table 3a shows that equation constants B, C, and especially D are, as might be expected from the discussion in section I, 7, very erratic where the number of animals are few. In two cases the values of D are negative, an impossible situation, since the cows could not gain weight on less than nothing. The following list of explanations of the erratic results are intended to supplement the discussion given in I, 7:

a. The smaller the number of animals in the group to which equation 1a was fitted, the less the “degree of freedom,” the less the compensatory smoothing effect the less the dependability of the resulting equation constants of the fitted equation. From this point of view, the number of animals in the Exposition subgroups, and in the Pennsylvania group are too few. The fewness of animals in the Pennsylvania group is compensated by the excellency of the observations. Observational perfection can not however eliminate inherent biological variations in maintenance cost and composition of weight gains. To present an equation based on 5 to 28 animals as a reasonable statement of the partitioning of the TDN into its various uses and as a tool for determining net efficiency, would be comparable to using a mortality table based on the statistics of one town as a statement of mortality and as a guide in determining insurance rates.

b. A given gain in live weight does not always have the same energetic significance because the composition of the gains vary. One time a given gain in weight may be largely water; another, fat; another, “flesh,” that is protein, mineral, water, fat in varying proportions. (For discussion of literature on this problem see S. Brody, Annual Review Bio-
chemistry, Vol. 4, pp. 299-404, 1935. Mitchell and Carman reported that weight gains in uniformly fed rats ranged in heat content from 0.32 to 3.9 Calories per gram.) The value of D in equation 1a should therefore be expected to vary with the nature of the weight gains.

c. It is well-known that there are differences in maintenance costs of animals. Some animals, referred by farmers as "hard keepers," are muscularly active (restless, nervous) and therefore have a relatively high maintenance cost (high-value of C in equation 1a); others, referred as "easy keepers," are quiet, phlegmatic, and therefore have a relatively low maintenance cost (low value of C). The nature of the average results of equation 1a is such that whatever affects C (maintenance) also affects B (milk cost). If the maintenance costs of a "hard" and an "easy" keeper are averaged, then obviously the "easy keeper" will be overcharged with maintenance, with the result that the net efficiency (ratio of milk to TDN above that going for maintenance) will appear higher than it is; opposite results will be obtained for the "hard keeper." Variability in maintenance cost will therefore influence profoundly the apparent individual net efficiencies of milk production.

d. Maintenance cost, C, is also influenced by fatness. It is well-known that a fat individual tends to have a lower maintenance cost than a thin one of the same live weight. Two animals having the same live weights, producing the same amounts of milk, at the same gross efficiency, may yet produce milk at different net efficiencies on account of differences in body fatness and consequently differences in maintenance costs.

e. Maintenance cost, C, is moreover influenced by nutrition plane. The energy cost of "handling" unit feed (mastication, digestion, assimilation, intermediate changes, excretion of end products) increases with amount of feed consumed and with percentage of protein in feed. Differences in values of equation constants between the several Exposition sub-groups may be due to differences in nutritional level, particularly to differences in protein percentages in the feeds of the several subgroups (see Table 1).

f. Errors in weighing, or in estimating body weights will result in corresponding errors in maintenance cost (C in equation 1a). An error in the maintenance cost, C, for an individual is associated with a corresponding error, but of opposite sign, in milk production cost, B, of the individual. The unusually high net efficiency values shown by the Illinois superior Holstein data are probably due to systematic over-estimates of live weights.

g. Another possible source of error may be noted as regards the Exposition and the Illinois superior Holstein data. Cattle feeders often look on roughages merely as fillers, and therefore tend to be careless in weighing them. The following experience illustrates one practical feeder's
attitude. He was instructed to keep accurate individual feed records of cows. His records showed remarkable uniformity in hay consumption. On questioning it developed that instead of weighing the hay consumed by each cow separately, he divided the total hay consumed by the number of cows in the group. He fully appreciated the importance of weighing the individual grain consumption but not the hay. In this case the larger cows were probably undercharged in comparison to the small. It was suggested in Res. Bull. 222 that larger cows tend to be overfed in comparison to small.

h. The amount of TDN required to gain unit weight (D in equation 1a) probably depends on the amount of weight gained. Investigations by Spillman, Jull, Titus and Hendricks indicate the applicability of the law of diminishing increments to weight gains: the greater the weight gains the greater in proportion the net TDN cost per unit weight gain. If the law of diminishing returns is applicable to milk secretion, then the greater the milk production, the greater the net TDN cost (B in equation 1a) per unit FCM produced.

i. It must be remembered that the TDN energy for the present computation was not determined directly but computed with the aid of Morrison’s conversion tables. The errors introduced by use of such factors are compensated, when dealing with large numbers of individuals, as in the case of the experiment-station cattle group, but they are likely to affect the results adversely when dealing with small numbers of individuals, as in the case of the Exposition subgroups.

j. Errors tend to fall most heavily on D (weight-gain cost) because, as shown by the beta coefficients, the relative importance of the TDN used for weight-gain is small (16%, compared to 35% for maintenance and 25% for milk production).

The above list of influencing factors on the constants of equation 1a, and consequently on the apparent net efficiency of milk production, indicates that the results presented in this bulletin on net efficiency of milk production must be considered as preliminary explorations rather than as final conclusions. Moreover, whatever final conclusions may be formulated by the present statistical method will have to be confirmed, before final acceptance, by an experimental method such as the one used by Dr. Graham, previously noted.

3. Comparison of gross efficiency of milk production with gross efficiency of muscular work and gross efficiency of growth.—As shown in Table 3a, the gross efficiency of milk production of good dairy cows is of the order of 30%. That is, the percentage ratio of

\[
\frac{\text{Milk energy produced}}{\text{TDN energy consumed}} \times 100
\]
is of the order of 30. But some individuals reach much higher efficiency levels. We found, with the aid of the nomograph in Missouri Station Bulletin 351, that the gross energetic efficiency of milk production of the Jersey champion cow Stonehurst Patricians Lily is 47.5%. This is the highest gross efficiency that we encountered. It is instructive to compare the gross efficiency of milk production with gross efficiency of other processes.

We have shown (see Missouri Research Bulletin 209) that the maximum attainable gross efficiency of work (pulling loads on a horizontal platform) in horses is of the order of 25%. Unlike the efficiency of milk production, the figure for efficiency of work did not include the maintenance cost during the time the horses were not working, nor the expense of “handling” the feed. Moreover, the work was carried out under ideal conditions quite unlike farm practice. The actual gross efficiency of work as carried out under farm conditions is probably a small fraction of the 25% maximum, and consequently a small fraction of the efficiency of milk production.

