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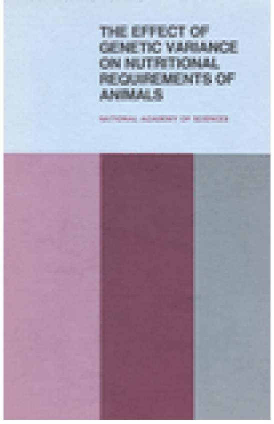

The Effect of Genetic Variance on Nutritional Requirements of Animals: Proceedings of a Symposium

Subcommittee on Genetic Variance in Animal Nutrition,
Committee on Animal Nutrition, Board on Agriculture
and Renewable Resources, National Research Council

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The Effect of Genetic Variance on Nutritional Requirements of Animals

Proceedings of a Symposium
University of Maryland
College Park, Maryland
July 31, 1974

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Committee on Animal Nutrition
Board on Agriculture and
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National Research Council
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Preface

The symposium reported herein was held under joint sponsorship of the Committee on Animal Nutrition of the Board on Agriculture and Renewable Resources, National Research Council, and the American Society of Animal Science at the 1974 meeting of the society at the University of Maryland, College Park, Maryland. It sought to review and interpret the knowledge accumulated thus far on the interactions of genetics and nutrition of animals. In assessing the importance of research in this area for animal production and human welfare, it is hoped that this symposium will stimulate more cooperation and interdisciplinary research between nutritionists and geneticists.

The organizers and the committee are grateful to the officers of the American Society of Animal Science and, in particular, to Dr. Frank H. Baker, president, and Dr. T. J. Marlowe, secretary–treasurer, who were instrumental in making many of the on-site arrangements. We are grateful, too, to the specialists who appeared on the program and to their colleagues and institutional officers who cooperated to make participation possible.

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Introduction

M. L. Sunde*
University of Wisconsin

It was thought by the National Research Council's Committee on Animal Nutrition two or three years ago that a symposium attempting to cover the existing literature on the interaction of genetics and nutrition would be valuable to both disciplines. The idea was to try to cover the literature for several species of animals and then publish the information to stimulate additional work in the area. The publication of the proceedings would serve as a reservoir of information for the scientists involved and enable them to proceed more rapidly in their research work in this area.

A review of nutrition and disease by Dr. Howard Schneider (presently with the Rockefeller Institute)† contains the following statement:

> It may be that thus far the nutritionist has had to pay scant heed to Mendelian genetics because he has taken his problems where he found them and in retrospect he found them where genetic influence is not sharply particulate and hence not prominent. Growth, for example, is a biological character which is controlled by so many genes that it is extremely unlikely that breeding methods, even carelessly pursued, result, in the animals, in any embarrassing excursions up and down the scale of rate of growth. . . . The mere fact that this possibility has been excluded by

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† Schneider, Howard. 1946. Nutrition and disease. Vitam. Horm. 4:60.

> the biological basis of growth has made it possible to neglect genetics to a large extent. At my home University, the University of Wisconsin, nutritional investigations are pursued in the Biochemistry Building. Right next door is the Genetics Building. The two buildings might well be in different worlds.

Unfortunately the overall situation at many of our experimental stations, including the one mentioned above, has not changed very much in the intervening years. Nutritionists have explained away many unanswered nutritional quirks as being confounded by genetics; the geneticist, in turn, has been plagued with differences from generation to generation that he has had to explain as environmental or nutritional.

A strain of inbred Ancona chickens maintained in our laboratory has a high zinc requirement for normal feathering. This strain shows a very different requirement for arginine than a strain of crossbred New Hampshire × Single Comb White Leghorn chicks.

A strain of Royal Chinese geese was imported recently from Ecuador. When goslings of this strain were fed a good diet, they grew very rapidly—in fact, to over 5 pounds at 28 days. Four out of 31, however, developed bone abnormalities in the legs, even when all the nutrients that were supposed to prevent this condition were provided in generous amounts. Perhaps the condition of accelerated growth provided stress to a bone system that would have otherwise been adequate. A number of years ago, Dr. Leslie E. Johnson of South Dakota, and later at Iowa, had noted this same condition in swine.

The material that follows may stimulate research on questions such as these and decrease the time necessary to review the literature on this important subject.

Genetic Variation in Nutrition of Cattle for Meat Production

E. J. Warwick[*] and E. H. Cobb[†]
U.S. Department of Agriculture

Genetic differences may be expressed in a number of ways and may be influenced by uncontrolled or uncontrollable environmental factors. Inherited traits, especially as they relate to overall efficiency in cattle production, are greatly influenced by management variables—such as type of ration, age, or weight at measurement or at slaughter. Goals for slaughter weight and body composition dictate the genetic types and management regimes selected. An effort is often made to take advantage of interactions between genetic variability and environmental and management variables to optimize efficiency of the production processes.

Six of the more readily apparent ways in which genetic variability could be expressed will be discussed, followed by an attempt at synthesis and projections for genetic improvement in efficiency of production per unit of feed consumed.

ABILITY TO DIGEST NUTRIENTS

Very few attempts have been made to determine the heritability of digestive abilities within types of cattle. T. W. Dowe (personal

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communication, 1973) accumulated data for such an attempt but found within-sire animal variation to be too large to arrive at meaningful h heritability estimates with limitations imposed on numbers by the necessarily costly and time-consuming procedures. Reid (1962) concluded from a comprehensive review of the literature that variability in digestive powers between individuals was so low that possibilities for genetic improvement were very small—probably too small to justify selection studies.

Several studies have compared digestive ability of beef breeds of the *Bos taurus* species with that of *Bos indicus* (Zebu types) and their crosses. Tests have been conducted in several parts of the world with feedstuffs differing widely in nitrogen content and in digestibility of dry matter. Working in East Africa with Zebu and Zebu–Ayrshire crosses, French (1940) observed in the Zebus a greater, but not statistically significant, ability to digest dry matter. Duckworth (1946) reviewed a large number of digestion trials with both *Bos indicus* and *Bos taurus* and regressed digestibility of organic matter on crude-fiber content of rations. The resulting equations suggested a higher digestibility by *Bos taurus* at low fiber levels, with the difference disappearing at higher levels. At a crude-fiber level above 38 percent, Zebu types would be expected to excel in digestive ability. Phillips *et al.* (1960), working in East Africa, reported dry-matter digestibilities of 67.7 and 65.0 percent for Zebu and mixed-breed grade European steers, respectively. More recently Karue, Evans, and Tillman (1972) compared Boran and 3/4 Hereford-1/4 Boran crossbred steers and found a slightly, but not significantly, higher digestibility for both energy and dry matter by the Borans. The Borans had a significantly higher digestibility of nitrogen (56% versus 51%), which was associated with a higher nitrogen intake. Howes, Hentges, and Davis (1963) in Florida compared digestibility of a variety of feeds in Hereford and Brahman females. Differences in percentage of dry-matter and apparent crude-protein digestibility over all rations favored the Brahmans (61% versus 63% and 46% versus 50%, respectively) but were statistically significant only for apparent crude-protein digestibility. There was a tendency for the superiority of the Brahmans to be greater on low-protein roughages, but the statistical significance of the trend was not explored.

The greatest volume of research on this problem has been by the Division of Animal Genetics at Rockhampton, Queensland. Ashton (1962) compared grade Brahman, Hereford, and crosses of Brahman and Africander with Shorthorns and Herefords on rations of "natural pasture hay" and the same hay in varying combinations with lucerne (alfalfa) hay. The pasture hay ranged from 3.5- to 4.4-percent crude protein and from 15.5- to 17.4-percent alfalfa. Steers with Zebu backgrounds had significantly higher dry-matter and apparent nitrogen digestibilities. Figures for dry-matter digestibility were 56.0 and 53.3 percent for Brahmans and Herefords, respectively, with crossbreds being intermediate. For apparent digestibility of nitrogen, corresponding figures were 53.0 and 49.8 percent, with the crossbreds similar to the Brahmans. In a trial with Brahman × Hereford and Hereford steers, Vercoe (1966) fed high-quality, hammermilled lucerne (alfalfa) hay at three levels of intake. He found significantly higher dry-matter and nitrogen digestibilities by the crossbreds. In a follow-up study with the same animals on a low-quality diet of blue grass–spear grass hay, he (Vercoe, 1967) found no breed differences in digestibility. This paper refers to an additional crossover trial at one season that again showed breed differences on a high-quality, but not on a low-quality, diet. Vercoe and Frisch (1970a) found no overall significant differences for either dry-matter digestibility or apparent nitrogen digestibility between breeds when Brahman, Africander, and Shorthorn × Hereford male cattle were compared on varying levels of lucerne (alfalfa) hay. There were tendencies—either statistically significant or approaching significance—for both dry-matter and apparent nitrogen digestibilities to decrease with increased feeding level in Brahmans and Africanders, but this was not the case in the Shorthorn × Hereford crossbreds.

Colditz and Kellaway (1972) studied the effect of diet and heat stress on the nitrogen metabolism of Friesians, Brahman × Friesian crossbred, and Brahman heifers. On the high-quality diet, dry-matter and nitrogen digestibilities were similar for all genotypes; on the low-quality diet, Friesians had the highest percentages for both. These responses were confounded with differences in intake: Nitrogen utilization was similar for the three genotypes within diets. Apparent nitrogen digestibility was similar for the three genotypes at both 17 and 38 °C. The dry-matter digestibility for the Friesians was higher than that for the Brahman × Friesian crossbreds at 17 °C and for both the other genotypes at 38 °C.

Moore (1974) used 36 bull calves representing 6 breeds—Angus, Hereford, Barzona, Santa Gertrudis, Brahman, and Shorthorn—to determine breed differences in ability to utilize three different rations varying in energy and roughage content. Hereford bulls fed the high-energy ration had significantly higher dry-matter digestibility and digestible-energy values than did Brahman bulls. The dry-matter digestibility and digestible-energy values for the Brahman bulls fed the low-energy ration were significantly higher than comparable values for Hereford bulls. No differences in digestibilities were noted among the breeds on the medium-energy ration. Hereford bulls exhibited significantly higher nitrogen retention values than Brahman bulls on the high-energy ration, but no differences in nitrogen retention values were noted among breeds fed the medium- and low-energy rations.

Overall, Zebu and Zebu-cross cattle appear to be slightly more efficient than British breeds in digesting dry matter and crude protein (nitrogen), but results are not consistent. Causes of inconsistency are not fully understood.

True digestibility of nitrogen is differentiated from apparent digestibility by detection of metabolic nitrogen with undigested nitrogen in conventional digestion trials. Moran and Vercoe (1972) reviewed a total of 107 digestibility trials involving comparisons between Zebu-type cattle—Brahman, Africander, and their crosses with British breeds—and British breeds or crosses for factors affecting apparent nitrogen digestibility. Statistical approaches utilizing data on apparent nitrogen digestibility, and on its relation with dry-matter intake and percent nitrogen in the ration, were used to estimate metabolic fecal nitrogen and true nitrogen digestibility. It was concluded that Zebus may have a slightly higher true nitrogen digestibility and a lower metabolic fecal nitrogen level than British cattle. Differences were small and could not be subjected to statistical tests.

It appears that genetically determined differences in ability to digest feedstuffs, if they exist, are of such small magnitude as to be of doubtful practical significance. Presumably, either in evolutionary history or in most modern production situations, advantages in digestion potential would give animals possessing them selection advantages. Thus, if genetic variation within species occurs, it is likely that a genetic homeostatic situation has been reached—at least for types of feedstuffs normally used in feeding cattle for beef production.

NUTRIENT REQUIREMENTS FOR MAINTENANCE

For practical cattle production, *maintenance requirement* can be defined as the nutrients required to keep an animal in a state of balance so that he neither gains nor loses body substance. It must provide for basal metabolism and for energy expended in standing, moving about, and—if ambient temperatures deviate from thermoneutrality—maintaining constant body temperature.

No known studies have been made of the heritability of differences in fasting metabolism within breeds or types of cattle. Blaxter and Wainman (1966) compared the fasting metabolism of steers of a dairy type (Ayrshire) and a beef type (Black Aberdeen Angus) ranging in weight from about 200 to 300 kg. They established average metabolizable energy (ME) requirements of 90.7 and 72.4 kcal/kg $W^{0.75}$ per day, respectively; where $W^{0.75}$ is the power function of body weight. Vercoe (1970a) observed average values of 86.4, 102.5, and 97.4 kcal/kg $W^{0.75}$ per day for Brahman, Africanders, and Hereford × Shorthorns, respectively. Most of his experimental animals were bulls averaging 13–22 months of age for the 3-year span of the trials. Weights averaged 303, 266, and 262 kg for the three breed types.

Extensive studies at Missouri (Kibler and Brody, 1950, 1951; Worstell and Brody, 1953) on heat production of Brahman, Holstein, Jersey, and Brown Swiss cattle over a considerable range of live weights, physiological states, environmental temperatures, and nutritional regimes do not permit estimates of fasting metabolism. A comparison by Worstell and Brody (1953) of Brahman and Brown Swiss heifers under similar intakes of total digestible nutrients, but with differences in growth rate and weight, suggested that Brahmans have a lower heat production.

Vercoe (1970a) hypothesized that the lower fasting metabolism of the Brahmans was probably due to more efficient use of the energy released by the biochemical processes occurring at basal conditions so that less appears as heat, rather than to a lower basal ME requirement. The ability of individuals and breeds differing biochemically to produce different fasting metabolisms was pointed out. Vercoe (1970a) found the between-animal, within-breed coefficient of variation to be ±13.2 percent per kilogram/$W^{0.75}$. This is approximately twice as large as the ±7.4 percent reported within-animal by Blaxter and Wainman (1966).

Blaxter (1962) pointed out that individual variation in basal metabolism is quite considerable. He also pointed out from a review of available data that fatty tissue in cattle has a maintenance cost comparable to that of the body as a whole.

Evidence is conflicting on the broader question of whether or not genetic differences exist in maintenance requirements. Taylor and Young (1967, 1968) maintained 22 unmated Ayrshire females on constant levels of food intake for several years until equilibrium weights were reached. Six equally spaced feeding levels were used. The coefficient of variation in equilibrium weights for unrelated animals within feeding level averaged ±5.5 percent, whatever the level of constant food intake. This can be related to average equilibrium weights of about 135, 225, 315, 450, 540, and 630 kilograms for the six constant feeding levels. Overall, the average weight eventually maintained at the different feeding levels was directly proportional to food intake and significantly different from weight to the 0.75 power. Di- and monozygotic twins were included in the design, permitting partitioning of variance into genetic and nongenetic fractions. A heritability estimate of 0.89 ± 0.37 percent together with a coefficient of genetic variation of about 4–6 percent, suggested that direct selection for efficiency of maintenance could lead to rapid improvement.

Vercoe (1970b) observed that Brahman × British (BX) crossbred steers were maintained at higher live weights than British crossbreds (SH) when both types ate the same quantity of low-nitrogen diet over about a 200-day period. Three BX and three SH steers were fed 4.28 kg of dry matter per day of a low-quality, tropical pasture hay (1.5 percent nitrogen, 35 percent cellulose, dry-matter basis). The BX animals were maintained at about 328 kg, while the SH steers were weight-constant at about 290 kg. Digestibility and nitrogen measurements were made over 10-day periods during the last 90 days of the study, and gas exchange measurements were made at the end after a 96-hour fast. It was concluded that the more efficient maintenance of the BX steers was attributable to a higher efficiency of utilization of metabolizable energy. (Digestibility did not differ between groups, and fasting metabolism was higher for the BX steers, thus excluding these as possible explanations.) No significant breed differences were observed in dry-matter digestibility, urinary nitrogen, or heat production; but the SH steers produced significantly more methane.

Garrett (1971) observed that Holstein steers had an approximate maintenance requirement that was 5-percent higher than that of Herefords in one trial, and 12-percent higher in another. Other studies have not demonstrated differences in maintenance between breeds.

Klosterman, Sanford, and Parker (1968) found that maintenance requirements of Hereford and Charolais cows were proportional to body weight. Similar inferences can be drawn from studies at Fort Reno, Oklahoma (Ewing *et al.*, 1968), and the Texas Agricultural Experiment Station (Melton, Cartwright, and Kruse, 1967), in which cows of markedly different weights of either the same or different breeds were fed individually in dry lot for extended periods. In all cases, however, these cows were lactating for portions of the year, thus making maintenance estimates rather uncertain.

Stonaker *et al.* (1952) compared Hereford females of three sizes (large, intermediate, and compact) and found that, within age group, the amount of hay eaten per 1000 pounds of body weight maintained was independent of the size of the animal.

To summarize, evidence on genetic variability in maintenance requirements is scanty and conflicting. The most critical past studies strongly suggest the existence of such variability. In view of the fact that maintenance overhead represents such a large fraction of feed costs in beef production, further critical studies of sufficient scope to provide comprehensive parameter estimates are indicated. Klosterman (1972) observed that only 13 percent of the metabolizable energy fed to the cow and to the calf to attainment of the "slaughter condition" for approximate USDA average choice was recovered as net energy in the empty body at slaughter. Thus 87 percent was required for maintenance and other nonproductive functions. If a possibility exists for reducing this large fraction of production costs, we should be aware of it and develop methods for optimum breeding plans to take advantage of it.

SPECIFIC NUTRIENT REQUIREMENTS FOR NORMAL HEALTH AND PRODUCTIVITY

Will one animal maintain normal health and perform at an optimum rate when fed at one level of a specific nutrient or additive, while another animal of similar age and weight will require a higher level? Very little is known about this question in cattle. Field observations in England (Hignett, 1950) indicated that low dietary-phosphorus levels relative to calcium adversely affected reproduction. Guernseys were affected the most followed by Jerseys and Herefords; Friesians appeared to be the most tolerant, with Shorthorns and Red Polls next.