According to Terroine and Wurmser’s computations the average gross efficiency of embryonic growth of the chick and silk worm is 60% to 70%, that is, about twice as great as of milk production by good cows. However, embryonic growth and milk production are expressed in different units; in embryonic growth efficiency is computed with reference to egg yolk, while in milk production it is computed with reference to TDN. Gross efficiency of postnatal growth is much less. According to Rubner gross efficiency of early postnatal growth is about 34%. (According to Rubner, 4.8 Calories are required to produce 1 gm of body substance containing 1.7 Calories. The gross efficiency is therefore \( \frac{1.7}{4.8} = 34\% \).) The following brief examination of growth data indicates that on “ordinary” diets growth efficiency tend to fall below 34%, particularly in the later ages. Efficiencies of the order of 34% are obtained only on excellent diets.

For convenience of computation we assumed that 1 gram of body weight uniformly contains 2.0 (rather than 1.7) Calories, and 1 gram of TDN contains 4 Calories. Using the above conversion factors the gross efficiency of growth of dairy cattle in our herd is as follows:

<table>
<thead>
<tr>
<th>Age Months</th>
<th>Holstein heifers</th>
<th>Jersey heifers</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>35</td>
<td>37</td>
</tr>
<tr>
<td>2</td>
<td>29</td>
<td>25</td>
</tr>
<tr>
<td>3</td>
<td>26</td>
<td>23</td>
</tr>
<tr>
<td>4</td>
<td>18</td>
<td>17</td>
</tr>
<tr>
<td>5</td>
<td>17</td>
<td>15</td>
</tr>
<tr>
<td>6</td>
<td>14</td>
<td>13</td>
</tr>
<tr>
<td>7</td>
<td>13</td>
<td>11</td>
</tr>
<tr>
<td>8</td>
<td>10</td>
<td>9</td>
</tr>
<tr>
<td>9</td>
<td>10</td>
<td>9</td>
</tr>
<tr>
<td>10</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>11</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>12</td>
<td>9</td>
<td>9</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Age Months</th>
<th>Holstein heifers</th>
<th>Jersey heifers</th>
</tr>
</thead>
<tbody>
<tr>
<td>13</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>14</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>15</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>16</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>17</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>18</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>19</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>20</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>21</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>22</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>23</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>24</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>25</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>26</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>27</td>
<td>1</td>
<td>7</td>
</tr>
</tbody>
</table>

Percentage Gross Efficiency of Growth (1 gm TDN = 4 Cal., 1 gm weight gain = 2 Cal.)
Percentage gross efficiency of growth of young rats on an optimum diet may be computed from data by Palmer et al., Minn. Tech. Bul. 92.

<table>
<thead>
<tr>
<th>Weeks Efficiency</th>
<th>146 Males</th>
<th>141 Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 2 3 4 5 6</td>
<td>25 23 21 20 19 18</td>
<td>23 19 17 15 14 13</td>
</tr>
</tbody>
</table>

Percentage gross efficiency of growth of chickens, computed from data by Card and Kirkpatrick, Storrs Bul. 96, indicates a decline in efficiency from 21-25% 1st week, to 3-5% 24th week.

<table>
<thead>
<tr>
<th>Age, Wks.</th>
<th>1 2 3 4 5 6 7 8</th>
</tr>
</thead>
<tbody>
<tr>
<td>W. Leghorns</td>
<td>26 22 19 18 20 19 16 13</td>
</tr>
<tr>
<td>R. I. Reds</td>
<td>21 17 25 22 19 18 20 17</td>
</tr>
</tbody>
</table>

We are indebted to Professor Gustave F. Heuser for sending us unpublished data from the Poultry Department, Cornell University on unusually rapid growing chicks and the amount of feed consumed by them; from which we computed the following growth efficiency values. In these computations we assumed that the energy content of 1 gm of their feed was 3 Cal. TDN. and 1 gm weight-gain 2 Calories. The 1st group was composed of 10 males and 1.4 females; the 2nd group, 15 males and 10 females.

<table>
<thead>
<tr>
<th>Age, weeks</th>
<th>1 2 3 4 5 6 7 8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Efficiency Group 1</td>
<td>34.8 38.3 33.3 41.8 28.8 25.4 18.2 25.7</td>
</tr>
<tr>
<td>Efficiency, Group 2</td>
<td>38.9 38.6 32.6 32.8 29.1 28.2 21.8 23.7</td>
</tr>
</tbody>
</table>

If our conversion factors are roughly correct, then the gross energetic efficiency of growth of these rapidly growing chicks on the given diet (Diet: yellow cornmeal 57.75 group 1 and 57.25 group 2; wheat flour middlings 20.00; egg white 10.25 group 1 and 8.25 group 2; dried liver 7.50 group 1 and 10.00 group 2; cod liver oil 1; steamed bone meal 2.00; limestone 1.00; salt 0.50.) is of the same order as the gross energetic efficiency of milk secretion.

The characteristic feature about gross-efficiency of growth is that it declines rapidly with increasing age. Some of the decline of growth...
efficiency with increasing age is only apparent, due to the decrease in water concentration in the body. But most of it is real because the older the animal the greater the maintenance expense in comparison to weight gain. Thus growth efficiency of "feeder" steers (Winters and McMahon, U. Minn. Tech. Bul. 94, 1933) during a period of about 200 days, weight about 500 pounds at the beginning of the trial, ranged from 5% for experiment 1, to 9% for experiments 2 and 3. In other words, the gross energetic efficiency of a good cow as a converter of feed into final product is 3 to 10 times as great as of a feeder steer. This fact is of great interest from the standpoint of national economy. The differences between gross efficiency of growth and milk secretion would be greatly increased if we carried out the computation on the edible product rather than on the whole body. All the produced milk is edible, but of the steer body, only 55-64% is "dressed" and perhaps only 50% edible. While gross efficiency of growth of the entire body appears to be the same in small and large animals, there may be a difference with regards to the efficiency of "dressed" carcass.

IV. FACTORS INFLUENCING GROSS AND NET ENERGETIC EFFICIENCY OF MILK PRODUCTION WITH SPECIAL REFERENCE TO THE APPLICABILITY OF THE LAW OF DIMINISHING RETURNS

This section discusses two questions: (1) To what extent does body size affect gross energetic efficiency of milk production? (2) To what extent does milk production level affect the energetic efficiency of milk production?

1. Influence of body weight on gross energetic efficiency of milk production.—It is well known that other conditions (especially fatness) being the same, large animals produce more milk than small. Under farm conditions, as illustrated by dairy cattle herd improvement association records, there is an increase in yearly yield of approximately 10 pounds of fat or 250 pounds of FCM (4% milk) for each increase of 100 pounds of body weight. Under official-test conditions, there is an increase of about 20 pounds of fat, or 500 pounds of FCM, for each 100 pounds increase of body weight. Since a large cow tends to produce more milk than a small, then if the profit per pound of milk is the same then clearly the large cow producing more milk than the small, will also bring in the greater total monetary return per cow than the small. This, however, does not answer the question whether a large cow is more or less efficient energetically as converter of feed into milk than a small cow (or whether the profit per pound of milk is the same in the large as small cow).
On pages 10 and 13 of Missouri Research Bulletin 222, group averages of gross energetic efficiencies were plotted against corresponding group averages of live weights of the experiment-station cows. The resulting curve declined from 32.6% gross efficiency for 750 pound cows to 29.9% efficiency for 1150-pound cows, and remained roughly constant between the far greater range of 1150 and 1450 pounds. No attempt was made to fit an equation to represent the trend of the data. It seemed interesting to replot the same data but by individuals rather than by groups, and to fit a linear equation to the data by the method of least squares. The result is shown in Fig. 2b. Solid lines represent the entire group; broken lines represent separate trends for Holstein and Jersey (together with a few Guernsey) data.

The solid (average) line in the lower half of Fig. 2b shows that the FCM production tends to increase with increasing live weight according to the equation:

\[ FCM = 18.58 + 0.0089M \]

This means that an increase in body weight tends to be accompanied by an increase of about 0.9 pounds FCM production per day (or about 330 pounds per year).

The upper chart of Fig. 2b shows that the gross efficiency tends to decrease with increasing live weight according to the equation:

\[ \text{Gross Efficiency} = 37.42 - 0.0068M \]

This means that an increase of 100 pounds in live weight tends to be accompanied by a decrease in gross efficiency by 0.68%.

The differences in gross efficiency between small and large cows is statistically significant although, as shown by the distribution of the data points in Fig. 2b, many small cows show no larger, and often smaller, efficiencies than large cows. In Research Bulletin 222 we suggested that differences in efficiency between large and small cows may be due not to differences in body size, but to differences (for reasons there explained) in fatness, nutritional level, selective breeding associating size with productivity.

Messrs. Kruger and Reece of this Department suggested the following line of reasoning in explanation of the apparent efficiency decline with body-weight increases, especially below the 1100-pound body-weight level. (see pp. 10 and 13 of Missouri Research Bulletin 222). Dairymen judge cows by their milk production and not energetic efficiency. For example, 900 and 1100-pound cows are judged to be equally good if they give the same amounts of milk, in spite of the fact that the 900-pound cow is more efficient if she produces as much milk as the 1100-pound cow. Such selection on the basis of production regardless of size results in selection of relatively high-efficient small cows with relatively low-efficient large cows. The smaller the cow the greater, so-to-speak, is her struggle
Fig. 2b.—Gross efficiency (upper chart) and FCM production (lower chart) of the 243 experiment-station cows. Heavy continuous curves represent averages of all cows; broken curves represent Holsteins (the longer curve) and Jerseys and few Guernseys (shorter curve).

for survival in the herd; the more she must compensate for her small size by high efficiency. In other words, our present system of judging cows by milk production level regardless of size favors only such very small and small cows as are unusually efficient producers. The conclusion is that Fig. 2, Mo. Res. Bull. 222, and Fig. 2b in this bulletin, represent not a functional relation between body weight and milk-production efficiency based on random sampling, but an apparent relation due to selective sampling. This line of reasoning also emphasizes the importance of comparing milk-producing abilities not by amount of milk produced, but by energetic efficiency which “corrects” for differences in body weights of cows.
Fig. 2c.—Gross efficiency and FCM production of the superior Holstein (Illinois milk testing plant) cows and the Pennsylvania (Forbes) cows.

Fig. 2c presents FCM production and gross efficiency of milk production as functions of body weight of the Illinois Testing Plant superior Holstein cows (continuous curve) and the Pennsylvania (Forbes') data (broken curve).

The continuous lower line of Fig. 2c shows that the FCM production of the Illinois cows increases with increasing live weight according to the equation:

\[ \text{FCM} = 37.2 + 0.0105M \]

This means that an increase of 100 pounds in live weight tends to be accompanied by an increase of about 1 pound of FCM production per day (or about 360 pounds per year).

The continuous upper line in Fig. 2c shows that the gross efficiency of the Illinois cows tend to increase very slightly with increasing live weight, as indicated by the equation:

\[ \text{Gross Efficiency} = 32.17 + 0.0016M \]
Fig. 2d.—Milk (FCM) production and gross efficiency of milk production as functions of body weight of the cows on test at the Exposition ("World's Fair"). Equations for the trend curves for milk production: Jersey FCM = 13.82 + 0.0335M; Shorthorn, FCM = 34.15 - 0.00127M; Holstein, FCM = 51.22 - 0.00187M; Brown Swiss, FCM = 23.94 + 0.0132M. Equation for the gross efficiency curves: Jersey, Eff = 30.52 + 0.00346M; Shorthorn, Eff = 43.46 - 0.0111M; Holstein, Eff = 40.74 - 0.00498; Brown Swiss, 39.21 - 0.00844M. FCM and M represent respectively 4% milk and live weight, in pounds.

This means that an increase of 100 pounds in live weight tends to be accompanied by an increase in gross efficiency of milk production by 0.16%. In other words, 1800-pound cows tend to produce milk with an efficiency about 1.4% greater than 900-pound cows.

Fig. 2d presents similar data for the “World’s Fair” cows. The gross efficiency of milk production is there seen to increase with increasing live weight for the Jersey cows, and decrease for Holstein, Shorthorn and Brown-Swiss cows.
These results do not substantiate the hypothesis that there is a functional relation between live weight and gross energetic efficiency of milk secretion. Increasing live weight decreased the gross efficiency for the experiment-station data, increased for the Illinois Holstein data, increase the Exposition Jersey, decrease the Exposition Holsteins, Shorthorns and Brown-Swiss data. The slopes of the efficiency curves in Figs. 2c and 2d, whether positive or negative, are not significant statistically (cf. R. A. Fischer's "Statistical Methods for Research Workers," 1932, pp. 118 and 158). The negative slope in Fig. 2b is statistically significant, but the significance is of a low order, and as pointed out, may be due to relative overfeeding of the large cows, or to selection, rather than to influence of size as such. The decline of efficiency with increasing live weight of Brown-Swiss and Shorthorns was possibly due to the fact that larger individuals of these breeds tend to be beefier, fatter, than smaller. It is obvious that extra fat or beef will increase maintenance without increasing milk production. It is significant that the gross efficiency of the Exposition Holsteins and Jerseys are the same (34%) in spite of the size difference, and in spite of the fact that the FCM production of Jerseys was 45.6 pounds per day while of Holsteins 48.8 pounds per day. The greater production of the Holsteins appears to have been just paid for energetically by their greater maintenance cost. Size and breed appear to be without influence on efficiency.

Our present conclusion, then, is that the gross energetic efficiency of milk production is not functionally related to live weight. However, we realize that this conclusion must be substantiated on better data having a wider range in live weights. Data on dairy goats when compared with data on dairy cattle would furnish the necessary range in live weight now lacking and we should try next to secure those data.