There is some evidence that, at least for some types, Zebu and Zebu crossbred cattle have a lower requirement for protein than European types (Elliott and Topps, 1963). This is expressed by the apparent better ability of the Zebus to survive on lower protein hays (Livingston, Payne, and Friend, 1962) and their ability to maintain normal protein metabolic processes under these conditions. The Zebu propensity to voluntarily consume more total feed on low-protein grasses and hays is probably a factor in their greater survival ability. The Commonwealth Scientific and Industrial Research Organization (CSIRO) group at Rockhampton, Queensland (Vercoe, 1966, 1967, and 1969; Vercoe and Frisch, 1970a,b) has made extensive studies of nitrogen metabolism in Brahman, Brahman × British crossbreds, and British types. Although greatly affected by live weight and by ration, the Zebu types tended to have higher plasma and urinary excretion of creatinine, greater urinary urea, and lower urinary ammonia. The observations are consistent with the concept that, under submaintenance conditions, Zebu-type animals may derive a higher proportion of their energy requirements from catabolism of tissue protein. When put under temperature stress sufficient to raise rectal temperature by 1.3 °C, both British and Brahman × British crosses increased urinary nitrogen by similar amounts but the ambient temperatures for effecting the increase in rectal temperature were 31° and 45°, respectively.

At given environmental temperatures and levels of feed intake, water consumption of Zebus was found to be less than that of European breeds (Winchester and Morris, 1956). LeRoux (1952) in South Africa found that Africanders lost much less weight and reduced feed intake less than European exotics when water was withheld for 24 of 48 hours. Phillips (1960) reported a lower water requirement for Zebus compared to grade Herefords and a significantly smaller ratio of water drunk to hay eaten for Zebus. He concluded that Zebu steers seem to be better adapted to dry conditions and that the effect of limited water supply in reducing food intake will be less for Zebus. Thus, there is strong evidence that *Bos indicus* and *Bos taurus* have different water requirements.

SPECIFIC NUTRIENT REQUIREMENTS FOR OPTIMUM EFFICIENCY OF PRODUCTION

Nutrient requirements at productive levels for cattle may differ from simple maintenance requirements. For example, if there are two steers of the same age and body composition, could there be genetic differences that would permit one to gain 2 1/2 lb/d on a ration that was 10-percent protein while the other would require a 12-percent protein ration to achieve the same rate of gain? Innumerable similar questions for other nutrients and production situations could be raised.

No experimental work bearing directly on this question is known to have been done. It would appear that the problem is of sufficient potential economic importance to justify research to ascertain if differences exist.

METABOLIC PATHWAYS OF FEED UTILIZATION

Many experiments have shown that breeds differ markedly in carcass composition at either similar weights (Mason, 1971; Cole *et al.*, 1963) or similar ages (Bond *et al.*, 1972). There are also genetic differences within breeds in carcass composition (Shelby *et al.*, 1963). The references given are only a few of many that could be quoted and are given as entrees to the literature and as some of the more striking examples.

Thus, evidence shows conclusively that there are genetically determined metabolic differences in utilization of digested nutrients that lead to marked differences in product composition. Genetically determined differences in product composition are easy to demonstrate at comparable weights or ages; they are probably much less apparent at comparable stages of maturity. Unfortunately, the differences in physiological and biochemical mechanisms and pathways by which one animal produces proportionally more fat and another proportionally more lean tissue are almost completely unknown.

ABILITY TO CONSUME FEED

Regardless of efficiency or inefficiency of maintenance, the animal that consumes feed only at a level sufficient to maintain body weight is completely inefficient as a meat producer. With *ad libitum* feeding of any given ration every nonlactating, nonreproducing animal will reach this state at maturity. In the period prior to this, ability to consume feed at rates proportionally high above maintenance will contribute to gross or apparent efficiency.

Brown and Gifford (1962) reported heritability of feed consumed as 0.76 in Angus and Hereford bulls fed for 154 days in post-weaning tests in Arkansas. Brown and Gacula (1964) later reported a heritability of 0.43 for total feed consumption. Koch *et al.* (1963) found a heritability of 0.64 for feed consumed in a combined analysis of data from Angus, Hereford, and Shorthorn bull and heifer calves fed rather different types of rations in Nebraska and Oklahoma. Intake data were adjusted for differences in live weight in this study.

Swiger *et al.* (1961) found that heritability of feed consumption ranged from 0.07 to 0.77 depending on the length of the feeding period. Swiger *et al.* (1965) reported a heritability of 0.64 for daily total digestible nutrient (TDN) intake from an analysis of 480 calves in a heterosis experiment at Fort Robinson involving 9 breeding groups of Hereford, Angus, and Shorthorn straightbreds and their crosses.

Utilizing data from identical and fraternal twin females, Kress *et al.* (1971) found significant set by diet interactions for feed consumption, TDN consumption, and TDN consumption available for growth. The interaction accounted for about 4 percent of the total variation of these traits. One explanation for the significant interactions was the possible difference in capacity for feed consumption between sets.

Bogart and England (1971) found significant differences between lines for feed consumed by Hereford and Angus calves fed a completely pelleted ration composed of two parts alfalfa and one part concentrate. The calves were fed to gain 136.2 kilograms or until they reached 313.2 kilograms of body weight. The heritability of feed consumption was estimated as 0.38 ± 0.15.

Olbrich, Martz, and Hilderbrand (1973) found no difference in voluntary intake between Zebu and Scotch Highland heifers when compared at 9, 18, and 31 °C and fed high-roughage or high-concentrate rations. There was a significant breed–temperature–ration interaction for voluntary intake.

Several studies, Frisch and Vercoe (1969), Rogerson *et al.* (1968), Ledger *et al.* (1970), have found that Brahman and Brahman–British crossbred cattle have lower feed intakes than British breeds at comparable weights on rations of high-quality forage or rations high in concentrates, when all are maintained at ambient temperatures below those producing thermal stress. However, on low-quality forage rations, Zebu-type cattle have usually been observed to have a higher voluntary intake (Karue *et al.*, 1972). Also, at ambient temperatures above the stress level for British breeds but below those for Zebus, feed intake of the latter is usually higher (Vercoe and Frisch, 1970b).

Overall, it appears that genetic differences in voluntary feed intake are of a magnitude that makes selection rather effective. Genetically determined differences between Zebu types and the British beef breeds in feed intake are dependent in their expression upon type of feed and environmental conditions as regards temperature.

FEED REQUIRED PER UNIT OF GAIN IN LIVE WEIGHT AND CARCASS COMPONENTS

Evaluation of feed required per unit gain in live weight or per unit of carcass component, often referred to as efficiency of gain, presents many difficulties. Similar terms are often used with widely varying connotations in both industry and research reports. Gross differences in feed required per unit gain in either live or carcass weight are dependent upon many factors including types of feed, temperature, and other environmental conditions; live weight during the period evaluated; composition of gain; state of health; and perhaps others. Thus, we will attempt to consider feed requirements taking proper note of these.

Over a period of many years, rather large differences in feed required per unit of live-weight gain have been observed both within and between breeds and types. Mason (1971) has reviewed and summarized a massive amount of data, including that on efficiency of live-weight gain, on the large dairy and dual-purpose breeds of Europe. Usually, although there are exceptions, the larger, faster growing types have required less feed per unit of live-weight gain than slower growing kinds when evaluated over reasonably comparable age and size ranges.

A number of studies in the United States comparing British breeds with straightbreds (a few cases) of the muscular, fast-growing continental European breeds or crossbreds of these breeds with British breeds have consistently shown more efficient live-weight gain in time-constant feeding periods for the continental European breeds and their crosses (Lasley, 1968; ARS–USDA, 1974). In each of these cases, the fast-growing types and their crosses were less fat at the end of the trial. Klosterman, Cahill, and Parker (1968) reported no significant differences in efficiency between Hereford, Charolais, and Hereford–Charolais crossbred steers when fed to similar degrees of fatness. Brungardt (1972) found no difference in efficiency between Charolais and British breeds when fed to the same degree of finish.

Many trials have shown Holstein steers to be more efficient in live-weight gain than British types (see Bond *et al.,* 1972, for an example and references to earlier work) when fed through comparable time-constant, age-constant, or weight-constant periods. Here, too, the grossly more efficient dairy types were less fat at the termination of the trials.

Heterosis effects on different measures of feed efficiency were summarized by Cundiff (1970); they were found to be small and generally not significant.

The importance of genotype–environment interactions in cattle is not well documented. Pani and Lasley (1972) and Warwick (1972) have summarized the existing information on the importance of genotype–environment interactions on feed efficiency. Genotype–environment interactions appear to be important, but the studies carried out cover only a limited range of environments and management systems. If genotype–environment interactions are real for feed efficiency and nutrition of beef cattle, then the selection and testing of animals should be done under the environments where they are to be maintained. The comparison of feeds and management systems would logically be made on animals similar to those recommended for use by industry.

Within breed a number of studies have indicated a reasonably high heritability for differences in feed required per unit of live-weight gain. [See Petty and Cartwright (1966) for a detailed listing of studies to that date and Koch *et al.* (1963) for one of the more definitive individual studies.] Most of these studies have been on *ad libitum* feeding regimes, making it difficult or impossible to determine whether observed differences are due merely to the apparently more efficient animals consuming more feed over that required to meet maintenance requirements or to true differences in efficiency. Further, in many of the studies carcass composition has not been determined. In order to eliminate the feed intake variable, Fitzhugh and Cartwright (1971) fed steers of 18 half-sibling groups, restricting feed consumption to the minimum expected for any contemporary steer. Significant differences in gain between half-sibling groups suggested that additive genetic variation existed for efficiency of feed utilization; however, composition of gain was not reported. Varying fat content of tissues produced may be related to apparent efficiency.

If genetic differences in true maintenance costs are small, the cattle breeder need not consider these differences in breeding programs. Rather, he should emphasize ability to consume feed at high levels, ability to use net energy consumed for production of the product or combination of products most desired, and mature sizes optimum for minimizing total feed requirement at the desired slaughter weight. Critical research is needed to establish or disprove the assumption made above. If proven to be essentially correct, computer simulation will serve as a key factor in guiding decisions in selection programs or in combining breeds for maximum economic efficiency, even though differences in true biological efficiency may be minimal.

SUMMARY AND CONCLUSIONS

Genetic variability in efficiency of production per unit of feed consumed in cattle may occur in several ways. Differences in ability to digest nutrients is one of these. The evidence is that genetic differences in ability to digest feedstuffs are nonexistent or of small magnitude. Another way in which genetic differences may be expressed is as nutrient requirements for maintenance. Such variability is suggested by available data, but the evidence is scanty and conflicting.

Other possible sources of genetic variation are specific nutrient requirements for normal health, productivity, and optimum efficiency of production. Here again, the evidence for genetic variation within breeds does not seem to be available; whereas some evidence of breed differences does exist.

Genetically determined metabolic differences in uses of digested nutrients have been clearly demonstrated, but virtually nothing is available on the physiological and biochemical pathways by which different animals produce differences in proportions of fat and lean.

Genetic variation in voluntary feed intake and in feed required per unit of live-weight gain has been clearly established within and between breeds.

If genetic differences in true maintenance costs are small, the breeder should emphasize ability to consume feed at high levels, ability to use net energy consumed for production of the products desired, and mature sizes optimum for minimizing total feed requirement at the desired slaughter weight.

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Genetic Variation in Nutrition of Dairy Cattle

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Feed costs are a major part, perhaps 35–55 percent, of the total cost of milk production, and cows respond to differences in amount and type of diet. Selection applied to populations of dairy cattle has produced a genetic increase in milk production. Major research efforts have been applied to nutritional and genetic problems related to the ability of dairy cattle to produce food. These research disciplines have largely, but not completely, approached problems independently; consequently, the knowledge relating genetic variability to how cows use nutritional inputs is limited. Considerable work has been done, however, in two broad and important areas: (1) genetic differences in gross feed efficiency and (2) genotype by feeding regime interactions.

The general lack of knowledge concerning genetic effects on nutrient utilization in dairy cattle is not surprising. Large numbers of observations are usually needed to accurately measure quantitative genetic differences, and most genetic-nutritional relations that have been investigated are quantitative. Most nutritional work requires relatively detailed observation of each cow; obtaining this kind of detailed knowledge on large numbers of animals is expensive. Energy and protein levels are normally the most critical part and make up the largest and most expensive part

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of the diet of dairy cows. The utilization of these nutrients depends, to a large extent, on rumen function and the microbial alteration of feed in the rumen. Because of the latter, studying genetic differences for individual nutrients is difficult. This is probably why most genetic input has been applied to the less specific aspects of the problem like gross feed efficiency or commonly used feeding regimes.

Nutrient requirements for dairy cattle are given by the Subcommittee on Dairy Cattle Nutrition (National Academy of Sciences, 1971). The requirements are given relative to acceptable standards of growth, levels of production, maintenance needs, and reproduction. It is well-known that genetic differences exist in milk production and growth. The evidence for this is the large number of heritability estimates that are greater than zero for various measures of milk production, including the solid components of milk (Wilcox *et al.,* 1971), and growth or body weight at different ages. That genetic differences exist among cows in the ability to produce milk and nutrient requirements differ by levels of production implies that genetic differences exist among cows in the ability to use feed for milk production. This has now been demonstrated since the heritability of gross feed efficiency is estimated at 0.3–0.5 percent, as will be discussed later. The NRC publication on nutrient requirements for dairy cattle (National Academy of Sciences, 1971) states that "variation among animals in ability to digest feed is relatively small, but large differences exist in feed capacity, appetite, growth rates and level of milk production." The evidence that "variation among animals in ability to digest feed is relatively small" is not clear. Certainly, large variation has been observed for coefficients of digestibility between cows. It seems important to quantitate this statement because the magnitude of this variation might be important in deciding future research objectives. However, if the variation among animals to digest feed is small, then other physiological attributes seem to contribute to heritable differences in gross efficiency.

GENETIC DIFFERENCES IN DIRECT MEASURES OF EFFICIENCY

The ability of dairy cattle to convert feed into milk has generally been termed *feed efficiency*. Many ways to measure physiological efficiency have been proposed and are useful. Gross energetic feed efficiency, or some ratio of the energy produced in milk to the total energy consumed by the animal, seems to be the only measure for which genetic differences have been observed. This is one of the easiest measures of efficiency, and—because relatively large numbers of cows are needed to measure genetic differences—it is not surprising that this method has been used. Also, if any use is to be made of the information in practical selection, the measure must be relatively easy to use so enough cows can be measured to practice selection effectively. As different measures of efficiency are discussed, they will be defined briefly in the text or tables where a brief definition can be found associated with reference numbers.

Breed Differences

Most studies of efficiency have been conducted with a single breed. Breed comparisons from different data sets are likely to be misleading, unless the work was designed to make such comparisons.

Using data from 57 Ayrshire (A), 68 Brown Swiss (S), and 57 Holstein (H) cows that produced contemporarily in the Beltsville herd, Dickinson *et al.* (1969) concluded that the differences between these breeds were real for efficiency [100 × (energy in milk)/(energy in feed)]. Even though the number of cows was small for each breed, the cows were purchased to be representative of the breeds and were sired by 36 Ayrshire, 48 Brown Swiss, and 40 Holstein bulls. Brown Swiss were the least efficient (54.3 percent), Ayrshires were next (60.3 percent), with Holsteins the most efficient (61.0 percent). Brown Swiss differed significantly ($P<0.01$) from the other two breeds. At a given body weight, chest girth or wither height, Holsteins were more efficient (Pg;0.05) than the other breeds. Breed differences should be investigated more extensively, particularly for efficiency of feed conversion from such diverse sources as roughage and grain.

Heritabilities

Heritability estimates of feed efficiency for milk production, the measures used, and sources of these estimates are given in Table 1. Heritability is the ratio of the additive genetic variance in the population to the total variance. The latter includes both environmental and genetic portions of the variation. Operationally, heritability is the fraction of the selection differential, or the total selection practiced, that is expected to result in genetic improvement in the next generation. The estimates in Table 1 are not all independent, since parts of some data sets are included in more than one estimate. It was not possible to separate unique sets of data from the published reports. No estimates found in the literature were omitted.

The data in Table 1 indicate heritability of feed efficiency is greater than zero and is, in fact, relatively large. The definitions of efficiency different among studies, but all were attempts to measure a ratio of energy input to energy output. The data are from Norway, Sweden, and the United States and represent several breeds of cattle with differing housing systems, management, diet, etc. Some of the details and conditions concerning these heritability estimates have been discussed critically by Freeman (1967) in a previous review of this subject. In the work done by U.S. Department of Agriculture (USDA) workers (Plowman, personal communication, 1967; Hooven *et al.,* 1968, 1972; Miller *et al.,* 1972a; Miller, 1972) cows were fed to approximately 115 percent of Morrison's (1957) standards considering needs for production and maintenance. Estimated net energy (ENE) was not determined directly but from published values for the feeds used. Milk production was adjusted to a fat-corrected basis (FCM) to account for differences in milk composition.

Cows were generally fed according to needs by some standard in all of the references cited, and in all studies allowances were made for changing production. The feeds comprising the diets differed. All cattle received liberal amounts of roughage plus concentrates, and dietary energy was changed through lactation by adjusting the concentrates fed.

Hooven and Matthews (1958) found significant differences between six sire progeny groups in gross feed efficiency. These differences were also significant when production was treated as a covariate, indicating that differences between sires were significant with milk yield held constant. Repeatability (the correlation between successive lactations of the same cow) of efficiency was about two-thirds the magnitude of milk yield.

TABLE 1 Heritability Estimates of Feed Efficiency for Milk Production

Measure	Estimate	Source
FCM/FU Consumed	0.48 ± 0.07	Mason *et al.* (1957)
FU/kg Butterfat	0.40	Venge (1956)
Production FU/kg butterfat	0.23	Venge (1956)
FCM/therm NE Consumed	0.45	Plowman (Personal communication, 1967)
TDN/45.4 kg FCM	0.20 ± 0.41	Gray (Personal communication, 1967)
TDN/45.4 kg FCM	0.36	Gray (Personal communication, 1967)
FCM/100 FU-Calculated index	0.12	Syrstad (1966)
FCM/Total ENE	0.46 ± 0.10	Miller *et al.* (1972a)
FCM/ENE Consumed	0.56 ± 0.07	Hooven *et al.* (1972)
FCM/ENE	0.46	Miller (1972)
FCM/FU Consumed	0.39	Gjelstad (1953)

NOTE: FCM=fat-corrected milk; FU=feed unit; NE=net energy; TDN=total digestible nutrients; ENE=estimated net energy.

The data summarized in Table 1 leave little doubt that genetic differences within breeds are large enough that genetic progress could be made if selection is practiced for increasing feed efficiency for milk production. Also, nutritionists can expect cows to make greater or smaller responses in efficiency because of their genetic ability. These conclusions seem true, generally, for several breeds in different management conditions when fed different feeds, although all feeding was generally according to need and for rather different measures of efficiency, as seen in Table 1.

Crossbreeding

Heifers of the Ayrshire, Brown Swiss, and Holstein breeds were the foundation cows for a crossbreeding experiment reported by McDowell and McDaniel (1968). Breed comparison of these samples of the breed were those discussed earlier by Dickinson *et al.* (1969). All possible two-breed crosses were produced from these three breeds. Three-breed crosses were produced by mating two-breed cross females to the breed of a sire not represented in the two-breed cross females. The crossbred progeny were reared on a normal diet of grain, hay, and corn silage. During lactation, cows were offered 10 percent in excess of Morrison's net energy standards. Hay and corn silage was offered to appetite, and concentrates were supplied to make up the difference between the amount of energy consumed from roughage and the calculated requirements based on body weight, milk yield, and percentage of fat.

These results (McDowell and McDaniel, 1968) are for first lactations. Three measures of feed efficiency were used: (1) total therms produced/total therms consumed; (2) kilogram FCM/therm ENE consumed; and (3) estimated protein yield/estimated feed protein consumed. These three measures of efficiency essentially ranked crossbred groups the same and, for all practical purposes, can be considered as one. These measures of efficiency are not independent because of a part-whole relation and because parts of each measure were calculated from estimated values.

For yield traits, the Ayrshire, Brown Swiss, and A × S crosses were significantly lower than the other six groups. The differences in yield traits among Holsteins, two-breed crosses that were half Holstein and all three-breed crosses were small and nonsignificant. The A × H, S × H, and three-breed crosses were generally superior to all purebreds for the three measures of efficiency. The energy content of the milk between these groups and Holsteins compensated for the 4–7 percent lower milk yield. Heterosis (differences between crossbred performance and the average of the parental breeds) for production traits was a positive 8–10 percent for the A × H and S × H and slightly negative for the A × S cross. The level of heterosis for efficiency traits was about half that for production in the A × H and S × H crosses and zero for the A × S cross. Generally, three-breed crosses showed more heterosis than two-breed crosses for both production and efficiency, but the three-breed cross data are difficult to interpret because all reciprocals were not available. Knowledge of the amount of heterosis between breed crosses is useful in considering alternative breeding programs and indirectly indicates type of gene action; however, the performance of breed crosses relative to the best of the purebreds is of immediate concern. When data from the Ayrshires, Brown Swiss, and all-breed crosses were expressed as a difference from the contemporary Holstein average, the following resulted; (1) All groups were inferior to Holsteins in milk yield; (2) the A, S, and A × S were significantly below the Holstein's mean in production and efficiency; and (3) the A × S, S × H, and three-breed crosses were slightly lower in milk and FCM but generally superior in fat yield and the three measures of efficiency. A comparison of the economics of these crosses had not yet been made.

Plowman and Hooven (1963) compared feed efficiency in growing heifers (lb gain/therms consumed) from 12 to 16 months with first lactation production and efficiency. They used outbred, linebred, A × H and S × H crosses. All heifers received hay *ad libitum* and 1.4 kg concentrates per day. There were differences between groups and sires within groups for gain and therms consumed but no real differences in efficiency of gain. In FCM yield, the linebreds, outcrosses, and A × H did not differ from each other but did differ from the S × H. Similar results were found for gross feed efficiency (FCM/ENE consumed). The within-sire and group correlations between growth traits (including efficiency) and production and between production and efficiency were nonsignificant except for a negative correlation between therms consumed for growth and FCM. These data suggest little relation between growing efficiency and production efficiency. Using the same data but with slightly fewer numbers and a different analysis, Hooven *et al.* (1964) found a significant correlation of 0.21 between efficiency of growth and gain from 12 to 16 months.

Martin and co-workers at Purdue have investigated the effects of crossbreeding with breeds not commonly used in the United States. Scott and Martin (1963) used dual-purpose cattle to determine the effects of crossbreeding on various expressions of feed efficiency and growth. Red Dane, Red Poll, and Milking Shorthorn cattle were mated to produce purebreds, all possible two-breed crosses and three-breed crosses (half one breed and a quarter each of the two other breeds); 110 steers were fed for

22 weeks starting at 227 kilograms. Three-breed crosses were superior to two-breed crosses who were superior to purebreds in feed required per kilogram of gain in feed required per kilogram of gain over maintenance requirements, and in gain per day. These differences were not generally significant, but agree with most results in beef cattle indicating substantial heterosis and crossbred advantage in gross efficiency.

T. G. Martin (personal communication, Purdue University, 1973) has preliminary results from a Holstein–Red Dane crossbreeding experiment. Generally, analyses of body size data showed nonsignificant heterosis in females. In steers, heterotic effects were significant in about half of the analyses of body measurements and weight at different ages. Steers were fed more liberally than females. Feed efficiency (kg gain/kg feed) showed about 6 percent heterosis, but the differences were not significant. In lactation comparisons, Holsteins produced more milk (about 907 kg), consumed more feed and were more efficient than Red Danes. Crossbreds consumed 279 kilograms more feed and produced 843 kilograms more FCM, which resulted in a superiority in efficiency of 8.5 percent over purebreds and 2.1 percent over Holsteins. These comparisons relating to lactation were generally significantly different. Preliminary results from the Red Dane–Holstein experiment indicate that 90 percent of the variance in feed consumption is explained by FCM production and the three-fourths power of body weight. In general, the crossbreeding work shows some heterosis in gross feed efficiency for growth and production, particularly when the Holstein is included. This indirectly indicates some nonadditive genetic effects on efficiency. The economic value of this heterosis is questionable because of the high production level of the Holsteins.

Sampling Parts of the Lactation to Estimate Total-Lactation Efficiency

Determining feed efficiency for a total lactation is expensive, so an obvious question is whether data collected from portions of the lactation can be effectively used to estimate total-lactation efficiency. Gross efficiency generally declines as lactation progresses (Miller and Hooven, 1969). Body weight change affects efficiency as body stores are either catabolized or replenished. Other variables, usually handled as classification variables in most analyses, affect efficiency. Parity number has a large effect in most studies; days not pregnant and year and season of calving are usually shown to have a relatively minor effect on gross efficiency during lactation.

Hooven *et al.* (1972) estimated genetic parameters for part lactations.

They estimated the heritability of whole-lactation (total-lactation) gross efficiency to be 0.56 ± 0.07. The estimates for part-lactation efficiencies were 31–60 days, 0.44 ± 0.07; 121–150 days, 0.44 ± 0.07; and 181–210 days, 0.34 ± 0.07. The day intervals are the periods for which data were used.

Genetic correlations between part- and total-lactation efficiencies indicate the extent to which the same genes control efficiency through the lactation. The correlations between total lactation and the three sampling periods were 0.81, 1.00, and 0.94; between 31–60 days and the last two periods, 0.88 and 0.61; and between the last two periods, 0.94. These data indicate that efficiency is partly controlled genetically for segments of lactation, and there is some indication that different genes control efficiency at different times during lactation (genetic correlation, $r_G < 1.0$). These results come from 306 daughter–dam pairs with 276 degrees of freedom within sires, so additional data are needed to substantiate these conclusions.

The relative efficiency of selection for total-lactation feed efficiency from part-lactation data was estimated by Hooven *et al.* (1972). The estimated relative efficiencies of selection were 0.72 for 31–60 days, 0.89 for 121–150 days, and 0.73 for 181–210 days. If selection were practiced to improve efficiency, collection of data for the 30-day period only, from 121-150 days, where the relative efficiency of selection is nearly 90 percent, would seem desirable so that more cows could be evaluated for the same expenditure.

Laflamme (1972) used feed intake from 90–150 days to study intake and efficiency and considered model building with many variables calculated from the input and output measures. No genetic inferences were possible from these data.

The work considered on sampling part lactations to estimate total-lactation efficiency addresses an important question. More evidence is needed than is now available to answer this question for one lactation. Shouldn't such information, including correlated response, be known for lifetime production?

GENETIC DIFFERENCES IN CONSUMPTION

Ability to consume large amounts of forage and grain is necessary to achieve and sustain high levels of production. Much research effort has been expended relating appetite or consumption to growth or production responses on many dietary regimes. Most of these have made nutritional comparisons without relating them to genetic differences; substantial amounts of work, however, have been done where genetic inferences can be made. Only the latter type of work will be considered.

A gross indication of genetic control over a trait is the difference between breeds. Contemporary comparison of breeds with cows being representative samples from the breeds, particularly when small numbers of cows are compared, is usually needed to make valid inferences. Also, the way various feeds are offered may influence the results. Legates *et al.* (1956a) compared the consumption of alfalfa hay by Ayrshire, Guernsey, Holstein, and Jersey cows where grain provided 40 percent of the maintenance requirement. Breed differences in hay consumption per 27 kilograms of body weight were significant. The number of cows from each breed was small. In the experiment of McDowell and McDaniel (1968), the cows chosen to be representative of the Ayrshire, Brown Swiss, and Holstein breeds were fed 10 percent in excess of needs. The percent ENE consumed was nearly the same for each breed, but the Brown Swiss were lower in efficiency.

Mather (1960) wrote an excellent summary and review of the literature addressing the question, "Can dairy cattle be bred for increased forage consumption and efficiency of utilization?" The data available then indicated that repeatability (correlation between repeated measurements on the same cow) of roughage consumption from month to month within a year was about 0.5; from month to month across years, about 0.2; and yearly averages, about 0.4. Because of differences in the methods and times of collection, it was difficult to pool all the estimates; however, some of those assembled by Mather (1960) and from other studies are given in Table 2. Mather (1960) answered the question that was the title to his talk in the affirmative but clearly stated some of the unknowns and the need for more evidence.

Additional evidence since Mather's (1960) paper was reviewed by Freeman (1967). Freeman considered the additional work of Stone *et al.* (1960), who pooled the results from 12 forage experiments; Gray *et al.* (1967); and Plowman (Personal communication, USDA, 1967). Details of the work of these authors will not be repeated, but collectively these studies indicate that repeatability is large enough for cow culling to be effective in improving consumption and that selection for improved consumption would be effective. The total numbers of animals represented in these studies to this time were not large.

Several good experiments have been reported since 1968, which clearly show genetic difference in nutrient consumption. A summary of some of the repeatability and heritability estimates from these and earlier work is given in Table 2. The times, relative to the lactation period, during which food intake was measured, vary in the studies reported. Estimates were given separately for the forage, grain, and total intake in some experiments and only for one of these three in others. Different breeds were included, although most of the estimates were from Holsteins. In all studies, the estimates were made within breeds. The cows were fed according to estimated requirements for production and maintenance in nearly all the reported work. Forage was offered free choice in most experiments, and the difference between the nutrients supplied and those needed was adjusted by the amount of grain fed. The repeatabilities in Table 2 are generally high, ranging from 0.22 to 0.86, and depend on the lactation period during which intake was measured. Repeatabilities of adjacent weekly or monthly intakes are higher than the correlation between intakes over longer periods of time. The heritabilities, in general, are clearly greater than zero, indicating that a substantial portion of the total variation in feed intake is controlled by largely additive genetic effects. The variation in these estimates is expected because of the small number of cows used to compute each estimate, because of differences in measures, and because of some inaccuracies of measurement. No zero estimates

TABLE 2 Heritability and Repeatability Estimates of Food Intake

Measure	Repeatability	Heritability	Source
Weekly forage intake	0.70		Stone *et al.* (1960)
3-Month forage dry-matter intake	0.32	0.09 (daughter–dam) 0.23 (paternal half-sibs)	Gray *et al.* (1967)
Therms intake per lactation	0.45	0.21 (first lactation) 0.45 (all lactations)	Plowman (Personal communication, 1967)
28-Day total feed intake from fourth to eighth month	0.71 ± 0.86	(first lactation)	Griffin *et al.* (1971)
Forage consumption/454 kg body weight	0.54	(monthly values in same year)	Mather (1960)
Forage consumption/454 kg body weight	0.37	(yearly averages)	Mather (1960)
Forage consumption/454 kg body weight	0.22	(monthly values–any year)	Mather (1960)
Grain consumption		0.26 ± 0.09	Miller *et al.* (1972a)
Forage ENE		0.19 ± 0.09	Miller *et al.* (1972a)
Forage ENE/grain		0.12 ± 0.08	Miller *et al.* (1972a)
Total ENE		0.42 ± 0.10	Miller *et al.* (1972a)
Forage ENE/$W^{0.75}$		0.03 ± 0.09	Miller *et al.* (1972a)
Therms consumed/lactation		0.26 ± 0.06	Hooven *et al.* (1972)

of either repeatability or heritability were found in the literature, but such estimates may not be reported even if found.

The relation between total- and part-lactation feed consumption was investigated by Hooven *et al.* (1972) and gives a good picture of consumption through lactation. This work is based on 425 first lactations. Total ENE consumed was lowest (601 Mcal) the first 30 days of lactation, increased to a maximum of 734 Mcal for the 61–90- and 91–120-day periods, and gradually and consistently declined to 647 Mcal for the 271–300-day period for Holsteins. Large differences in consumption were associated with parity; differences in consumption were also associated with years, seasons, and body weight (Gray *et al.*, 1967; Hooven *et al.*, 1968). The phenotypic relations between part- and total-lactation ENE consumption and gross efficiency were very similar. Correlations between ENE consumed in adjacent periods of 30 days through lactation ranged from 0.75 to 0.91. Correlations between the 10 parts and total lactation ranged from 0.51 to 0.87. The four 30-day periods from day 60 through 180 all had phenotypic correlations of over 0.7 with lactation total consumption. Results very similar to these were reported by Griffin *et al.* (1971) who analyzed 225 first lactation records of daughters of 13 sires.

The genetic correlations between consumption in parts and all of the lactations were generally high. Griffin *et al.* (1971) found genetic correlations of 0.71–0.86 from the fourth to eighth month with lactation total intake. These correlations were all greater than the 0.76 correlation between the 30-day sampling periods and total lactation consumption in the work of Hooven *et al.* (1972).

CORRELATED RESPONSES

A discussion of quantitative genetic effects on the use of nutrients by dairy cattle must consider correlated responses of economic traits associated with feeding cows. Milk production and changes in body weight are joint responses to nutrient intake. The heritability of milk and milk fat yield is generally considered to be about 0.2 to 0.3. The fat, protein, solids-not-fat, and total solids components of milk, when expressed as a percentage of total yield, have been shown to be rather highly heritable, about 0.3 to 0.6. Further, these components were correlated both phenotypically and genetically, and these parameters are estimated rather precisely by the interregional study on milk composition (Wilcox *et al.*, 1971). Body weight at given ages and changes in body weight are heritable (Touchberry, 1951; Johansson, 1954; Hooven *et al.*, 1968; Miller and Hooven, 1969). The output traits (milk yield, milk

TABLE 3 Phenotypic Correlations among Measures of Consumption, Efficiency, Yield and Weight

	Consumption			Efficiency				Weight			
Trait	Grain	Forage	Total ENE	FCM/FU	FCM/100 FU Maintenance	FCM/ENE (Mcal)	TDN to Produce 100 lb FCM[a]	Average Body Weight	Heart Girth	Weight Gain	End of Lactation
Yield											
FCM	0.83^{b}	0.10^{b}	0.72^{b} 0.68^{c}	0.82^{d}	0.95^{e}	0.82^{c}	-0.71^{f}	-0.11^{d} 0.44^{g}	0.02^{e}	-0.53^{g}	
Milk	0.83^{b}	0.10^{b}	0.70^{b}	0.84^{i}				0.01^{d} 0.42^{g}		-0.53^{g}	-0.17^{h}
Consumption											
Grain		-0.23^{b}				0.74^{b}		-0.18^{b}		-0.48^{b}	
Forage						-0.32^{b}		0.49^{b}		0.08^{b}	
Total ENE	0.58^{b}	0.66^{b}				0.17^{b} 0.14^{c}		0.41^{b}		-0.28^{b}	0.27^{h}
Total therms								0.64^{g}		-0.33^{g}	
TDN Intake							-0.20^{f}				
Efficiency											
FCM/FU								-0.10^{d}			
FCM/100 FU Maintenance									-0.29^{e}		-0.41^{h}
FCM/ENE therms								-0.04^{g}		-0.51^{g}	
TDN To produce 100 lb FCM								0.08^{f}			

[a] Sign differs because of definition.
[b] Miller *et al.* (1972a).
[c] Hooven *et al.* (1972)
[d] Gjelstad (1953).
[e] Syrstad (1966).
[f] Stone *et al.* (1960).
[g] Hooven *et al.* (1968).
[h] Miller *et al.* (1972b).
[i] Mason *et al.* (1957).

composition, and body weight and body weight change) are not individually controlled by independent sets of genes; rather, many of them have genes in common which influence their expression. That is, they are genetically correlated. The practical result of two traits being correlated genetically is that, if selection for only trait one is effective in changing trait one, then an automatic change in trait two can be expected without any selection being purposely applied to trait two. Phenotypic correlations simply measure the degree of association of two traits in the same animal.