It is instructive to note in this connection that notwithstanding the conclusions of published investigations on this problem, the published data themselves do not indicate that energetic efficiency of milk production is significantly influenced by live weight. The following examples substantiate this statement:

a. Gaines conclusion (J. Dairy Sc., 14, 1931) that McDowell's data (U. S. D. A. Circ. 114, 1930) indicate a decline in efficiency with increasing body weight is due to Gaines' assumption that maintenance varies directly with body weight. If Gaines had assumed that maintenance varies with surface area (with weight \( \frac{3}{3} \)) then he would have found the decline much less significant.

b. Gaines (U. Ill. Bul. 308, p. 418) cited the following data on feed consumption, milk production and live weights of 3 groups of cattle investigated in Denmark. We added to his table (see Table 4a) the gross
energetic efficiency of milk production computed by aid of equation 1b and the assumption that 1 "feed unit" ("1 kg. barley") is equivalent to 3200 Calories of TDN. The efficiency values are seen to be exactly the same for the three groups of cows in spite of the fact that average weight of the Jerseys was 796 pounds; Crossbreds 913 pounds; Red Danish cows 1021 pounds.

c. W. B. Nevens (J. Dairy Sc. 2, 99, 1919) arranged F. W. Woll’s data (Wisconsin A. E. S. Res. Bul. 26, 1912) in accordance with live weight. These data are cited in Table 4b to which we added columns for FCM pounds and Calories, TDN-Calories and gross energetic efficiencies of milk secretion. The efficiencies were computed on the assumption that 1 pound of Woll’s “feed unit” is equivalent to 2000 Calories of TDN. The efficiency values show no relation to live weights. Nor do the efficiency values which we added to Table 4c taken from Woll’s bulletin 26 show any relation to body weight. (Note: both Woll and Nevens, as McDowell after them, concluded that efficiency increases with increasing live weight.)

The compilation by R. I. Grady (Ohio A. E. S. Monthly Bull. 2, 334, 1917) is also of interest. Grady presented his data with reference to 1000 pounds live weight, assuming that the average weight of the Jerseys was 850 pounds; Holsteins 1200 pounds. We added the columns for FCM pounds and Calories, TDN Calories, gross and net energetic efficiency, assuming that the maintenance cost per 1000 pounds live weight is 14,200 Calories for Holsteins and 15,450 Calories for Jerseys.

The above citations lead us to believe that, gross energetic efficiency of milk production is functionally independent of body size as such.

The following four pieces of evidence from data on energetic efficiency of other functions and of growth substantiate the idea that the gross energetic efficiency of milk production is probably independent of body weight:

a. The limiting (maximum) gross energetic efficiency of pulling loads is practically the same in large (1500 pound) Percheron horses and in small (600 pound) Shetland ponies as illustrated in Figs. 6 to 8, Missouri Research Bull. 209.
<table>
<thead>
<tr>
<th>Class</th>
<th>No. of Cows</th>
<th>Ave. Live Weight lbs.</th>
<th>Milk lbs.</th>
<th>Solids lbs.</th>
<th>Fat lbs.</th>
<th>Feed Units</th>
<th>FCM lbs.</th>
<th>FCM Cals.</th>
<th>TDN Cal.</th>
<th>Efficiency %</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>HOLSTEINS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1000 and less</td>
<td>16</td>
<td>927</td>
<td>13192.7</td>
<td>1589.6</td>
<td>456.93</td>
<td>7905</td>
<td>33.2</td>
<td>11302</td>
<td>43315</td>
<td>26.1</td>
</tr>
<tr>
<td>1001-1,100</td>
<td>21</td>
<td>1081</td>
<td>14411.7</td>
<td>1689.1</td>
<td>483.15</td>
<td>7543</td>
<td>35.4</td>
<td>12019</td>
<td>41332</td>
<td>29.1</td>
</tr>
<tr>
<td>1101-1,200</td>
<td>42</td>
<td>1170</td>
<td>14089.5</td>
<td>1683.6</td>
<td>480.73</td>
<td>7650</td>
<td>35.2</td>
<td>11968</td>
<td>41918</td>
<td>28.5</td>
</tr>
<tr>
<td>1201-1,300</td>
<td>25</td>
<td>1274</td>
<td>15616.5</td>
<td>1865.6</td>
<td>529.27</td>
<td>8145</td>
<td>38.9</td>
<td>13212</td>
<td>44631</td>
<td>29.6</td>
</tr>
<tr>
<td>1301-1,400</td>
<td>26</td>
<td>1377</td>
<td>16414.7</td>
<td>1845.1</td>
<td>527.86</td>
<td>7950</td>
<td>39.7</td>
<td>13501</td>
<td>43562</td>
<td>31.0</td>
</tr>
<tr>
<td>1401-1,500</td>
<td>10</td>
<td>1474</td>
<td>15359.9</td>
<td>1875.0</td>
<td>544.71</td>
<td>8180</td>
<td>31.2</td>
<td>13335</td>
<td>44822</td>
<td>29.8</td>
</tr>
<tr>
<td>Over 1,500</td>
<td>8</td>
<td>1669</td>
<td>17017.1</td>
<td>2042.4</td>
<td>592.07</td>
<td>8675</td>
<td>43.0</td>
<td>14613</td>
<td>47535</td>
<td>30.8</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td></td>
<td>1225</td>
<td>14712.3</td>
<td>1833.2</td>
<td>505.32</td>
<td>7890</td>
<td>37.8</td>
<td>12850</td>
<td>43233</td>
<td>29.7</td>
</tr>
<tr>
<td><strong>GUERNSEYS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>800 and less</td>
<td>5</td>
<td>762</td>
<td>6935.6</td>
<td>983.5</td>
<td>351.36</td>
<td>5989</td>
<td>20.6</td>
<td>6998</td>
<td>32817</td>
<td>21.3</td>
</tr>
<tr>
<td>801-900</td>
<td>32</td>
<td>863</td>
<td>7579.4</td>
<td>1073.8</td>
<td>384.24</td>
<td>6109</td>
<td>24.1</td>
<td>8194</td>
<td>33474</td>
<td>24.5</td>
</tr>
<tr>
<td>901-1,000</td>
<td>56</td>
<td>962</td>
<td>8623.0</td>
<td>1208.8</td>
<td>427.63</td>
<td>6394</td>
<td>27.0</td>
<td>9187</td>
<td>35036</td>
<td>26.2</td>
</tr>
<tr>
<td>1001-1,100</td>
<td>29</td>
<td>1068</td>
<td>9165.4</td>
<td>1270.3</td>
<td>444.794</td>
<td>6739</td>
<td>28.3</td>
<td>9629</td>
<td>36929</td>
<td>26.1</td>
</tr>
<tr>
<td>1101 and over</td>
<td>19</td>
<td>1202</td>
<td>9446.7</td>
<td>1334.0</td>
<td>479.111</td>
<td>6930</td>
<td>30.0</td>
<td>10214</td>
<td>37973</td>
<td>26.9</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td></td>
<td>987</td>
<td>8548.9</td>
<td>1199.7</td>
<td>425.55</td>
<td>6458</td>
<td>26.2</td>
<td>8900</td>
<td>35387</td>
<td>25.0</td>
</tr>
<tr>
<td><strong>JERSEYS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>800 and less</td>
<td>10</td>
<td>766</td>
<td>6065.5</td>
<td>862.5</td>
<td>309.51</td>
<td>4985</td>
<td>19.4</td>
<td>6586</td>
<td>27315</td>
<td>24.1</td>
</tr>
<tr>
<td>801-900</td>
<td>34</td>
<td>866</td>
<td>7031.8</td>
<td>970.2</td>
<td>360.87</td>
<td>5614</td>
<td>22.5</td>
<td>7664</td>
<td>30762</td>
<td>24.9</td>
</tr>
<tr>
<td>901-1,000</td>
<td>21</td>
<td>945</td>
<td>7180.3</td>
<td>1038.4</td>
<td>373.99</td>
<td>5666</td>
<td>23.3</td>
<td>7929</td>
<td>31047</td>
<td>25.2</td>
</tr>
<tr>
<td>1001 and over</td>
<td>11</td>
<td>1109</td>
<td>7897.9</td>
<td>1124.6</td>
<td>402.46</td>
<td>5535</td>
<td>25.2</td>
<td>8565</td>
<td>30329</td>
<td>28.3</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td></td>
<td>909</td>
<td>7063.0</td>
<td>997.17</td>
<td>364.31</td>
<td>5534</td>
<td>22.6</td>
<td>7690</td>
<td>30324</td>
<td>25.3</td>
</tr>
</tbody>
</table>