The previous discussion has dealt with genetic influences on forage consumption, grain consumption, and total consumption on both a total- and part-lactation basis. As will be discussed later, these input traits are also correlated genetically. Efficiency deals with both input and output traits and, as expected, is genetically correlated with both input and output traits. Even though data are not available from large populations of cows under commercial conditions, it is clear that the genetic relation among the physiological traits that collectively control nutrient use in dairy cows is indeed complex. Some of these relations have been studied and will be considered next. The total complex of these traits should be considered in both genetic and nutritional studies, even though the experiment concentrates primarily on one trait.

In general terms, yield and efficiency are expected to be functionally related. They are, of course, part-whole related, but the amount of milk that cows produce will vary much more than the amount of feed they consume, under normal conditions, and will force efficiency to be dependent on yield. McGilliard (1959) pointed this out and discussed this general dependence. As yield and feed level increase, the proportion of feed consumed that is used for maintenance requirements becomes less. The other major variable is body weight or its change.

Part or all of the relation between yield, consumption, gross efficiency, and body weight has been investigated by many people. Estimates of some of the published phenotypic and genetic correlations among nutritional inputs, outputs, and efficiency are summarized in Tables 3 and 4. Estimates including the same data were not included in these tables where it was possible to avoid them, but it was not possible to separate all of them. Additional evidence concerning these relations is available, but is not easily summarized in tabular form. Most of these data came from experiments where the cows were fed according to estimated nutrient requirements based on immediate past production and body weight. The diets could generally be considered as common ones for the areas where the experiments were conducted. The association

TABLE 4 Genetic Correlations Among Measures of Consumption, Efficiency, Yield and Weight

	Consumption				Efficiency				Weight		
Parameter	Grain	Forage	Total ENE	Therms	FCM/FU	FCM/100 FU Maintenance	FCM/ENE Mcal	FCM/ENE Therms	Average Body Weight	Heart Girth	Weight Gain
Yield											
FCM	1.0^a	0.32^a	0.82^a 0.86^b 0.83^c	0.89^d	0.94^e	0.88^f	0.93^b	0.88^c	0.29^e 0.28^d -0.11^c	-0.08^f	-0.77^c
Milk	1.0^a	0.20^a	0.77^a 0.76^c	0.86^d	0.95^g			0.86^c	0.19^e 0.30^d -0.12^c		
Consumption											
Grain		0.33^a					0.90^a		-0.21^a		-0.95^a
Forage							-0.11^a		0.93^a		0.26^a
Total ENE	0.84^a	0.80^a					0.50^a	0.47^c	0.44^a		-0.43^a
Total therms							0.61^b	0.64^d	0.44^c 0.80^d		-0.39^c
Efficiency											
FCM/FU									0.13^e		
FCM/100 FU Maintenance										-0.55^f	
FCM/ENE Therms									-0.17^d -0.51^c		-0.88^c

[a] Miller *et al.* (1972a).
[b] Hooven *et al.* (1972).
[c] Miller (1972).
[d] Hooven *et al.* (1968).
[e] Gjelstad (1953).
[f] Syrstad (1966).
[g] Mason *et al.* (1957).

among traits might be different if a constant amount of feed or more liberal grain or roughage were offered, or if some other system of feeding were used. At present there seems to be no direct evidence of the effect of different feeding systems on the genetic control of associated traits.

Phenotypic correlations measure the degree of association between traits that is caused by both genetic and environmental effects. The correlations in Table 3 indicate the phenotypic association among different measures of yield, consumption, efficiency, and weight. The correlations between yield and consumption and between yield and efficiency are generally high, about 0.6–0.95, except forage intake with yield. Total ENE is highly correlated with grain and forage intake, as expected. Grain and forage intake are negatively correlated because the cows were fed so that the difference between requirements and total consumption was met by varying the amount of grain offered. It seems the feeding regime induced this correlation; this, however, is not a criticism of the work because estimation of this correlation was not the objective of the study. Correlations between measures of consumption and efficiency were low except for grain consumption and efficiency. The correlations between measures of weight and yield, weight and consumption, and weight and efficiency are quite variable. Generally, weight gain is negatively associated with efficiency, yield, and consumption. Average body weight was measured at different times in the studies summarized; even so, considering the data in Table 3 and other work, the phenotypic correlation between body weight and yield is probably positive and small. Average body weight and grain consumption are negatively correlated, and most measures of weight or weight gain with efficiency seem to be negatively correlated.

Knowledge of the correlation among the traits given in Table 3 should be useful in designing experiments where response to any of these traits is of concern. Cows are often allocated into subclasses, such as blocks in a randomized complete block design, based on early lactation yield of milk or FCM. Because of the high correlations between yield and consumption and yield and efficiency, the blocking on yield is also reasonably effective in blocking for consumption and efficiency. This may or may not be desirable depending on the objectives of the work.

Genetic correlations measure the net effect of pleiotropic genes, that is, those genes that affect more than one trait. Genetic correlation estimates are in Table 4. Because of the limited number of animals involved, their standard errors can be expected to be large, especially for r_G estimates not close to ± 1.0. For traits not involving weight, the genetic correlations are generally similar in sign to the phenotypic correlations and larger in magnitude. The genetic correlations involving yield, efficiency, and consumption are large except for those including forage intake. Even for forage consumption, the genetic correlations are larger than the corresponding phenotypic ones. It can be concluded, on the basis of these limited data, that the same genes affecting yield also exert major effects on consumption and efficiency. Most of the genetic correlations between body weight and yield and between body weight and consumption are positive. The latter correlation tends to be somewhat larger than the former. The genetic correlations between weight gain during lactation with yield, consumption, and efficiency are all large and negative, except for forage consumption and weight, which is estimated as 0.26 from one study.

The relation of weight with other variables is difficult to interpret. Weight (or change in weight) from animal to animal or from time to time for the same animal probably represents large differences in body composition because of the proportion that is body fat or metabolic water. This, of course, represents large differences in the amount of energy required to change body weight.

The correlations in Tables 3 and 4 give general relations among the variables. The genetic correlations among yield, efficiency, and consumption are generally large and positive. This suggests that selection for any one would produce a generally positive effect in the other traits. If selection were to be practiced for increased yield and efficiency and decreased consumption, the heritabilities and genetic and phenotypic correlations could be used to indicate what progress would be expected. Average body weight tends to be positively associated with yield and consumption, but negatively associated with efficiency. Heavier weight per se is not necessarily desirable, particularly when it is negatively correlated, phenotypically and genetically, with efficiency.

The relations among some of these variables tend to be nonlinear in much of the reported work where nonlinearity has been investigated. The intrasire regression of efficiency on average body weight in first lactations was distinctly quadratic in the work of Hooven *et al.* (1968). Cows with a body weight of about 550 kilograms were distinctly more efficient (FCM/therms ENE) than either heavier or lighter cows. Efficiency increased about 4 percent as body weight increased from 450 to 550 kilograms, but decreased about 10 percent as body weight increased from 550 to 700 kilograms. Miller and Hooven (1969), whose data include that reported by Hooven *et al.* (1968), showed that the regression of efficiency for average body weight was nonlinear for 30-day segments and for total lactation. The general shapes of the curves peaked at intermediate body weights, except for the 31–60 day segment of the lactation. Dickinson *et al.* (1969) found linear regressions of efficiency for body weight for each of the Ayrshires, Brown Swiss, and Holstein breeds. The regressions of efficiency for weight gain and chest girth were not linear, but the regressions of efficiency for wither height and body length were. Working with associations among measures of economic efficiency, Miller *et al.* (1971) showed the regression of income over feed cost for body weight to be quadratic, peaking at 500–550 kilograms of body weight in first lactations. Although not all work is in complete agreement on the nonlinear relations among these variables, there seems to be sufficient evidence to consider many of the phenotypic associations involving weight to be quadratic.

Many authors have considered the correlated response in feed efficiency when selection is only for yield. Because these traits are highly correlated genetically and because the heritability of each is positive, selection for only one trait would be expected to automatically improve the other, and vice versa. Freeman (1967) summarized this aspect of the work and concluded that selection for milk production would make between 70 and 95 percent as much improvement in efficiency as direct selection for efficiency, when the selection intensities are equal for the two traits. It is much easier to measure milk production than efficiency for large numbers of cows. In practice, the selection intensity for production would surely be much larger than for efficiency. This indicates that efficiency can be increased more rapidly by selection for production than by direct selection for efficiency. This conclusion has also been expressed by Hooven *et al.* (1968) and seems valid based on the rather limited data available. Essentially the same conclusions were made by Hooven *et al.* (1972) when efficiency was measured for a part of the lactation.

Changes in body weight as correlated responses to selection for yield should also be considered as possible and likely. These responses imply that selection goals should consider changes in body weight. Body weight with other traits has been considered by Wallace (1956), Mason *et al.* (1957), Hooven *et al.* (1968), and Dickinson *et al.* (1969), but are only ancillary to this discussion.

The projection of correlated responses should be viewed with some reservation. They are expected responses and have not been demonstrated experimentally. These expected responses, under mass selection, are subject to large sampling errors as demonstrated by Searle (1965). The parameters (heritabilities, genetic correlations, etc.) used to make these estimates are not precise because of the limited data from which they were estimated and because the feeding regimes used were only a few of the many possible regimes. These projected responses could conceivably differ by feeding regime.

GENOTYPE BY ENVIRONMENT INTERACTION

Genotype by environment interactions occur when the responses among genotypes are not the same from environment to environment. Such interaction would be of concern to both nutritionists and breeders. If possible, rather careful definitions of environments and genotypes should be made, which are realistic for the situation under consideration. For example, a genotype by environment interaction is obvious when British breeds of dairy cattle are taken to the tropics and when tropical breeds produce in highly specialized dairy farms in temperate zones. The British breeds do very poorly or even die in the tropics without major environmental modifications, and tropical breeds do not compete economically in highly specialized dairy farms in temperate zones. The following discussion will consider designed experiments with specific dietary regimes and conclusions drawn from field data in the temperate zones.

Designed Experiments Not Using Twins

Richardson *et al.* (1971) reported the response of 228 daughters of 13 Jersey sires that were randomly assigned, within progeny groups, to an all forage or forage plus grain ration. The sire by ration interaction for milk and FCM was significant between the 5 and 10 percent levels, but it only accounted for 4 percent of the total variation. The interaction was significant ($P < 0.001$) for gross efficiency. This might be expected because gross efficiency is a ratio; the amount of grain fed was controlled by production, and, in the all forage groups, there was little difference between cows in the amount of forage consumed. Sires ranked similarly under the two feeding regimes, with three noteworthy exceptions. For the three bulls, the interaction constants exceeded standard errors. The authors concluded that this genotype by level of nutrition interaction was probably negligible within the range of commercial dairying in the United States.

Two experiments were conducted at Utah (preliminary, unpublished data) with designs similar to the Tennessee work of Richardson *et al.* (1971). The first experiment used progeny of 10 bulls randomly divided within progeny groups to all forage and forage plus grain diets. The latter received 1 kg grain/3.5 kg FCM. The second experiment split progeny of eight sires with one group receiving alfalfa hay plus 1.36

kilograms of grain per day regardless of yield and the other group receiving alfalfa hay plus 0.6 kg grain/4 kg FCM above 4.5 kg/d. In the first experiment, the sire by ration interaction was significant ($P \simeq 0.05$) for gross efficiency and ($P > 0.05$) for yield. There were some rank changes among sires on the two diets. Mean-yield difference was 1409 kilograms for the two diets; there was no difference between rations in efficiency. This suggests that cows could not consume enough hay to produce to their potential. In the second experiment, the interaction of sires by rations was not significant for yield or efficiency. There were fewer changes in rank of sires between the two rations in this experiment than for those in the first experiment, even though the mean ration difference in yield was 1864 kilograms of milk. The difference in efficiency between the two rations was significant. For both traits in both experiments, sire differences tended to be greater on the higher plane of nutrition. Variation in efficiency was less under the more favorable environments. This was not true for yield. There was no large difference in variability of feed intake on the different diets. For milk yield, a large F value for sires was due to an increase in the component for sire differences, but for efficiency this was due to a reduction in the residual variance. These results indicate that genetic response is more fully expressed when diets have more available energy. These three experiments do indicate that genotype by ration interactions depend upon the nature and concentration of ration fed.

Designed Experiments Using Twins

In an experiment at Iowa State University (Rindsig and Freeman, 1973) identical and fraternal twins were used to estimate a ration by genotype interaction. After 9 months of age, the high-grain group received 2.72 kg/d of grain and the low-grain group no grain until calving. After calving, the high-grain group received 1 kg grain/2 kg milk on all milk over 4.54 kilograms daily and the low-grain group received 1 kg grain/6 kg milk on all over 4.54 kilograms daily. All twins were offered roughage free choice. Pairs were allocated to rations, with both members of one pair receiving a high ration; the next two pairs were split with one member of each pair on each ration; and both members of the fourth pair were on a low ration. A total of 129 pairs were used. Body measurements were taken at 3-month intervals to 36 months and 1 month after each calving. Of all possible tests of pair by ration interaction in growth traits, 14.1 percent were significant. The only trait that showed a consistent pattern of significance across consecutive ages was wither height. For wither height, the interaction accounted for 9.2 percent of the total variance, averaged across all ages. The point estimates of the interaction for other traits seemed to be distributed around zero at the various ages. The effects of contemporaneity on growth were generally very large at early ages, diminished as the twins grew older, and were not important after 2–3 years of age. Effects of contemporaneity accounted for over 50 percent of the variation in body weight, heart girth, paunch girth, and pelvic width from 3 to 9 months of age. Contemporaneity effects result from all things common to a pair of twins, except their genetic likeness, that are not common to individuals randomly drawn from the population being sampled. These contemporaneity effects may be due to both intrauterine and extrauterine effects.

The mean difference in first lactation mature equivalent production was 875 kilograms of milk, but there was less difference in later lactations. Five out of a possible 56 interaction terms were significant for production traits, providing little evidence of a meaningful interaction of genotypes by ration levels. These estimates were from a conventional analysis of variance. Using a weighted least squares analysis with a model that included rations, contemporaneity, additive genetic effects, rations by additive, and error—no interaction effects for production traits were larger than their standard errors; thus, a confidence interval would include zero. No interaction accounted for more than 2 percent of the total variance; thus, there is no evidence of a real ration by genotype interaction with these rations.

Bonnier, Hansson, and Skjervold (1948) used 14 pairs of monozygotic twins in two experiments. In one, ration differences were maintained up to calving and then fed according to production; in the other experiment, ration differences were maintained throughout life. The ration differences were significantly different from zero, but the rank order of twins across rations was nearly the same. The authors considered the interaction practically unimportant. Hancock (1953) used 15 pairs of monozygotic twins in a balanced incomplete block design where twins were allocated to three ration comparisons. He found no evidence of an important genotype by ration interaction in spite of rather large ration differences in milk yield.

Hansson *et al.* (1953) found no differential response in 16 Swedish Red and White identical twin pairs to different feeding regimes for growth traits up to 25 months of age. Later studies by Hansson *et al.* (1958) indicate highly significant and nonlinear interactions between twin pairs and milking interval for milk and fat production. Some evidence also was found for such an interaction for production of protein and lactose.

Brumby (1961) split 120 identical twin pairs between 40 New Zealand herds, 20 of which were high-producing and 20 low-producing. He found that the correlation between the deviation in milk yield from the herd mean of a monozygotic twin in a high herd with the deviation of its co-twin in a low herd was 0.11 ± 0.11. Twin members did not rank the same at the different levels of production. Based on the work of Hansson *et al.* (1953), Brumby concluded that the interaction was not due to plane of nutrition, but he speculated that milking technique in low-producing herds was less adapted to the individual cows than in high-producing herds and contributed to the large interaction.

Everson (1960), using data from the Moorman twin herd, estimated that the proportion of variance due to pair by ration interactions was negligible for growth traits from 3 to 9 months of age, but as high as 23 percent for some traits between 12 and 24 months.

Johansson and Rendel (1971) found two indications of interaction between genotypes for milk yield. The correlation between first lactation milk yield of monozygotic pair members split across high and average level herds was 0.28, compared with 0.87 for pairs in the same herds. Split monozygotic pairs had relatively low rank correlations compared with intact pairs. No such interactions were found for fat content. This excellent paper reviews and discusses much of the twin work where interaction between genotypes and herd levels were investigated.

The Animal Breeding Research Organization in Scotland has conducted rather extensive twin research. Watson (1960, 1961) reviewed experiments where twins were allocated to high- and low-producing commercial herds and other comparisons were made including commercial and research herds. This work was not designed to test genotype by environment interactions but to characterize the variation between and within monozygotic and dizygotic twin pairs in commercial and experimental herds. The papers clearly show the importance of contemporaneity (due to time of calving and lactation number), the effects of which reduced the intraclass correlation between members of twin pairs by about 20 percent for milk yield. Other sources of environmental variation common to twin pairs reduced this intraclass correlation a further 25 percent.

Many other experiments have been conducted investigating genotype by environmental interactions in dairy cattle. The environments included (1) different levels of the same dietary ingredients; (2) different dietary ingredients; (3) climate; (4) various time-oriented definitions, such as stage of lactation, and summer and winter feeding conditions; (5) milking stimuli; and (6) housing and other classification variables.

Designed experiments considering these environmental variables, and the literature relating to genotype by environment interaction in domestic animals, dogs, rats, and mice has been summarized in a comprehensive review by Pani and Lasley (1972).