*Table 2 was compiled by sorting according to live weight and breed the records of all cows for which live weights are given and which completed records in the Wisconsin cow competition as stated in Wisconsin Research Bulletin No. 26.
b. The gross energetic efficiency of development of a finished embryo appears to be independent from size or species. It is said to be the same for the chick as for the silk worm (the finished chick embryo is 50,000 the size of the finished silk worm embryo) and perhaps frog and minnow, namely 50 to 65%. (see Needham’s Chemical Embryology for references and discussion.)

c. The gross energetic efficiency of early postnatal growth is said to be the same in all warm blooded species. See Lusk’s Science of Nutrition for a discussion of Rubner’s “law of constant energy expenditure” which reads: The amount of energy (calories) which is necessary to double the weight of the newborn of all species (except man) is the same per kilogram no matter whether the animal grows quickly or slowly.

We computed gross energetic efficiencies of growth (gain in weight) in early postnatal life of mice, rats, chickens, swine and cattle and found greater variations in percentage efficiency between members of the same species, than between species averages. These computations are cited in detail in section III, 3, of this bulletin.

d. Kleiber found that the ratio of maximum available food energy consumption to basal metabolism is practically the same for steers, chickens, rabbits. (The ratio was 4.4 for a group of chicks; 5.0 for a rabbit; 4.2 and 5.6 for two steers.) The available consumed energy is of course used for only two purposes, namely maintenance and storage. If the ratio of available energy consumed to maintenance is the same, regardless of size or species, then the gross energetic efficiency of growth would be expected to be the same, regardless of size or species.

Against the above voluminous body of direct and indirect evidence favoring the independence of gross energetic efficiency from live weight as such, one can cite much fewer evidence favoring the opposite conclusion: First, is the slight but statistically significant decline in gross efficiencies between live weights 800 to 1000 pounds (decline from 32.4% to 30.2%) shown in Table 2, p. 10, and Fig. 2 p. 13, Missouri Research Bulletin 222. Second, is the fact shown in Fig. 4, p. 17, Res Bul. 222 that the FCM production of Jersey Register of merit cattle lags somewhat behind in its increase with increasing body weight in comparison to the increase in maintenance cost. But, as explained in Res. Bull. 222, it is possible that factors other than simple live weight might have been responsible for this decline in efficiency with increasing body weight.

It is reasonable to assume that some heavy cows are so because they tend to be fat and “fleshy.” The current feeding standards, which assume a direct proportionality between live weight and maintenance cost, help to produce this result (see Fig. 1, Missouri Res. Bul. 222). The fact that a large cow produces more milk than a small may also perhaps stimulate the feeder to overfeed the large cow in comparison
Fig. 3.—Rise and decline of egg production with increasing live weights of hens. This chart indicates the presence of an optimum body weight rather than a continuous rise or decline of egg production with increasing body weight.

to the small. Overfeeding, fleshiness, fatness, always tend to reduce efficiency by increasing maintenance. Moreover deposits of fat tend to inhibit (by simple mechanical obstruction) productive processes. An exaggerated illustration of this fact may be seen in the decline not only in gross efficiency but also in absolute egg production in fowls with increasing live weight shown in Fig. 3. In the case of curve 3, Rhode Island Reds, the egg production remains roughly constant at the 190-egg level between 4 and 5½ pounds live weight, then it drops steeply
down to the 100-egg level for $8\frac{1}{2}$ pounds—a tremendous reduction. Each breed and group of birds is seen in Fig. 3 to have its characteristic optimum body weight where egg production is a maximum. May there not be like optima body weights resulting in most efficient milk production for each group of cows? In other words, a decline of efficiency with increasing live weight for one group of cows may mean that the optimum body weight has been passed for this particular group, and not on account of a general functional relation indicating general decrease in efficiency with increasing live weight.

The above considerations lead to the tentative conclusion that while it is true that a small animal tends to produce more milk in comparison to its body weight than a large, it is also true that a small animal tends to spend more energy for its overhead maintenance in comparison to a large; the result may be that the gross efficiency, that is the ratio

$$\frac{\text{Milk energy produced}}{\text{Milk energy produced} + \text{Maintenance energy expense} + \text{Energy equivalent of work and wastes incident to milk production}}$$

tends to be independent of body weight. The final decision on the matter will have to await not only more and better data on dairy cattle, but also data on dairy goats, which will extend the live-weight range of the dairy animals under comparison.

We felt that it is important to state explicitely that we believe that while gross energetic efficiency of milk production is not dependent on live weight, monetary profitableness of milk production is decidedly dependent on live weight. An 1800-pound cow may have the same energetic efficiency as a 900-pound cow, and bring in the same profit per pound milk produced; but since the 1800-pound cow will produce more milk pounds, she will make a greater total profit. On the other hand, two 900-pound cows will produce more milk than one 1800-pound cow, and under certain conditions, two 900-pound cows will bring in a greater, monetary return than one 1800-pound cow. We must remember that energetic (or dollar) efficiency is a ratio; while profit is a difference and the relation between the two is not a simple one.