Considering all the designed experiments, there is slight evidence of some traits showing a real genetic by nutritional interaction. To make a general statement for a class of traits (i.e., growth, production, etc.) does not seem warranted because there certainly was no consistent pattern to the results.

It is clear from reviewing the results of the designed work with twins that the effects of contemporaneity should be considered by the experimenter before starting work with twins. Such effects are usually confounded with the between-pair differences, and there can be serious biases in both growth and production studies. Such biases may cause large errors in making any genetic inference from between- and within-pair variances of twin data. Conversely, such additional likeness might be used to advantage where additional similarity between twin members would not bias the inferences to be made from the experiment.

Genotype by Environment Interaction from Field Data

A large body of evidence is available on sire by herd or sire by herd-year-season interactions from cattle under commercial conditions. The stimulus for this research was to determine if sires used extensively in artificial insemination rank the same over wide levels of herd environments. Specific feeding regimes or levels of energy intake are not available from these studies, but wide differences exist among herds as judged by production differences.

Individual research will not be discussed, but authors and regions will be given to indicate the extent of this work. Each general study involved several thousands of records. Extensive studies are typified by those of Mason and Robertson (1956) in Denmark; Burnside and Rennie (1961) and Mao and Burnside (1969) in Canada; and Robertson *et al.* (1960) in Great Britain. In the United States, this problem has been considered by Hickman and Henderson (1955) and Van Vleck *et al.* (1961) in New York; Legates *et al.* (1956b) using data from all over the United States; Lytton and Legates (1966) comparing northern and southern regions of the United States; Wadell and McGilliard (1959) and Specht and McGilliard (1960) using Michigan data; and Bereskin (1963) and Kelleher *et al.* (1967) using Iowa data.

In these studies, the sire by herd or herd-year-season interaction varied from negative estimates to one account for up to 7 percent of the total variation. The magnitude of the interaction component averaged about 2–3 percent of the total variation in milk production. In these data, significance tests for interaction are rather meaningless because differences too small to be important might appear significant because of the large numbers of records involved, and with unequal subclass frequencies tests would usually only be approximate. Kelleher *et al.* (1967) selected balanced two sire by *n* herd-year-season sets of data and found that the interaction accounted for 2 percent of the total variance. The authors in these studies generally agreed that sire by environment interactions were small and unimportant considerations in sire evaluation.

One exception to this conclusion came from the work of Mao and Burnside (1969). Their data from commercial herds was classified by 10 environmental factors. Among these were level of grain feeding in summer and winter. The three levels of feeding were high and low grain fed according to production and no grain fed, or the cows were not fed according to production. A highly significant interaction of sires by summer level of grain feeding was found. It accounted for 17.4 percent of the total variance. There were 29 degrees of freedom for this interaction. Correlations between progeny tests of the same 29 bulls in the three levels of feeding were relatively low. No significant interactions were found for winter grain feeding levels, but correlations between progeny tests of 34 sires in the three levels were again low, which did not agree with the interaction analysis. The authors suggested the sire by summer feeding interaction needed further investigation.

Considering all the work done with genotype by environmental interactions, the results do not offer any real reason for concern for selecting breeding animals in the commercial population. Even if interactions of moderate magnitude do exist when genotypes are tested over a rather wide range of environments, large errors in estimating breeding values are not likely (Kelleher *et al.,* 1967). This is the case for sires progeny-tested in many herds, such as sires used in artificial insemination; but, if sires are progeny-tested in limited environments, say one or two herds, large errors in estimating breeding values are likely. The results of these experiments do indicate some caution should be exercised when planned experiments under limited environments are conducted by nutritionists, breeders, or other experimentalists. Some care should be taken to use experimental material (cows, heifers, etc.) and environments that are representative of the populations and environments to which inferences are to be made.

RELATED CONSIDERATIONS

Feeding according to need was a common element of past work, where genetic inferences could be made relating to nutrition. Many other conditions did differ, such as dietary ingredients and environmental influences. There seems to be little or no evidence to indicate whether, for example, the heritability of efficiency would be different if cows were fed a relatively concentrated diet free choice. Obviously, many similar questions could be asked relating to correlated responses.

The dairy industry in highly developed countries can be characterized by herds increasing in size with more mechanization and less labor per cow. This implies that individual cows are not likely to be fed very carefully according to need. It is a common practice for cows to be fed essentially all they can eat, or to be allocated to lots according to production level; then, lots of cows are fed approximately to need according to the lot average. These industry changes strongly suggest that the genetic components of efficiency should be evaluated under different feeding regimes and under those characteristic of industry conditions. Even so, considering the different feeding regimes, management conditions, breeds, and measures of efficiency, the heritability estimates in Table 1 are reasonably similar.

Most, perhaps nearly all, nutritional research relates to formulating feeds or dietary regimes intended to maximize the economy of production, estimating parameters of feed use, or understanding basic physical and biochemical processes of feed use. This research is surely needed. It seems, however, that some research intended to maximize production regardless of cost is needed. What would the efficiency of feed utilization be in such diets? Provided such diets were available, attempts to adjust to commercial conditions could be made. Diets that maximize production would be of real experimental interest to geneticists. Also, in trying to determine diets that maximize production, nutritionists should be aware of the inherited ability of the experimental cows.

There is really no doubt that, at present production levels, when selection is applied, milk production can be increased. We have very little or no real knowledge as to the physiological changes caused by selection. Interdisciplinary research seems necessary to obtain these needed answers.

The genetic information relating to feed use; i.e., heritabilities and genetic and environmental correlations, includes parameter estimates based on components of variance and regressions that have genetic interpretations. These parameter estimates are certainly useful and allow predictions of expected response to selection. They certainly give an idea of the nature of quantitative genetic control over gross measures of feed use, but selection experiments or actual experience that allows measurement of genetic changes is needed to help verify the nature and magnitude of these responses.

Body size and body weight change related to productive ability and biological and economical efficiency is a complex problem that clearly needs research. Of course, inherent in this problem is the need to evaluate body composition as weight changes. The literature clearly indicates a phenotypic quadratic relation between gross efficiency of feed use for milk production and body weight. What is the nature of this genetic relation? Are such curves diet and genotype dependent? In brief, do we know what our selection goals should be relative to body size, and would such goals be dependent upon diet?

Many other problem areas related to genetic variation in nutritional response of dairy cattle could be enumerated, but this seems unnecessary. We seem to know just enough to begin to ask meaningful questions.

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Genetic Variation in Nutritional Requirements of Poultry

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The relatively short generation time and large number of offspring from the mating of two individual birds make study of genetic variations in nutritional needs somewhat easier with poultry than with other species of domestic animals. The variability encountered in nutrient requirements of poultry that may be ascribed to the genetic makeup of the animal has been evaluated from a nutritional, rather than a quantitative, point of view. In many cases breed, strain, and species differences in requirement are used as evidence for genetic variability rather than specific selection experiments.

A broad coverage of the literature is intended, but some important studies inevitably will be overlooked. Several authors have reviewed this subject from various points of view. Their papers should also be consulted (Hutt, 1961a, b; Olsen *et al.,* 1964; Nesheim, 1966; Quisenberry, 1969; Morris, 1972; Hvidsten and Kolstad, 1972).

FACTORS INFLUENCING EFFICIENCY OF FEED UTILIZATION

The efficiency with which an animal converts its food into body tissue or product is not a specific trait. In one sense, it is a function of the

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efficiency whereby each of over 40 nutrients is used by an animal. However, there are physiological functions that may affect several nutrients or broad classes of nutrients. The processes of digestion and energy deposition, maintenance, and energy losses during metabolism, are examples. For the most part, experiments on genetic variability in these functions are lacking, and conclusions drawn in a discussion of genetic variation will be largely speculative.

Digestion and Absorption

Chickens and other classes of poultry have the ability to digest and absorb food well. There is little evidence to suggest that chickens can be fed more than their digestive systems can assimilate. The amount of food consumed has relatively little influence on the metabolizable energy value per unit of food (Hill and Anderson, 1958). The ability to digest individual classes of nutrients appears to be good. Data from adult chickens with a colostomy (Katayama, 1924; Ekman *et al.,* 1949; Morimoto *et al.,* 1960; Squance and Brown, 1965) generally show that digestibility of dietary protein in common feed ingredients undamaged by processing and in mixed diets is between 80 and 90 percent. Similar results have been reported (Ekman *et al.,* 1949; Bolton, 1955) using indirect methods for measuring protein digestibility.

Fat absorption is efficient when the common fats or fat fractions of feeds are considered. At around 70 percent digestibility, beef tallow is the least well digested common feed fat; most others, such as lard and vegetable oils, are about 90–95 percent digestible by chickens (Renner and Hill, 1960). Only the very young chicken seems to lack the ability to digest fats at high efficiency (Renner and Hill, 1960; Carew *et al.,* 1972). Bolton (1955) has determined that starches and sugars in feeds are almost completely digested, while pentosans are only partially degraded. Cellulose and lignin were indigestible in his experiments.

The studies cited suggest that digestion and absorption of nutrients by the chickens investigated was quite efficient. If some method of selection for "better digestion" could be devised, improvement in efficiency might be quite small. The few published studies that compare stocks of different genetic background do not demonstrate wide variability in ability of these stocks to digest and absorb food.

Slinger *et al.* (1964) found small differences in metabolizable energy (ME) values of a ration fed to White Leghorn chicks and a crossbred broiler strain. In one comparison the Leghorns obtained about 1.6-percent more ME from a high-energy diet than the broiler chicks; the two breeds obtained the same ME value from a low-energy ration. Turkeys compared at the same time obtained 2-percent more ME from the low-energy ration but about the same as the broiler strain chicks with the high-energy ration. Differences of a similar magnitude between chickens and turkeys were found by Fisher and Shannon (1973). Sibbald and Slinger (1963) reported that White Leghorns obtained 2.6-percent more ME from a ration than did White Plymouth Rock chicks.

Other laboratories, however, have not found a consistent ME advantage for White Leghorn chicks (Stutz and Matterson, 1963). March and Biely (1971) found that broiler chicks and New Hampshire chicks had higher ME values on one diet than did White Leghorn chicks. Again the differences were small, amounting to 1–2 percent of the total dietary ME. Similar small differences were found between Brown Leghorns and Light Sussex hens in the ME value of a diet fed the two breeds (Foster, 1968). While these studies show that some differences in the digestion and absorption of a diet may be detected among breeds of chickens in carefully conducted experiments, they provide little indication that the variation is substantial and one that could be exploited if an efficient way of selecting for ability to digest and absorb food could be devised.

Utilization of Metabolizable Energy

The fate of energy entering the body as absorbed and retained metabolites determines the efficiency of utilization of energy for productive purposes. Some metabolizable energy is lost as heat due to the "heat increment" of feeding (Mitchell, 1962), and the "net energy" remaining can be used for maintenance or for production of new tissue or products. In general, little information is available as to the genetic variation associated with the utilization of absorbed energy.

The maintenance requirement of a laying hen represents a major portion of the daily energy requirement. Variation in metabolic rate or activity might be expected to have a major influence on efficiency. Mitchell (1962) found a rather high individual variation for basal metabolic rate (BMR) in a series of measurements of 14 hens and 7 cocks. The variation between individuals was considerably greater than the variation in repeated measurements made on the same individual. Males had a significantly higher BMR than hens in these studies.

There is no agreement in the literature on the differences in basal metabolic rate among various breeds, although some workers claim that White Leghorns have a higher BMR than heavy breeds (Ota and McNally, 1961; Huston *et al.,* 1962). Other studies have not confirmed such differences, particularly when metabolic rate is related to metabolic body size (Berman and Snapir, 1965). When high environmental temperatures were used, White Leghorns had a lower fasting metabolic rate than Plymouth Rocks in studies by Berman and Snapir (1965). This was considered to provide a greater tolerance to high environmental temperature for the White Leghorns.

The influence of the sex-linked gene for dwarfing (dw) on efficiency has been studied in some detail by Guillaume (1969). When normal and dwarf sister pullets were compared during growth from hatching to 9 weeks of age, the dwarf chickens had a lower maintenance requirement and resting metabolic rate than full-sized sisters. In spite of the lower maintenance requirement, the dwarf chickens required more food per unit gain because they grew more slowly and their carcasses had a greater fat content. The overall efficiency of energy retention, however, was greater for the dwarf pullets. Guillaume suggested that the dwarf pullets were less active than their normal sisters, and later studies showed that they may have had less active thyroids (Mérat and Guillaume, 1969).

No available reports directly note individual or breed variation in losses due to heat increment of feeding. The total heat losses per unit of body weight per week were the same for a broiler "hybrid" and for Rhode Island Red × Light Sussex crossbred chicks in studies by Davidson and Mathieson (1965).

In view of the difficulties in making large numbers of measurements of the various aspects of energy metabolism, it is not surprising that relatively little information on genetic variation in these traits is available. More studies have been made of the differences in feed conversion between different stocks.

The amount of feed required to produce a broiler of a given weight or a dozen eggs is commonly used as a measure of feed efficiency. A large aspect of the profitability of poultry meat and egg production is the efficiency whereby feed is converted into product. This is a complex relationship because feed efficiency depends on many interrelated factors. Feed conversion depends on nutritional adequacy of the diet, the metabolizable energy content of the diet, environmental temperature, and, to a large extent, the rate of productivity. The faster a broiler reaches market weight or the greater the number of eggs produced by a hen in a laying year, the more efficient the conversion of food to product will be. This is due to the reduction in food needed for maintenance relative to product produced. Morris (1972) has estimated that efficiency of food utilization would improve by about 5 percent for every 20 eggs added to the annual production of a laying hen.

Because of the relationship of feed efficiency and productivity, selection for rapid growth rate in broilers and high egg production in laying hens also results, to a considerable degree, in selection for improvement in feed conversion. Little selection for improved feed efficiency independently of improvements in rate of productivity has been done in poultry. Few experiments have been reported in which individual food intake records have been kept, and the variation in feed efficiency has been studied independently of rate of productivity. This type of experiment is necessary to determine the genetic variation that exists in metabolic efficiency of energy utilization.

The problem of genetic variations in feed efficiency in growing broilers and in laying hens has been considered by several authors. Fox and Bohren (1954) studied the relationship between growth rate and feed efficiency with four breeds of chickens: New Hampshire, Dark Cornish, Purdue Dominant White, and White Leghorn. Chicks from these breeds were individually fed, and regression coefficients for the individual breeds for the relationship between body weight and feed efficiency were determined. This relationship was similar for the heavy breeds but different between the White Leghorn and heavy breeds. When the feed efficiency of the three heavy breeds was compared after adjustment for differences in growth rate, they were not significantly different. Fox and Bohren concluded that there is little justification for commercial breeders to practice selection on the basis of feed requirements.

Wilson (1969) attempted to determine the relationship between feed efficiency, rate of gain, and feed consumption in an effort to estimate whether metabolic efficiency was genetically controlled. Broiler type chicks were individually caged and fed from 5–10 weeks of age. Lines were differentiated by selection, over two generations, for average daily gain or for feed efficiency. A random control line was also maintained. Although the selection was of relatively short duration, Wilson concluded that selection for gain alone reduces the amount of food needed to produce a unit of gain about 75 percent as much as does direct selection for feed efficiency. This would suggest that some aspect of metabolic efficiency is under genetic control. Of course an apparent change in efficiency could be a reflection of a change in body composition rather than a true difference in efficiency of energy utilization.

Nordskog *et al.* (1972) discussed some unpublished studies from Iowa State University dealing with laying hens. Three Leghorn lines selected for high production, large body size, or small body size were compared according to feed requirements for maintenance and egg production. Although differences in gross feed efficiency could be demonstrated, the net efficiency of energy utilization for egg production did not seem to differ among the lines. They concluded from their data that variation in metabolic efficiency was probably low.

Frankham (1971) selected two strains of White Leghorns for increased production and found there was a large improvement in gross feed efficiency in the selected lines compared to an unselected control population. However, egg production was considerably greater and body weight lower in the selected lines. Although gross efficiency of egg production changed by this selection procedure, the effect on net efficiency of energy utilization cannot be determined, as individual feed intake measurements were not made.

Miller and Quisenberry (1959) found that feed efficiency varied markedly between a White Leghorn strain and two hybrid laying strains. They concluded that the major factors influencing the differences in feed efficiency were rate of production and body size of the hens. When feed conversion means were adjusted to remove linear effects of body weight and egg production, significant strain differences in feed conversion were still observed; however, this difference was small compared to the influence of body weight and egg production.

The results of the studies cited do not point to large genetic variations in metabolic efficiency in populations of chickens. The number and extent of such studies have not been large, however, and more definitive evidence seems to be needed. Most selection for feed conversion has involved growing birds, and little has been done in selection of laying hens for this trait. Selection for improved efficiency might be accomplished by selection for reduced activity, lowered body fat content, or some other related parameters. It seems unlikely, however, that breeders will commit resources to select poultry for food conversion efficiency as a separate trait on the basis of present evidence.

VARIATIONS IN PROTEIN AND AMINO ACID REQUIREMENTS

Although protein is usually considered a nutrient, the protein requirement basically represents the total nitrogen requirement, in which all the necessary amino acids are present in adequate amounts without marked imbalances. Therefore, except for digestion and some features of protein biosynthesis, the protein requirement represents the net effect of many metabolic processes in which amino acids participate.

The protein "requirement" of species of poultry varies markedly, depending on how one considers the requirement, as shown in Table 1. The bases for these estimates are included in the table. There are striking differences when the protein requirement is expressed as a percentage of the diet, in grams per 1000 kilocalories of metabolizable energy, and in amount per day; when expressed in terms of grams of protein required per gram of gain, however, the species and type differences largely disappear, at least in this early growth period.

Ducks seem to make more gain per unit protein intake than the other species listed. Since the wet carcasses of 3-week-old ducks are only about 16-percent protein compared to 18–19 percent for chickens and turkeys, some but not all of the apparent greater efficiency of the duck may be due to a different body composition.

As it is difficult to evaluate potential genetic differences in protein requirement (i.e., the factors of food intake, growth rate, and body composition all affect the protein requirement in one way or another), a more specific question seems to be whether there are differences in efficiency of protein utilization among individuals, strains, or breeds that could be exploited by selection. Few experiments seem to have been done on this point. Davidson and Mathieson (1965) compared the efficiency of protein deposition of Rhode Island Red × Light Sussex crossbred chicks to that of chicks from a "modern broiler hybrid." The faster growing broiler chicks converted a higher percent of the dietary protein to tissue protein. To achieve a given weight, however, the crossbred chicks had to be fed longer, and the apparent differences in protein efficiency may have been due to the relative amounts used for maintenance and growth. Data are needed comparing the net protein utilization for a given protein determined with chicks of different genetic background.

TABLE 1 Protein Requirements of Various Types of Poultry Expressed in Different Ways

	Protein Requirement			Gain per Protein Consumed (g/g)
Animal Type	% of diet	g/1000 kcal ME	g/d	
Broiler chick[a]	23	72	11.5	2.3
Egg-type chicken[a]	20	69	8	2.2
Turkey[a]	28	102	12	2.2
Duck[b]	19	75	18	2.9

[a] The data for protein required for early growth at various energy levels are taken from *Nutrient Requirements of Poultry* (Washington, D.C.: National Academy of Sciences, 1971). From the same publication, data were obtained for growth rate and feed intake for White Leghorn males to 500 g, and for male broiler chickens and male turkeys to 1000 g. The daily protein required was the average calculated from days required to reach above weights, and estimated protein intake during that period.

[b] Data for growth rate, feed consumption, and protein requirement of male ducks was supplied by Dr. B. J. Wilson, Poultry Research Centre, Edinburgh, Scotland. The ducks weighed 1200 g at 3 weeks of age and consumed 2020 g of a diet containing 2600 kcal ME/kg and 19 percent protein.

Egg Production

In studies of the protein requirement of the laying hen, some reports have appeared of strain or breed-diet interactions. Two main conclusions may be drawn by an evaluation of these studies. Differences in the percentage of protein required in a diet between strains in many cases can be explained by differences in food intake. Since hens differing in body size may consume variable amounts of food, the percentage of dietary protein required to achieve a given protein intake may differ considerably. In other cases hens seem to differ in their response to diets marginal or deficient in protein, but they may not differ in the grams of consumed protein required for maximum egg output.

The effect of food consumption on required dietary protein concentration is illustrated by the experiments of Sharpe and Morris (1965). Diets containing graded levels of protein were fed to Rhode Island Red × Light Sussex pullets and to "hybrid" pullets. The crossbred pullets weighed 33-percent more and produced 20-percent fewer eggs than the hybrid pullets. When expressed as a percentage of the diet, the protein requirement of the hybrid strain was about 16.5 percent while that of the crossbred strain was 12.5 percent for maximum egg production. However, since the crossbred hens consumed more feed than the hybrids, both types consumed about 20 grams of protein per day for maximum egg production. Perhaps the higher maintenance requirement of the heavy breed compensated for the greater production rate of the light breed.

The differing responses of hens to diets deficient in protein is illustrated by data published by Harms and Waldroup (1962). Two strains of White Leghorn hens (A and C) were fed diets containing 17-, 13-, and 11-percent crude protein. Egg production of the two strains was similar when they were fed the diets containing 17- and 13-percent protein, but at 11-percent protein, egg production of strain A was 59.5 percent compared to 53.8 percent for strain C. Strain A consumed 11.4 grams of protein per hen per day while strain C consumed 10.1 g/d. When the grams of egg output are plotted against grams of protein consumed, the two strains seem to follow a common regression line. Thus in this case the relatively small difference in response to protein deficiency between the strains seemed to involve the degree to which protein deficiency affected food intake.

A similar example of such a differential response to marginal levels of protein is shown by data published by Harms *et al.* (1966). Diets of 17-, 15-, 13-, and 11-percent protein were fed to hens of six different genetic backgrounds. Five of these groups were egg-production strains while the sixth was a strain of New Hampshires. In the Cornell random bred strain, egg production was reduced much more than in the other four egg-production strains, as the protein level was reduced from 17 to 13 percent. This strain, however, gained considerably more weight than the other strains as the protein level was decreased, and appeared to be less inclined to lay eggs at the expense of body tissue.

In the same study the New Hampshires were affected relatively little as the protein level was reduced from 17 to 11 percent of the diet. The egg output by this group, however, was not more than 29.6 grams per hen per day, which was similar to that achieved by the egg production strains fed 11-percent protein diets.

These experiments indicate that there are differences in response among strains of laying hens to diets containing different percentages of dietary protein. They provide less convincing evidence that substantial differences in efficiency of protein utilization occur among strains. Balloun and Speers (1969) studied three strains of Leghorns selected for production rate or for large or small eggs. One of these strains seemed to be less efficient in using protein for egg production than the other, so perhaps one cannot say such differences in efficiency do not exist.

Since protein utilization per se is metabolically very complex and involves individual utilization of all the amino acids, selection for egg production on low-protein diets may be unlikely to produce hens superior in protein utilization, especially when they are fed other low-protein diets differing in amino acid composition from the one on which selection was based. The responses to protein deficiency in food intake, weight gain, reduction in egg size, and sensitivity of egg production rate may be influenced by selection, but experimental proof of this needs to be obtained.

AMINO ACIDS

Arginine

Chicks fed diets deficient in arginine have been reported by many investigators to show very striking individual variation in response to the deficiency (Snyder *et al.*, 1956). Breed and strain variations in response to an arginine deficiency have been observed (Hegsted *et al.*, 1941; Nesheim and Hutt, 1962), and variation in degree of arginine deficiency among offspring of individual hens was reported by Griminger and Fisher (1962). In each case cited, the arginine deficiency was produced by feeding diets containing casein as a source of protein.

Two strains of White Leghorn chickens were selected for a high or a low requirement for arginine on the basis of growth rate when fed a diet low in arginine and containing casein as the source of protein (Hutt and Nesheim, 1966). Data showing the development of these strains over four generations are shown in Figure 1. Nutritional studies with these strains showed that the difference between them was not due to an uncomplicated variation in arginine utilization. When they were fed diets deficient in arginine, using an amino acid mixture with a composition different from that of casein, the strains differed much less (Nesheim *et al.*, 1967). Although paired feeding eliminated much of the growth differences between the strains on the arginine-deficient diets, food intake differences were not the primary problem causing them to respond so differently to the arginine deficiency. Force-feeding the high-arginine strain the amount of feed consumed *ad libitum* by the low-arginine strain caused a very fatty liver and, eventually, high mortality. In addition, metabolic studies showed a greater degradation of dietary arginine by chicks of the high-arginine requirement strain

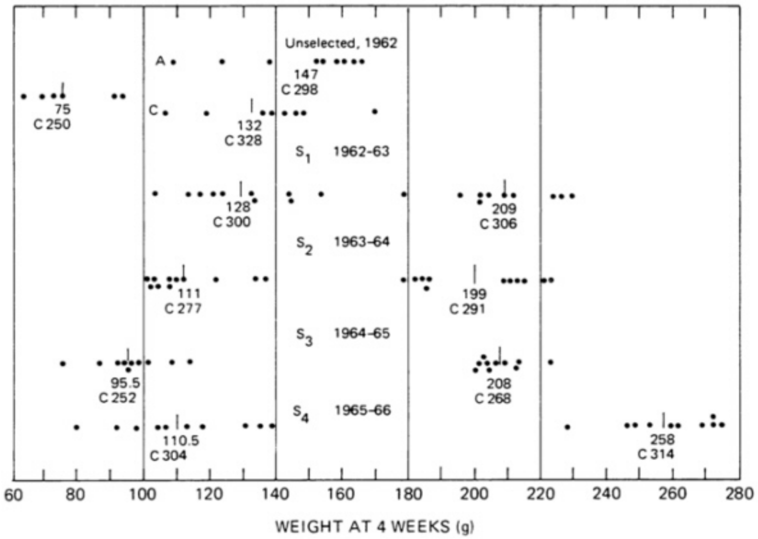

Figure 1 Differentiation of the two strains in four generations. Each dot represents average weight of chicks in one sire family after 4 weeks on an arginine-deficient diet. Average weights of all chicks on test, and of controls (C) are given for each generation below the distribution of sire families. The six dots at upper left represent sire families of a slow-growing strain subsequently discarded.

than by those of strains with a low requirement (Nesheim, 1968; Austic and Nesheim, 1970). The high-arginine strain developed high levels of kidney arginase activity when fed the diet containing casein. Arginase levels in kidneys of chicks from the low-arginine strain were not elevated under such circumstances (Nesheim, 1968).

The strains also varied in response to dietary excess of lysine. The lysine content of plasma and other tissue fluids was higher in chicks from the high-arginine strain than those of the low-arginine strain. When excesses of lysine were added to the diet of the two strains, a lower level of dietary lysine was required to depress the growth of the high-arginine strain compared to the growth depressing level for the low-arginine strain.

Several authors have described an antagonism between dietary lysine and arginine in chicks (Snetsinger and Scott, 1961; Jones, 1964; Boorman and Fisher, 1966; O'Dell and Savage, 1966). Excesses of lysine in diets for chicks caused a marked elevation in kidney arginase activity (Jones *et al.*, 1967). Since casein contains nearly twice as much lysine as arginine, the dietary requirement for arginine is elevated when casein diets are fed; this is due largely to the influence of lysine on the requirement for arginine. Thus the differentiation of the high-arginine and low-arginine strains of chicks appeared to be due to the differing of chicks of the two strains to lysine-arginine antagonism.

Lysine is degraded in chicks by a series of reactions initiated by the enzyme lysine-α-ketoglu tarate reductase (Grove and Roghair, 1971; Wang and Nesheim, 1972). The level of this enzyme found in several tissues of the chick appears to be a controlling factor in regulating body pools of lysine and the rate of lysine degradation.

Chicks of the high-arginine strain were found to have a significantly lower activity of lysine-α-ketoglutarate reductase in liver than those from the low-arginine strain. This was accompanied by a low *in vivo* lysine oxidation rate by the chicks of the high-arginine strain (Wang *et al.*, 1973). Present evidence indicates that the difference in arginine requirement of the high- and low-requirement strains is apparently due largely to a genetic difference in ability of the chicks from the two strains to degrade excesses of lysine. The test diet used to select chicks contained considerable lysine, since casein was used as the source of protein. Under these conditions lysine accumulated in plasma and body fluids of chicks that did not readily degrade lysine (high-arginine strain). The lysine caused an increase in kidney arginase activity of chicks from the high-arginine strain and a consequent increase in rate of arginine degradation. This could be compensated for by an increase in the arginine content of the diet.

The relation of lysine excess to the differentiation of the two strains

TABLE 2 Effect of Excess Lysine on Growth, Plasma Lysine and Arginase Activity in the High (HA) and Low-Arginine (LA) Strains of Chickens

Diet	Body Weight at 3 wk (g/chick)		Plasma Lysine Concentration (μg/ml)		Kidney Arginase Activity (urea in μmol/h/g kidney)		Lysine-α-ketoglutarate Reductase Activity (saccharopine in μmol/h/g liver)	
	HA	LA	HA	LA	HA	LA	HA	LA
Basal diet[a]	167	160	75	31	3018	3822	3.99	7.72
+ 0.25% L-lysine HCI	155	180	153	32	4297	3534	4.67	9.84
+ 0.50% L-lysine HCI	150	178	120	61	8734	3166	5.46	10.76
+ 0.75% L-lysine HCI	120	178	176	47	10046	3632	7.05	12.01
+ 1.00% L-lysine HCI	77	163	258	151	17108	3687	8.52	10.34

SOURCE: Data from Wang *et al*. (1973).

[a] Contained corn-gluten meal as source of protein, supplemented with 0.5 percent L-lysine HCI.

is clearly shown by the data in Table 2. As the lysine content of the diet was increased, growth of chicks of the high-arginine strain was depressed while that of the low-arginine strain was nearly unaffected. Plasma lysine levels of the two strains differed markedly at all levels of lysine fed. The arginase activity in kidney of chicks of the high-arginine strain increased as the lysine content of the diet increased, while that of chicks from the low-arginine strain was unchanged. The lysine-α-ketoglutarate reductase activity in liver was significantly different between the strains.

Properties of the lysine-α-ketoglutarate reductase from the two strains have not been determined. At present it cannot be ascertained whether the level of enzyme only has been altered by selection, or whether enzyme properties also vary.

These studies show that genetic variation in an amino acid requirement of chicks was made possible by a rather complex interrelationship between lysine excess and arginine. Although the selection was made under conditions of arginine deficiency, the basic metabolic changes occurred in lysine metabolism. When lysine is not in excess, the difference in arginine requirement of the strains is relatively small.

Rather marked variation was shown among chicks in ability to degrade lysine and to regulate body lysine pools. In spite of this, the low-arginine strain, with a high level of the lysine-degrading enzyme in liver, does not have a demonstrably elevated lysine requirement (Nesheim *et al.,* 1971). This appears to be due to the very low rate of lysine degradation that occurs when lysine intake is low.

Lysine

In addition to the studies cited of arginine and lysine relationships, several selection experiments have been carried out in an effort to alter the lysine requirement of chickens or quail. Enos and Moreng (1965) reported that the growth rate of offspring of 16 sire families differed significantly when they were fed a lysine-deficient diet. Subsequent selection for high and low growth rate of chicks fed a lysine-deficient diet was relatively unsuccessful in establishing strains with different lysine requirements (Enos *et al.,* 1971).

Selection for growth rate of Japanese quail fed diets deficient or adequate in lysine has been carried out for 15 generations (Godfrey, 1968, 1969). One line of quail (D) was selected for growth rate when fed a diet deficient in lysine. Another line (F) was fed the same diet supplemented with lysine. A third group (C) was kept as a randomly mated control line, but was fed the lysine-supplemented diet.

TABLE 3 Growth of Selected Lines of Quail Fed Diets Deficient or Supplemented with Lysine

	Average Weight at 4 wk by Quail Line[a] (g)		
Diet Type	F	C	D
Lysine-deficient	54	56	68
Lysine-supplemented	80	82	84

SOURCE: Data from Godfrey (1969).

[a] See text for description of lines.

Data showing the comparative growth of the strains are shown in Table 3. When fed the low-lysine diet, the quail chicks from the D line grew more rapidly than those from the F and C lines. Their growth rates were nearly the same when the diet contained adequate lysine. This selection experiment seems to have produced strains of quail with differing dietary lysine requirements, although no estimate of the size of this difference has been reported.

Some comparisons have been made of the lysine requirement of breeds of commercial strains of laying hens. Krautman (1971) studied 10 inbred lines of White Leghorns fed diets low in lysine, methionine, or protein. When expressed as a percentage of the growth rate of controls fed diets supplemented with lysine, the growth rate of chicks from the 10 lines ranged from 34.9 to 50.2 percent.

Morris (1972) reported data of Pilbrow (1968) comparing the lysine requirement of eight strains of commercial laying hens. The lysine requirement seemed to vary between 0.55 and 0.76 percent of the diet for the strains. It seemed to differ less, however, when lysine intake was compared to egg output. The hens with the highest egg output required the greatest intake of lysine above that used for maintenance.

Lysine seems to be very efficiently transferred from diet to carcass or egg proteins. When diets containing lysine levels slightly below the requirement are fed, over 85 percent of the lysine consumed may be deposited (Nesheim, 1966; Morris, 1972). For this reason any substantial improvement in lysine utilization by chickens may be unlikely, simply because it is already very good.

Methionine

Breed differences between White Leghorn and Australorp chicks in growth responses to methionine supplements have been observed

(McDonald, 1957). The growth rate of White Leghorn chicks was improved by supplementing their diet with methionine, whereas the growth rate of Australorp chicks was not. In subsequent experiments (McDonald, 1958) the growth of the White Leghorn chicks was improved by both methionine and cystine dietary supplementation, whereas only cystine supplements improved the growth rate of the Australorps. These results suggested that the Australorps converted less methionine to cystine than did the White Leghorns. This was confirmed in later experiments by Miller *et al.* (1960) working with Leghorns and Australorps from a different source. Although no difference in dietary methionine requirement could be demonstrated between Leghorns and Australorps, the conversion of ^{35}S-labeled methionine to cystine was greater for White Leghorn chicks than for Australorps. Since the White Leghorns are a rapidly feathering breed and the Australorps are slow feathering, it is possible that differences between the breeds in the conversion of the labeled methionine to cystine was a reflection of relative demand for cystine for feathering. Neither influences of rate of feather development on the control of the conversion of methionine to cystine, nor enzymatic differences between these two breeds have been investigated.

Chickens homozygous for the autosomal recessive gene *sc* lack scales and most feathers. When such chickens were fed a low-methionine diet their growth was the same as that of comparable chicks receiving the diet supplemented with methionine (Abbott *et al.*, 1962). Under the same conditions, normally feathered chicks fed the deficient diet gained only 50 percent as rapidly as controls. Since heat production by the scaleless chickens was greatly elevated, they consumed from 11 to 17-percent more food than normally feathered chicks. Thus the deficiency of methionine was at least partially made up by consumption of greater quantities of the deficient diet.

Hess *et al.* (1962) attempted to select strains of chickens for slow or rapid growth rate when fed methionine-deficient diets. After four generations, 3-week old male chicks from the strain selected for slow growth weighed 73.9 grams when fed the methionine-deficient diet while those from the fast-growing strain weighed 115.9 grams. Chicks from a random bred control strain fed the same diet weighed 101 grams. When the fast- and slow-growing strains were fed a normal diet, they weighed the same at 3 weeks of age. This experiment suggested that the strains differed in response to the methionine deficiency. The methionine requirement was not directly estimated in these experiments.