2. **Influence of milk production level on gross energetic efficiency of milk production.**—The TDN cost of milk production was subdivided in equation 1a into: (A) TDN cost of maintenance apart from milk production; (B) TDN cost of milk production apart from maintenance. The maintenance cost is an overhead cost, which goes on regardless of the production level. The higher the production level, the smaller the overhead maintenance charge per unit of milk production, and consequently the higher the gross production efficiency. The gross energetic efficiency of milk production must therefore increase with increasing
Fig. 4.—Decline in slope of gross energetic efficiency of milk production with increasing milk production. Gross efficiency of milk production increases with increasing milk production level but at decreasing rates in accordance with the law of diminishing returns, approaching a theoretical maximum of about 60%.

milk production, although it can never reach the net efficiency, that is the efficiency of the mammary gland as converter of TDN into milk aside from the overhead maintenance cost of the cow.
Since the higher the production level the greater the spread of the maintenance charge, or the smaller the maintenance tax per unit milk produced, therefore the successive increments in gross efficiency will decline with successive increments in milk production. If gross energetic efficiency is plotted against milk production, the resulting curve will not be a straight line, but its slope will decrease so that gross efficiency will approach net efficiency as limit. Such declines on gross efficiency increments with milk production increments for cows of different live weight are illustrated in Fig. 4, based on the data of the 243 experiment-station cows. Fig. 3 shows that a 1000-pound cow producing 70 pounds FCM per day is not twice as efficient as one producing 35 pounds FCM per day, but only about 28% more efficient.

In the data illustrated in Fig. 3, the net efficiency is of the order of 60%; the gross efficiency can therefore never exceed 60% for this particular group of cows. (It is of course conceivable that the net efficiency as thus defined is greater in some cows, or in some species, or under some conditions, in which case the gross efficiency may be correspondingly higher.) While the theoretical maximum gross efficiency is of the order of 60% the actual maximum gross efficiency is of the order of 48%.

(The gross energetic efficiency of milk production computed with the aid of the nomograph in Missouri Station Bulletin 351 is 43.5% for the champion Holstein Carnation Ormsby Butter King “Daisy” and 47.5% for the champion Jersey Stonehurst Patrician’s Lily.) The “working range” for improvement is therefore only between the actual present maximum of 48% to the theoretical, practically unattainable, maximum of 60%. The rapidly decreasing slope of the curve in Fig. 4 indicates that there are correspondingly rapid increasing difficulties for successive unit increases in gross energetic efficiency. This is, of course, only one illustration of the general law of “diminishing increments”, or “diminishing returns” known under various names, such as “Mitcherlich’s law,” “Spillman’s rule” etc.

The fact that very high-producing cows do not have proportionately high gross energetic efficiencies may be illustrated by a numerical example from Fig. 3 and Table 3a. From Fig. 3, a 1000-pound cow producing 70 pounds FCM per day is not twice, but only 28% more efficient than one producing 35 pounds FCM. A 1000-pound cow producing 70 pounds FCM is seen from Fig. 3 to have a gross efficiency of about 45%; while a 1000-pound cow producing 35 pounds FCM has a gross efficiency about 35%. From Fig. 3 the experiment-station cows produced their 28.3 pounds FCM with a gross efficiency of 30%; the “World’s Fair” cows produced their 41 pounds FCM with an efficiency of 31.8%; a 37% (\(\frac{11}{33}\)) increase in milk production was accompanied by a 5.5% (1.7/31) increase in energetic efficiency.
To avoid misunderstanding, it is necessary to repeat that the above discussion is concerned with efficiency and not profit. Efficiency is a ratio (ratio of milk energy to TDN energy); profit is a difference (difference between milk price and feed price). These two concepts must not be confused. While successive efficiency increments obviously tend to decrease with increasing milk production, successive monetary profit increments tend to remain constant with increasing milk production. A detailed analysis between profit and efficiency of milk production will be presented in the forthcoming bulletin (Missouri Res. Bul. 239).

3. Influence of milk production level and lactation stage on net energetic efficiency of milk production.—Equations 1a and 3a were formulated on the assumption that the net TDN cost (not including maintenance cost of the cow) per unit of FCM produced is the same regardless of the milk production level. This section attempts to show that the tentative assumption that net efficiency is independent of milk production level is not likely to be true.

If the net TDN cost per unit FCM produced (and consequently net efficiency) is the same regardless of milk production level, then for each unit TDN consumed above maintenance, there is a proportional increase in FCM produced (assuming that body consumption and weight remain constant). Of course, sooner or later a production limit is reached beyond which milk production does not increase at all. The question that we wish to pose in this connection is which of the following two assumptions is the more reasonable: (a) There is a constant FCM return per unit TDN consumption until the upper milk-production limit is reached abruptly; (b) The upper milk-production level is approached gradually in such manner that the successive milk increments for additional TDN increments decline gradually.

A consideration of other types of biological transformations suggest that the second assumption is more reasonable. Thus Liebig suggested, and Mitscherlich formulated, what is known as the "law of diminishing increments" to represent an analogous quantitative relation between plant growth and limiting fertilizer supply. Spillman, Jull, Titus and Hendricks found that the law of diminishing increments also represents the relation between animal growth and food consumption. According to this "law," the weight-gain per unit food intake diminishes with increasing food intake; the greater the food intake the less the successive weight gain per unit additional food intake. Following Hendricks and associates, this statement may be written in the form of the differential equation

\[
\frac{dW}{dF} = K(A - W) \tag{4a}
\]
or the integral equation

\[ W = A - Be^{kF} \]

Equation 4a shows that the body weight increment, \( dW \), per unit food increment, \( dF \), is proportional to the difference between the present body weight of the animal, \( W \), and the maximum body weight, \( A \), which the animal can attain. This difference of course diminishes as the animal's weight increases due to increased food consumption.

The essential problem that we should like to solve is: does the law of diminishing increments, which represent the relation between weight-gain and food consumption, also represents the relation between milk production-gain and food consumption? In other words, would equations 4a and 4b hold for milk production if we replaced in it body weight, \( W \), by milk yield, FCM? Granted that the amount of body weight gained per unit TDN (or F) consumed (aside from TDN cost of maintenance) decreases with increasing body-weight gains, does the amount of milk produced per unit of TDN consumed (aside from TDN cost of maintenance or live-weight gains) likewise decrease with increasing milk production?

It is difficult to test the applicability of the law of diminishing returns to milk production by partition equation 1a. To do this the first and third first-power terms would have to be replaced by exponential terms, when it would become difficult if not impossible to fit the resulting exponential equation to the data by the method of least squares. Under these circumstances it would not be possible to test this question rigorously; but it may be tested roughly, under the following simplified assumption:

Since the proportion of TDN used for live-weight gains is relatively insignificant, it will make no practical difference whether we assume that the TDN used for live-weight gains increases linearly or exponentially with live-weight gains. The live-weight gain term, \( \Delta M \), in equation 1a may therefore be left undisturbed in its present linear form. The difficulty is then narrowed to the FCM term in equation 1a. Does the TDN used for milk secretion increase linearly or exponentially with FCM production?

Since replacing the linear form of the FCM term in equation 1a by an exponential form would make it impossible to fit the equation to the data by the method of least squares, we may replace it instead by a simple power form; that is, we will assume, for purposes of convenience, that the TDN for milk production increases not with simple milk production, but with milk production raised to some power, \( n \), as shown by the following equation:

\[ \text{TDN} = B(\text{FCM})^n + C(M)^{0.73} + D(\Delta M) \]
This is frankly a compromise; the power function of equation 1c is more nearly the exponential function than the linear function of equation 1a. Besides, if the data follow a linear course, the value of n will be 1. On the other hand, if the function is not linear, and if the "law of diminishing increments" holds, then the value of n will be greater than 1. Thus if the value of the exponent n is 1.5 (instead of 1.0) it will mean that if milk production is increased by 100% above a certain level, the needed TDN consumption will have to be increased not by 100% but by about 150% above the corresponding feed level (assuming that maintenance TDN and live weight gains did not change with changing milk production level). Such a result would mean that the mammary gland (apart from the expense of normal maintenance of the rest of the body) does not operate at a constant efficiency, but that its efficiency decreases with increasing milk production especially in the upper production levels.

The modified partition equation 1a was fitted to the several groups of data by: (1) deducting from the total TDN consumed the amounts used for maintenance (CM0.73), and for weight gains (DΔM), as determined from equation 1a previously fitted to the corresponding groups. The remaining TDN, designated by TDN", was then related to the FCM by the equation

$$\text{TDN"} = B (\text{FCM})^n$$

The resulting values of n are shown in Table 4.

Table 4 shows that the average value of n is 1.5 for the Exposition data, 0.96 for the experiment-station data, and 0.72 for the Illinois Superior Holstein data. Table 4 also shows that of the Exposition subgroups, the relatively high producing cows (Holstein, Jersey, Class A) had very low values of n (.43, .59, .34) while the relatively low-producing cows (Shorthorn, Brown-Swiss, Class C, Class B) had high values of n (1.1, 1.3, 1.5, 1.5). Does this variability of the values of n reflect errors in the data, or is there a physiological mechanism responsible for it? It is conceivable that the differences in value of n, Table 4, are due to differences in shapes of lactation curves in different classes of cows as illustrated in Fig. 4a, and explained below.

The milk production level is a function of many influencing factors, such as: number of secreting cells; quality of secreting cells; concentration of actuating hormones or enzymes; concentration of milk precursors or substrates in blood; ability of animal to consume and rapidly assimilate large quantities of feed; relative tendencies to use nutrients for fattening and milk production, etc. The shape of the lactation curve when plotted against TDN" consumption will vary with the relative influences of the several factors. Thus when concentration of actuating hormones or enzymes is low in comparison to milk precursors or substrates, as in case of low-producing cows, the secreting cells operate at a
Table 5.—Numerical Value of n (and Incidentally B) in Equation 1d

\[ \text{TDN}^* = B(\text{FCM})^n \]

<table>
<thead>
<tr>
<th>Data</th>
<th>Number of Cows</th>
<th>n</th>
<th>B</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Experiment Station group:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All breeds</td>
<td>243</td>
<td>0.955</td>
<td>0.357</td>
</tr>
<tr>
<td>Guernsey</td>
<td>18</td>
<td>0.913</td>
<td>0.413</td>
</tr>
<tr>
<td>Holstein</td>
<td>157</td>
<td>0.920</td>
<td>0.407</td>
</tr>
<tr>
<td>Jersey</td>
<td>68</td>
<td>0.896</td>
<td>0.419</td>
</tr>
<tr>
<td><strong>La-Purchase Exposition:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All breeds</td>
<td>73</td>
<td>1.550</td>
<td>0.035</td>
</tr>
<tr>
<td>Brown Swiss</td>
<td>5</td>
<td>1.293</td>
<td>0.115</td>
</tr>
<tr>
<td>Holstein</td>
<td>15</td>
<td>0.432</td>
<td>2.425</td>
</tr>
<tr>
<td>Jersey</td>
<td>25</td>
<td>0.594</td>
<td>1.484</td>
</tr>
<tr>
<td>Shorthorn</td>
<td>28</td>
<td>1.070</td>
<td>0.170</td>
</tr>
<tr>
<td>Class A</td>
<td>45</td>
<td>0.342</td>
<td>3.739</td>
</tr>
<tr>
<td>Class B</td>
<td>65</td>
<td>1.509</td>
<td>0.040</td>
</tr>
<tr>
<td>Class C</td>
<td>34</td>
<td>1.510</td>
<td>0.039</td>
</tr>
<tr>
<td><strong>Illinois Testing Plant Sup.</strong></td>
<td>42</td>
<td>0.724</td>
<td>0.715</td>
</tr>
<tr>
<td>Holsteins</td>
<td>10</td>
<td>1.260</td>
<td>0.114</td>
</tr>
</tbody>
</table>

Fig. 5a.—Milk production (FCM) plotted against TDN* (TDN* is total TDN consumed less TDN used for maintenance and for live-weight gains; that is TDN* is that part of the TDN used for milk production only). This chart illustrates the applicability of the law of diminishing increments to FCM production and to the net efficiency of milk production (broken curve) of high-producing cows (curve II) and low producing cows (curve III), or during high and low production, during a lactation cycle.

low efficiency (that is, the secreting cells produce little milk in comparison to their overhead maintenance cost). In such case the “working range” will embrace the declining region (the rise in milk production is slow with increasing TDN* consumption as indicated by curve III, Fig. 5a) and the value of the exponent n in Table 4 will tend to be high. But when the concentration of actuating hormones or enzymes is high, as in the case of relatively high-producing cows, the secreting cells operate at a high efficiency (the cells produce much in comparison to their overhead maintenance cost). In such case the “working range” will be about the inflection region (rise in milk production is rapid with increasing TDN* consumption as indicated by curve II (Fig. 5a) and the value of the exponent n in Table 4 will tend to be low.
Fig. 5b.—The curves in this chart, plotted from Table 6, based on the Pennsylvania (Forbes) data substantiate the theory that the law of diminishing returns is applicable to net efficiency of milk production as explained in the text, and illustrated in Fig. 5a. Note the similarity between the shape of the net efficiency curve on the right in this chart and the broken curve on the left of Fig. 5a. While similarities between shapes of curves do not constitute proof of a theory, they substantiate the theory circumstantially. The shape of the lactation curve of net efficiency of the left side of this chart likewise substantiates, the theory expounded in the text.