Later studies by Lepore (1965) attempted to measure the methionine requirement of strains selected for two generations on the basis of growth rate when fed a low-methionine diet. Chicks from these strains were fed diets containing graded levels of methionine or protein, and the dietary requirement for these nutrients was estimated. No difference in methionine or protein requirement of the strains was detected. In contrast to the selection studies by Hess *et al.* (1962), the lines selected by Lepore also differed in growth rate when fed diets containing adequate methionine. It appeared that selection was made primarily for growth rate per se rather than in response to a methionine deficiency. The question of altering the methionine requirement of chicks by selection still seems to be unresolved, although the experiments thus far published do not give much encouragement.

Some variation among strains in methionine utilization may occur. Krautman (1971) reported that 10 inbred lines fed low-methionine diets differed significantly in growth rate from hatching to 3 weeks of age. Since his experiments seem to be complicated by protein deficiency as well, the strain difference due to methionine deficiency alone is hard to evaluate.

Morris (1972) discusses some experiments aimed at estimating the methionine requirement of individual laying hens. When the intake of methionine needed to stabilize body weight was considered, 335 milligrams per hen per day were required with a standard deviation of 35.6 mg/d. The data were corrected to adjust for differences in mean body weight and egg output. The variation was quite substantial, although it is difficult to estimate how much of the variation was due to true genetic differences and how much to experimental error.

Selection for improved utilization of methionine, using egg production as a criterion, would be very difficult since the utility of matings could not be assessed until progeny were laying. This would be more time-consuming and require greater resources than selecting desirable matings on the basis of chick growth studies over a short feeding period. It is doubtful that such a selection program would be very productive.

The metabolism of methionine is very complex. There are numerous functions for this amino acid in addition to protein biosynthesis. Methionine is a donor of methyl groups and, after conversion to cystine, participates in synthesis of glutathione, the formation of inorganic sulfur compounds, bile salt formation, and mucopolysaccharide synthesis. It would not be surprising to find genetic variation in the control of methionine utilization through these various pathways.

Several human genetic disorders involving sulfur amino acid metabolism are known (Stanbury *et al.*, 1972). Methionine is also limiting in many natural protein sources, however, so that natural selection for efficient methionine utilization by chickens may have operated for a very long period of time.

VARIATIONS IN VITAMIN REQUIREMENTS

Thiamin

Breed differences have been reported in the response to a thiamin deficiency. White Leghorn chickens survived longer than Rhode Island Red chicks when fed thiamin-deficient diets (Lamoreux and Hutt, 1939). In these early studies, the diets were made thiamin-deficient by autoclaving, and other deficiencies were probably also present. Scrimshaw *et al.* (1945) found that eggs from White Leghorn hens contained an average of 104.5 milligrams of thiamin per 100 grams of egg contents compared to 64.4 and 66.1 mg/100 g for eggs from Rhode Island Reds and Barred Plymouth Rocks, respectively. These results were confirmed by a later study (Howes and Hutt, 1956) in which four heavy breeds were found to lay eggs with substantially less thiamin than White Leghorn hens fed the same diet. These results were interpreted as indicating that White Leghorns used thiamin more efficiently than the heavy breeds. This conclusion was probably not justified, as later studies (Thornton and Shutze, 1960; Thornton, 1960) showed. When diets with graded levels of thiamin were fed to White Leghorn chicks or to New Hampshire X Delaware crossbred chicks, the dietary level of thiamin required for optimum growth was similar. The Leghorn chicks showed a slightly higher mortality and symptoms of polyneuritis compared to the heavy breed.

The data on egg thiamin are of considerable interest. Apparently nearly all the egg thiamin is present in egg yolk, being deposited there during yolk formation in the ovary. The differences in thiamin concentration in egg yolk probably represent differences in thiamin transfer from blood to egg yolk by the hen. The riboflavin content of eggs from White Leghorn hens is also higher than the level found in heavy breeds (Mayfield *et al.,* 1955). The transfer of riboflavin to eggs depends on a riboflavin-binding protein in plasma that is produced under the stimulus of estrogen (Clagett *et al.,* 1970). Perhaps the breed differences in egg thiamin are mediated in a similar manner, although as yet a thiamin-binding protein in plasma or egg yolk has not been described.

Riboflavin

Prior to the discovery of riboflavin and the development of dietary riboflavin sources, a deficiency of this vitamin caused major problems in the poultry industry. Most poultry rations, composed of cereals and protein supplements, require additional riboflavin to meet requirements for development of young chicks, egg production, and hatchability. It is not surprising that considerable research on the genetic variation in riboflavin requirements of poultry has been reported.

In two experiments chicks were selected for growth rate when fed riboflavin-deficient diets (Lamoreux and Hutt, 1948; Lerner and Brid, 1948). An attempt was made in both studies to select chicks "resistant" to riboflavin deficiency. This would presumably result in chicks with a dietary riboflavin requirement lower than that of the populations from which they came. Lamoreux and Hutt also selected for a "susceptible" strain. After six generations of selection, they reported the successful production of two strains differing in response to a riboflavin deficiency. When chicks of the two strains were fed a riboflavin-deficient diet, those from the resistant strain gained 89.9 grams to 5 weeks of age, while chicks from the susceptible strain weighed 49.4 grams. These results were from offspring of progeny-tested dams. Subsequent tests showed that chicks from the two strains gained at nearly the same rate when their diet was supplemented with riboflavin. Comparable differences in mortality of chicks from the two strains were also observed. The degree to which selection altered the quantitative requirement for riboflavin was not studied. The scant knowledge of riboflavin metabolism in 1948 precluded study of the mechanism whereby these strains differed in riboflavin requirement. It would be of interest to know what aspect of riboflavin metabolism was subject to genetic variation in the chickens studied. Although Lerner and Bird (1948) were less successful than Lamoreux and Hutt (1948) in clearly differentiating strains, they concluded that genetic differentiation of the ability to grow on a riboflavin-deficient diet was possible but would need to be approached on a larger scale than they had attempted.

A more specific genetic problem in riboflavin utilization by chickens involves a riboflavin transport protein. Maw (1954) reported studies that began with three closely related hens in a pedigreed breeding flock laying fertile eggs that would not hatch. By astute observation of the affected embryos, riboflavin deficiency was suspected. This was confirmed by riboflavin analysis of the eggs. Eggs from these hens would still not hatch when the laying diet was enriched with riboflavin. When eggs were injected with riboflavin, embryos developed normally and hatched. Maw concluded that the lack of ability of these hens to lay eggs with sufficient riboflavin for embryo development was the result of the action of a recessive gene (rd) in the homozygous state. Boucher *et al.* (1964) showed that the free riboflavin content of the blood in hens homozygous for this gene (rd rd) did not increase at the onset of egg production as in normal hens (Rd Rd). Hens heterozygous for this gene (Rd rd) had a rise in blood riboflavin only about half that seen in normal hens.

Subsequent studies with hens from the mutant strain showed that a riboflavin-binding protein (RBP) was absent in blood, egg yolk, and egg albumen while such a protein was present in normal hens (Winter *et al.*, 1967; Farrell *et al.*, 1969, 1970a,b).

The riboflavin-binding protein, first described by Rhodes *et al.* (1959) and later by Blum and Jacquot-Armand (1965), has a molecular weight of 32,000 and can bind 12.5 μg of riboflavin per milligram of protein (Farrell *et al.*, 1969). In normal laying hens, riboflavin is transported in the blood in the coenzyme forms, flavin-mononucleotide (FMN) and flavin-adenine-dinucleotide (FAD), as free riboflavin, and as riboflavin bound to RBP. Free riboflavin is rapidly cleared from the blood and excreted in the urine (Cowan *et al.*, 1966). Males and nonlaying hens lack RBP and have low levels of free riboflavin in blood. At the onset of laying, the level of RBP rises in blood and the blood riboflavin level increases markedly. This RBP may be transferred directly to egg yolk from plasma, and it may also be synthesized by the oviduct and secreted with egg albumen (Farrell *et al.*, 1970b). The synthesis of RBP is stimulated by estrogen, and estrogen-treated males will develop RBP in their blood (Clagett *et al.*, 1970). Hens homozygous for the recessive gene (rd rd) do not synthesize RBP under the stimulus of estrogen, nor do homozygous (rd rd) males treated with estrogen. Heterozygotes (rd Rd) have only half as much RBP in blood and egg proteins as normal hens. The frequency of this mutation in usual populations of hens does not seem to have been reported. Since offspring of the homozygous recessive individuals normally do not hatch, the presence of the gene must be somewhat limited in normal populations.

The understanding of riboflavin transfer in eggs achieved in the studies with the mutant strain probably provides an explanation for reported breed variations in egg riboflavin content. White Leghorn hens have been reported to deposit more riboflavin in their eggs than hens from heavy breeds when fed the same diet (Jackson *et al.* , 1946; Mayfield *et al.*, 1955). Morris (1972) shows data from an unpublished experiment by Tolan indicating maximum riboflavin content of albumen from eggs of Plymouth Rock and Rhode Island Red crossbred hens to be lower than that of White Leghorn hens, when both breeds were fed graded levels of riboflavin. This may be an indication that lower amounts of the riboflavin-binding protein were secreted into the albumen of the crossbred chicks than of the White Leghorns. The role of the riboflavin-binding protein in riboflavin transport also explains why egg riboflavin is not increased beyond a certain level as dietary riboflavin is increased. Once the available RBP is saturated with riboflavin, increases in absorbed riboflavin cannot be retained and are excreted. Blum *et al.* (1961) found that the egg riboflavin level varied in individual hens and with the stage of the laying year. The egg riboflavin is probably influenced markedly by estrogen secretion and variations between individuals and breeds may be a reflection of variation in estrogen secretion.

Although considerable research has been made on genetic variation in riboflavin requirements of chickens, some doubt remains as to the variations in requirement that may be present in normal populations. In general the variation seems to be low enough so that segregation of populations differing widely in riboflavin requirement would be difficult to achieve. Variation in egg riboflavin may reflect variation in the production of the riboflavin-binding protein in blood by individuals and breed groups.

Nicotinic Acid

The quantitative dietary requirement for nicotinic acid seems to vary markedly among various species of animals, particularly among classes of poultry. According to the National Research Council's *Nutrient Requirements of Poultry* (1971), the dietary requirement of growing chickens is 27 mg/kg of diet; for ducks, 55 mg/kg; and for turkeys and pheasants, 70 mg/kg. The wide variation in nicotinic acid requirement of various species may be related to the efficiency with which tryptophan is converted to nicotinic acid. Cats, for example, cannot use tryptophan as a source of niacin (DaSilva *et al.*, 1952); similar claims are made for mink (National Research Council, 1968).

During the degradation of tryptophan, several intermediates are produced, and many urinary metabolites have been described. Two major fates of tryptophan undergoing degradation, however, involve the conversion of a portion of the tryptophan molecule to nicotinic acid dinucleotide (NAD), or the complete oxidation of the molecule to carbon dioxide and water. These two pathways represent alternate fates of the intermediate, 3-hydroxy-anthranilic acid. These pathways are schematically shown in Figure 2.

3-Hydroxy-anthranilic acid, produced during tryptophan degradation, can undergo further degradation through a sequence of reactions leading to NAD formation or CO_2 and H_2O. Ikeda *et al.* (1965) have suggested that the activity of the enzyme picolinic acid carboxylase is a key factor controlling the alternate fates of tryptophan metabolites. In animals with high activity of picolinic acid carboxylase, the conversion of 3-hydroxy-anthranilic acid to CO_2 and H_2O is favored; if the activity of the enzyme is low, more of the tryptophan metabolite may be converted to NAD. The major example of this relationship has been in the cat, where picolinic acid carboxylase activity in liver is more than 30-times greater than in the rat. Tryptophan can serve as a source of nicotinic acid in the rat while it cannot for the cat. Henderson and Swan (1971) have suggested that the ratio of the activity of 3-hydroxy-anthranilate oxygenase to that of picolinic carboxylase represents a good measure of the relative efficiency of tryptophan—NAD conversion.

Whether differences in picolinic carboxylase activity among various species of poultry can explain the observed variations in nicotinic acid requirement remains to be seen. DiLorenzo (1972) observed that the picolinic acid carboxylase activity in livers of ducks and turkeys was 3

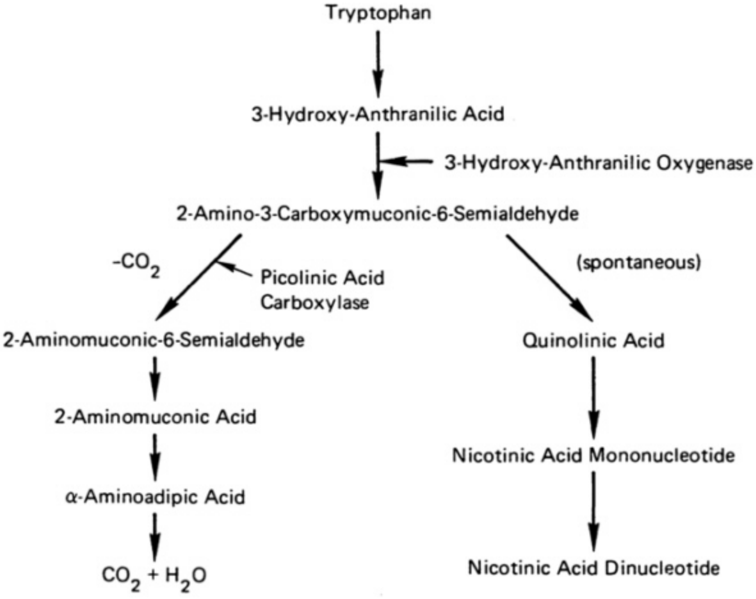

Figure 2 Alternate fates of 3-hydroxy-anthranilic acid during tryptophan degradation.

to 6-times that of chicks, but the usefulness of tryptophan as a nicotinic acid source for turkeys and ducks has not been studied in detail.

Nesheim (1972) described experiments in which two strains of White Leghorn chickens were selected on the basis of growth rate when fed nicotinic acid deficient diets. After four generations, chicks selected for poor growth (high nicotinic acid requirement) and fed the deficient diet weighed an average of 133 grams at 4 weeks of age with 18.3-percent mortality, while the chicks selected for fast growth (low requirement) weighed an average of 230 grams with 1.9-percent mortality when fed the same diet. Chicks from the two strains fed the diets supplemented with nicotinic acid weighed 288 and 279 grams respectively at 4 weeks of age. The selection appeared to be quite effective in differentiating strains of chicks as to their nicotinic acid requirements.

Further studies with chicks from these strains showed no difference in tryptophan requirement in the presence of sufficient dietary nicotinic acid, but a substantially different requirement resulted when no added nicotinic acid was included in the diet. These experiments suggested that the genetic variation was related to the relative ability of the strains to convert tryptophan to nicotinic acid (DiLorenzo and Nesheim, 1972). DiLorenzo (1972) also showed that the picolinic acid carboxylase activity in liver of chicks from the high-requirement strain was significantly higher than in livers of the low-requirement strain. This would be consistent, at least, with a change in the efficiency of the conversion of tryptophan to nicotinic acid between these strains. Further studies are needed to demonstrate this more convincingly.

Vitamin D

The dietary requirement of vitamin D seems to show remarkable variation among various species of domestic poultry. The minimum requirements established by the National Research Council for chickens, turkeys, ducks, pheasants, and Japanese quail are listed in Table 4. Turkeys and pheasants appear to require a considerably greater vitamin D_3 level in their diets than do chickens and ducks. The Japanese quail appears to be intermediate in the amount of vitamin D required for early growth and bone calcification. Less information on genetic variations within a species seems to be available. Olsson (1949) has reported that Rhode Island Red and White Sussex chicks required, respectively, 2.7 and 1.6-times more vitamin D per unit of diet than White Leghorns. Olsson used the distance between calcification zones of the distal tarsus and the metatarsus measured in x-ray photographs as the criterion of vitamin D adequacy. He also used cod liver oil as the source of vitamin D. In Olsson's studies the requirement of White Leghorn chicks and of turkeys was similar to those shown in Table 4 for the respective species.

Confirmation of these breed differences seems to be lacking in subsequent studies in which other criteria for vitamin D requirement were used. Waldroup *et al.* (1965) found that the NRC requirement of vitamin D_3 (200 IU/kg) was adequate for broiler chicks provided that calcium and phosphorous levels were balanced and sufficient calcium was present in the diet. Early studies by Baird and Greene (1935) also showed that 180 IU/kg of feed was sufficient for New Hampshire Red chicks in studies using cod liver oil as a source of vitamin D.

Titus *et al.* (1953) tested four purebred strains of New Hampshire chickens and numerous crosses of these strains for uniformity of response to a fixed allowance of vitamin D. By pretesting matings, it was possible to produce chicks with a tibia ash falling in a narrow range. For a given group of matings, a high correlation was found between the tibia ash from one hatch and from a later hatch. Using such chicks, Kennedy *et al.* (1953) showed that the precision of the vitamin D biological assay was improved. This represents a very useful application of genetic control of stock used for a nutritional problem.