The right curve in Fig. 5b, plotted from Table 6, brings out similarity between theoretical efficiency (broken) curve in Fig. 5a and the observed course of net efficiency with changing TDN"—consumption level; the left curve in Fig. 5b, plotted from Table 6, substantiates the statement that net efficiency of milk production declines with decline in concentration of activating substances or mechanisms, even if concentration of available nutrients remains the same.

It is generally agreed that in the early period of lactation of superior cows, when lactation rate is at maximum, nutritional factors ("substrates," "precursors") limit production rate. The animals can not consume enough food to maintain body weight. In the late period of lactation, when lactation rate is on the decline, activating factors or (hormones, enzymes, secreting cells) no doubt limit production. The production declines in spite of a food supply level which permits body-weight gains.
Table 6.—Course of Milk Production With Advancing Lactation and With Change in TDN and TDN*$ Consumption

<table>
<thead>
<tr>
<th>28-day Periods of Lactation</th>
<th>No. of Cows Included</th>
<th>Body Weight lbs.</th>
<th>FCM Lbs./day</th>
<th>Cal./day</th>
<th>TDN Lbs./day</th>
<th>Cal./day</th>
<th>Gross Efficiency %</th>
<th>Net Efficiency %</th>
<th>Ave. by TDN* Class</th>
<th>Net Efficiency %</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>9</td>
<td>1122</td>
<td>42.86</td>
<td>14572</td>
<td>16.40</td>
<td>29750</td>
<td>49.0</td>
<td>82</td>
<td>4-5.99</td>
<td>57</td>
</tr>
<tr>
<td>2</td>
<td>9</td>
<td>1116</td>
<td>44.03</td>
<td>14970</td>
<td>20.47</td>
<td>37133</td>
<td>40.3</td>
<td>72</td>
<td>6-7.99</td>
<td>66</td>
</tr>
<tr>
<td>3</td>
<td>10</td>
<td>1114</td>
<td>42.70</td>
<td>14518</td>
<td>21.08</td>
<td>38239</td>
<td>38.0</td>
<td>67</td>
<td>8-9.99</td>
<td>62</td>
</tr>
<tr>
<td>4</td>
<td>10</td>
<td>1119</td>
<td>40.10</td>
<td>13634</td>
<td>20.79</td>
<td>37713</td>
<td>36.2</td>
<td>62</td>
<td>10-11.99</td>
<td>60</td>
</tr>
<tr>
<td>5</td>
<td>10</td>
<td>1125</td>
<td>37.27</td>
<td>12672</td>
<td>20.67</td>
<td>37495</td>
<td>33.8</td>
<td>60</td>
<td>12-13.99</td>
<td>62</td>
</tr>
<tr>
<td>6</td>
<td>10</td>
<td>1133</td>
<td>34.70</td>
<td>11798</td>
<td>19.76</td>
<td>35845</td>
<td>32.9</td>
<td>62</td>
<td>14-15.99</td>
<td>60</td>
</tr>
<tr>
<td>7</td>
<td>10</td>
<td>1146</td>
<td>32.07</td>
<td>10904</td>
<td>18.82</td>
<td>34139</td>
<td>31.9</td>
<td>64</td>
<td>16-17.99</td>
<td>58</td>
</tr>
<tr>
<td>8</td>
<td>10</td>
<td>1148</td>
<td>28.93</td>
<td>9836</td>
<td>17.89</td>
<td>32452</td>
<td>30.3</td>
<td>63</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>10</td>
<td>1155</td>
<td>26.65</td>
<td>9061</td>
<td>17.30</td>
<td>31382</td>
<td>28.9</td>
<td>62</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>10</td>
<td>1155</td>
<td>21.52</td>
<td>7317</td>
<td>15.75</td>
<td>28933</td>
<td>25.3</td>
<td>61</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>7</td>
<td>1190</td>
<td>19.35</td>
<td>6579</td>
<td>16.40</td>
<td>29750</td>
<td>22.1</td>
<td>43</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>6</td>
<td>1141</td>
<td>9.42</td>
<td>3203</td>
<td>12.14</td>
<td>22022</td>
<td>14.5</td>
<td>58</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
SUMMARY AND CONCLUSIONS

Data on milk production, feed (TDN) consumption, live weights, weight-gains, were analyzed on four groups of cows total of 368 individuals with the objects of determining: quantitative partition of TDN consumed between its use for milk production, maintenance and live-weight gain; gross and energetic efficiencies of milk production; functional relation between live weight of cows and energetic efficiency of milk production.

This analyses led to the conclusions that: energetic efficiency of milk production is practically independent of live weight (apparently high efficiencies of small cows due to selection); energetic efficiency of milk production of good experiment-station dairy cows is of the order of 30%; successive efficiency increments decline exponentially with successive milk increments in their approach to a maximum efficiency (with respect to TDN energy) of about 60%. The gross energetic efficiencies of cows exhibited at the St. Louis "World’s Fair" were: 34.4% for Holsteins; 33.6% for Jerseys; 29.6% Shorthorns; 28.0% Brown-Swiss. A group of 42 very superior Holstein cows in Illinois produced milk with an efficiency of 34.3%. The highest energetic efficiency of milk production that we encountered (this was estimated from the nomograph in Missouri Station Bulletin 351) was 47.5% for the Jersey champion cow Stonehurst Patrician’s Lily, a 700-pound cow which produced 25,946 pounds FCM for the year. Much higher production records were made, but at lower energetic efficiencies. Thus the U. S. Holstein champion Carnation Ormsby Butter King “Daisy” produced 36,476 pounds FCM per year, which is 40.6% (= \( \frac{36,476 - 25,946}{25,946} \times 100 \)) above that of the Jersey champion production; but since the Holstein cow weighed 1700 pounds, which is 143% (= \( \frac{1700 - 700}{700} \times 100 \)) above that of the Jersey weight, and since the Holstein cow probably used about 91% (= \( \frac{12.09 - 6.33}{6.33} \times 100 \)) more TDN for maintenance than the Jersey, therefore the gross energetic efficiency of milk production of the Holstein was computed (from the chart in Missouri Station Bulletin 351) to be only 43.5% in comparison to gross efficiency of the Jersey of 47.5%. This 47.5% gross efficiency value with regards to TDN is probably near the limit of biological possibility.

The question of applicability of the law of diminishing returns to gross and net cost of milk production is discussed in detail, as also the
many factors which enter into the solution of the net-efficiency problem not only of milk production but also of growth and related processes. A historical review is presented of the attempts, since 1903, to solve this problem.

It is interesting to note that the gross efficiency of milk production of "good" dairy cows is of the same order as the gross efficiency of early postnatal growth on "good" diets; namely about 30%. Thus chicks and cattle grow at, roughly, the same gross energetic efficiency in early postnatal life, just as large and small cows tend to produce milk with equal gross energetic efficiency.