A curious condition due to vitamin D deficiency—blackening of feathers of certain breeds of chickens—has been reported by several workers (Decker and McGinnis, 1947; Glazener and Briggs, 1948). Lillie and Bird (1949) found that such feather blackening occurred when Buff Orpington and Rhode Island Red chicks were fed vitamin D-deficient diets but that Buff Rocks showed much less of the abnormality. Lillie *et al.* (1953) selected for resistance or nonresistance to blackening of feathers from a mixed population of Buff Rock and Buff Orpington chickens. After three generations, 33.8 percent

TABLE 4 Vitamin D Requirement of Various Species of Domestic Poultry

Animal Type	Vitamin D_3 Requirement (IU/kg of diet)
Chicken	200
Turkey	900
Duck	220
Pheasant	1200
Quail (Japanese)	480

SOURCE: National Research Council (1971).

of chicks from the line selected for resistance to black pigmentation showed black pigment when fed the vitamin D-deficient diet, while 96.8 percent of chicks from the nonresistant line developed the pigment. There was relatively little black pigment showing in either line when vitamin D-supplemented diets were fed. This seemed to be the only aspect of vitamin D deficiency affected by selection since both lines developed rickets when fed the low-vitamin D diet. The metabolic basis for the feather blackening in vitamin D deficiency does not seem to have been established.

The metabolic differences among species of poultry responsible for their different vitamin D requirements are not known. Since the metabolism of vitamin D has become much clearer as a result of recent studies in several laboratories, the investigation of species variation may be possible (Avioli and Hoddad, 1973). The action of vitamin D_3 requires its conversion to the metabolites, 25-hydroxycholecalciferol and 1,25-dihydroxycholecalciferol. Investigation of the effectiveness of these compounds in various species of poultry should prove interesting in relation to variations in vitamin D requirements of the various species.

Other Vitamins

Relatively little information is available as to the genetic variation in requirements for other vitamins in poultry. There are some isolated references in the literature to breed or strain differences, but few detailed studies.

Rhode Island Red chicks were reported to require about 0.75 mg/kg (12 percent) less pantothenic acid than White Leghorn chicks (Bauernfeind *et al.*, 1942). The data for this experiment are not reported, and the comparison with the Leghorns was not done simultaneously. Lucas *et al.* (1946) suggested that Rhode Island Rex × Barred Plymouth Rock crossbred chicks had a higher pyridoxine requirement than White Leghorns, although no direct comparison was made between the breeds. In another study, White Leghorn chickens had a higher rate of mortality than broiler chicks when fed diets low in vitamin B_6, but no difference in the amount required for optimal growth rate (Daghir and Balloun, 1963).

Nesheim (1970) reported that variability among chicks from 10 sire families in two strains of White Leghorn chicks fed choline-deficient diets was low compared to the variability in response to deficiencies of nicotinic acid or arginine.

White Leghorn chicks have been reported to be less susceptible to encephalomalacia than heavy breeds (Howes and Hutt, 1952). When vitamin E-deficient diets were fed for a 40-day period to White Leghorn, Rhode Island Red, and Barred Plymouth Rock chicks, there was higher mortality and a greater incidence of encephalomalacia in the heavy breeds. Since encephalomalacia occurs when chicks are fed diets high in unstable, unsaturated fats (Scott *et al.*, 1969), the greater feed intake of the heavier breeds with accompanying greater consumption of the unsaturated fatty acids may have precipitated the disease more rapidly in the heavy breeds. Further studies of the breed difference in other vitamin E deficiency diseases seem to be lacking.

Variations in the vitamin A requirement of strains and breeds of chickens have been studied to a limited extent. Olsen *et al.* (1964) found that the vitamin A requirement was similar for two strains of Columbian Rock chicks and one strain of New Hampshires, although the New Hampshires seemed to be more efficient than the Columbian Rocks in depositing vitamin A in the liver. Wide variations were reported in vitamin A requirements of breeds of chickens (Donovan, 1965), but the differences obtained in response to the vitamin A levels in these studies seem not to justify the widely differing vitamin A requirement reported.

Selection for high and low total blood carotenoid concentrations has been reported to be successful (Letendre *et al.*, 1968). After four generations the line selected for high blood carotenoid level had a mean of 8.9 μg/ml of blood as opposed to 5.8 micrograms for the line selected for low concentration. Blood carotenoids apparently have a reasonable level of heritability (Stone *et al.*, 1971). No studies have been reported on the potential effects of such selection on vitamin A requirement in such strains.

Bobwhite quail are reported to have a vitamin A requirement of 13,000 IU/kg of feed, nearly 10-times that of chickens (Nestler, 1946), but no additional experiments have been reported attempting to explain an apparent extraordinarily high vitamin A requirement for quail.

INORGANIC ELEMENTS

There are 14-15 inorganic elements that have been shown to be dietary essentials for chickens. Although relatively good information is available on the dietary requirement for these elements of growing chicks, little information is available with which to assess the variations associated with these requirements. There are breed and strain variations associated with metabolism of some of these elements, but these are somewhat hard to interpret.

Undoubtedly most information is available on the deposition of calcium in eggshells by laying chickens. The amount of calcium deposited in a shell has been shown to be under genetic control. Shell thickness, specific gravity, and shell strength have all been shown to vary with breed or strain of chicken, and a substantial portion of the variation in these traits within a population is genetic (Hutt, 1949; Lerner, 1958; Nagai and Gowe, 1969; Rodda, 1972).

Such variations in shell quality also represent variations in calcium metabolism, but they may not represent variations in nutritional requirements in the usual sense. Eggshell quality is a physiological trait affected by a great many factors. There is little evidence that hens laying good eggshells have a different dietary calcium requirement than those laying poor eggshells. There seems to be little published information on genetic variability in the absorption, bone deposition, or general dietary requirement for calcium that may not be influenced by other considerations, such as feed intake or rate of production. A full consideration of physiological factors affecting calcium utilization is beyond the scope of this paper.

Several investigators have reported breed differences in requirements of chickens for manganese. In a widely quoted study, Serfontein and Payne (1934) compared the incidence of perosis among offspring of 1 male mated with 7 females that never showed signs of perosis with the incidence of a similar breeding pen made up of individuals who had some degree of perosis from 3 to 8 weeks of age. Perosis occurred in 18.6 percent of the offspring of the "straight legged" mating during the first 6 weeks of life, while the chicks from the "crooked legged" mating had an incidence of 50 percent.

Although many nutritional deficiencies result in perosis (Scott *et al.*, 1969), most authors since have considered that Serfontein and Payne were observing manganese deficiency, as diets for poultry used at that time were generally low in managanese. Gallup and Norris (1939) found that 50 ppm of dietary managanese was required to prevent perosis in New Hampshire chickens, but 30 ppm was sufficient for White Leghorn chicks. Similarly, Barred Rocks showed a greater drop in hatchability than White Leghorns when fed a ration deficient in manganese (Golding *et al.*, 1940). Eight inbred lines of Brown Leghorns were found to differ markedly in their ability to transfer manganese to eggs (Bolton, 1957), and abnormalities in newly hatched chicks were alleviated in some strains by increasing the manganese content of the diets but not in others. Although the data cited suggest that some variation in manganese requirement exists in populations of chickens, no information is available as to the mechanism of such variation.

Only isolated evidence is available on genetic variation in requirements of other elements. Turkeys and chickens seem to differ in their ability to use anhydrous dicalcium phosphate as a source of dietary phosphorus (Gillis *et al.*, 1962). Three strains of White Leghorn chicks differed in rate of mortality when fed magnesium-deficient diets from hatching (Christensen *et al.*, 1964). The differences in mortality seemed to be due to differences in the uptake of magnesium from the egg by embryos during incubation. The chicks were then hatched with varying stores of magnesium.

WATER METABOLISM

Water is a nutrient, highly important to all animals, but often neglected in lists of required nutrients. Highly significant differences in water content of droppings were found among thirty entries in the Texas Random Sample Egg Laying Test (Quisenberry and Malik, 1963). This suggested that problems of wet droppings often reported in laying flocks may have some genetic basis. Individual laying hens producing wet droppings were not adversely affected when their water intake was restricted in studies reported by Lintern-Moore (1972). She concluded that wet droppings were the result of a primary polydipsia rather than an obligatory water loss followed by increased water intake.

The genetic basis for variations in water metabolism of poultry was demonstrated convincingly by Dunson and Buss (1968). An inbred strain of chickens was established which seemed normal in all respects except that excessive amounts of water were consumed and excreted. Water consumption of hens from the mutant strain averaged 25.3 percent of their body weight per day, whereas normal controls consumed an amount equivalent to only 7.2 percent of their body weight. Comparable differences were observed in water excretion between normal and mutant hens. Turkeys were also found showing similar characteristics of water intake. According to Dunson *et al.* (1972) the condition is inherited as a simple autosomal recessive.

The physiological mechanism controlling the polydipsia in these birds has not been completely established. When water intake was controlled to normal levels, no adverse effects were observed. The polydipsic hens had difficulty in concentrating urine when consuming solutions of fairly high salt concentration. Dunson *et al.* (1972) suggest that the defect may be caused by the inability of the kidney to respond to antidiuretic hormone. Although the hypothalamus seemed to contain normal amounts of arginine vasotocin, the neurohypophysis contained reduced amounts. This was suggested as evidence that increased neuro hypophyseal release of the arginine vasotocin may have occurred but that the kidney failed to respond.

The finding that genetic defects occur in control of water intake and excretion in chickens should shed some light on the field problem of wet droppings. The extent to which polydipsic individuals exist in present populations of poultry must be investigated. Attention to this trait by poultry breeders may result in improved condition of droppings in commercial flocks.

GENETIC VARIATION IN PHYSIOLOGICAL TRAITS RELATED TO NUTRITION

Numerous reports of genetic variations in physiological traits occur in the literature. For the most part, a discussion of these studies is beyond the scope of this paper. Some conditions related to nutrition have been described, however, that have not been discussed with specific nutrients.

A cartilage abnormality was described in chicks by Leach and Nesheim (1965) that was related in some way to the nutrition of the growing chick. Affected chicks had a cartilage plug, extending from the epiphyseal growth plate into the metaphysis of the tibiotarsus and tarsometatarsus, which was not replaced by bone and calcified as in normal chicks. In severely affected chicks the leg bones would twist and some lameness and trouble in walking was observed. Several other reports (Hemsley, 1970; Siller, 1970; Laursen-Jones, 1970; Riddell *et al.*, 1971) indicate that this abnormality is fairly widespread in commercial broiler flocks. A similar condition has been observed by McCapes (1967) in turkeys and by Wise and Jennings (1972) in ducks. The term *tibial dyschondroplasia* was used to describe the condition (Siller, 1970; Riddell *et al.*, 1971).

The incidence of tibial dyschondroplasia is generally low in a population of chickens. Leach and Nesheim (1965) found the abnormality in 10–15 percent of chicks studied, when they were fed a semipurified diet, but, when a practical chick starting diet was fed, the incidence was very low. This suggested that the diet affected the incidence of the disorder. Since nutritional studies were difficult when such a small proportion of the population showed the abnormality, a selection program was started for high or low incidence of tibial dyschondroplasia in a population of broiler type chicks. After eight generations, 70–80 percent of the chicks from the strain selected for a high incidence showed the abnormality when fed a semipurified diet, while only 2 percent of the chicks from the low-incidence strain were affected under the same conditions (Leach and Nesheim, 1972). The proportion of chicks affected was much higher when the purified diet was fed compared to a practical chick starting diet. White Leghorn chicks showed no evidence of the abnormality when fed either diet.

The selected strain was used in studies aimed at identifying the nutritional factors involved in the condition. No deficiency of known nutrients seemed to be involved in the development of tibial dyschondroplasia. The incidence of the condition could be affected by modification of the dietary mineral mixture to produce changes in the acid-base balance of the diet. When diets tended to produce a metabolic acidosis, the incidence was increased, whereas diets that caused a metabolic alkalosis resulted in a lower incidence. The precise metabolic cause of the cartilage abnormality is not yet known.

These experiments are an example of a condition of incompletely understood etiology that can be modified by selection. The physiological trait giving susceptibility to the cartilage abnormality apparently is inherited, but the susceptibility can also be modified by the diet fed to the chick. Leach and Nesheim (1972) have suggested that selection against the condition may be the best way for its control.

Plasma levels of uric acid have been shown to respond to selection (Cole and Austic, 1971). A strain of chickens was selected with a high incidence of articular gout and high levels of plasma uric acid. After four generations of selection the line selected for high blood uric acid had an articular gout incidence of 80 percent for the males and 91 percent for the females at 11 months of age. In a line of similar origin selected for low plasma uric acid levels, the incidence of articular gout was 8.7 percent for males and 1.3 percent for females at 11 months of age. Chicks from the high-uric acid line did not tolerate excesses of dietary protein as well as those from the low-uric acid line. Austic and Cole (1972) reported that hens from the high-uric acid line have a defect in the secretory mechanism for uric acid in the kidney, causing them to be less effective in excreting uric acid than normal hens. Uric acid production by the high-uric acid line was not elevated. The high-uric acid strain should be useful in the study of uric acid transport by kidney.

Another study of the effectiveness of selection for articular gout was reported by Peterson *et al.* (1971). These authors were able to select strains of chickens that differed markedly in incidence of gout when they were fed diets of 80-percent protein. The strains differing in susceptibility to gout also had different levels of uric acid in the blood when fed normal or excessive levels of protein.

The various species of poultry differ quite markedly in susceptibility to toxins produced by the mold *Aspergillus flavus*. Whereas only 0.03

milligrams of aflatoxin was reported to be toxic for ducks (Carnaghan, 1965), 0.25–0.5 mg/kg was required to depress growth of turkeys and pheasants (Muller *et al.*, 1970). Growing chickens seem to be able to withstand levels below 1.25 to 2 mg/kg with no apparent ill effects (Carnaghan *et al.*, 1966; Kratzer *et al.*, 1969; Smith and Hamilton, 1970). Strains of chickens also seem to show wide variation in susceptibility to the effects of dietary aflatoxin (Carnaghan *et al.*, 1967; Smith and Hamilton, 1970). The species and strain differences in susceptibility to aflatoxins suggest that there may be considerable variation in systems that metabolize these substances.

Some off-flavors in eggs may be the result of individual metabolic variations that are expressed when certain diets are fed. Several investigators (Miller *et al.*, 1972; Hobson-Frohock *et al.*, 1973; Vondell, 1948) have reported that individual hens from breeds laying brown eggs were found to produce eggs with off-flavors. These "tainted" eggs were found to contain trimethylamine in larger amounts than untainted eggs. If the individual hens identified as producing tainted eggs received trimethylamine in their diets, a high proportion produced eggs with off-flavor, but other hens not previously identified as producing off-flavored eggs had a lower proportion of affected eggs if fed trimethylamine. The tainted eggs were produced only when hens were fed certain diets. This condition seems to be related to metabolic differences among individual hens that are expressed only in certain environments.

Breed variations in response to antibiotic supplementation of poultry rations have also been reported (Nordskog and Johnson, 1953; King, 1970). The regulation of serum cholesterol level in chickens also seems to be under genetic control (Cherms *et al.*, 1960; Wilcox and Shaffner, 1963).

These studies are but a few examples of physiological traits that are under genetic control. They do not represent differences in nutrient metabolism directly, but do represent conditions where different genetic background – dietary condition interactions can be demonstrated.

Discussion

The utilization of major food components by poultry appears to be highly efficient, and little evidence of substantial genetic variation in efficiency of their use has been found in the literature covered by this review. This is not surprising since efficient absorption and nutrient metabolism would clearly have survival value, and would be expected to be favored in the wild ancestors of domestic poultry. Digestion and absorption seem to virtually be complete for compounds that can be substrates for enzymes found in the gastrointestinal tract. There seems to be slight prospect that selection can result in increased utilization of cellulose or hemicellulose components of diets fed to poultry, although there seems to be no direct evidence in the literature on this point.

The utilization of amino acids, when fed at growth-limiting levels in the diet, likewise seems to be quite efficient. The selection experiments aimed at improving the utilization of lysine or methionine that have been reported do not give very much encouragement that substantial changes can be made in efficiency of amino acid utilization by populations of chickens. Therefore, poultry with the same basic metabolic machinery for nutrient utilization will be used for food production in the future, even though selection for productivity may still achieve substantial improvements in overall gross efficiency. It should be pointed out, however, that such a conclusion is based on very meager experimental evidence, and that further investigation of metabolic variations that affect the utilization of energy and specific nutrients should be encouraged. In particular, the effect of selection for improved feed efficiency on the maintenance requirement for energy has not really been established in poultry.

The various species of poultry differ in quantitative nutritional needs. Turkeys, ducks, and chickens have somewhat different nutritional needs that seem to be based on substantial metabolic variation among species. Requirements of nicotinic acid and vitamin D represent two examples of this type of variation, although the metabolic basis for these variations is not known.

Broiler-type chickens are often fed different rations than are White Leghorn types (Scott *et al.*, 1969). The daily energy requirement and the daily protein needs of a growing broiler are quite different from those of a White Leghorn, and such differences are passed from one generation to another. But these differences in nutritional requirements seem to be more a consequence of differences in body size, or potential growth rate, rather than due to a fundamental difference in the metabolic efficiency of protein synthesis or the utilization of energy.

The genetic variations in nutrient requirements that occur seem to be mainly in metabolic detail. The variations in arginine requirement that were achieved by selection (Nesheim *et al.*, 1971) were the result of the metabolic problems caused by the presence of high levels of lysine circulating in body fluids. Individuals are present in populations of chickens that can degrade dietary excesses of lysine considerably better than others. These could be segregated by selection when an appropriate dietary condition was found that differentiated these individuals in the population. The average chicken, at least in many commercial strains, seems to be more like individuals from the high-arginine requirement strain (Nesheim *et al.*, 1971) than from the low requirement strain. There may be some advantage in having a poor ability to dispose of excesses of lysine that has not yet been discovered.

In many respects, the genetic variations that affect the nutrition of poultry are similar to the genetic variations in metabolism that have been found in man (Stanbury *et al.*, 1972). The single-gene mutations affecting riboflavin transport or water metabolism that have been discussed are clearly metabolic diseases that can be found in poultry populations. The individuals with abnormal water metabolism (Dunson and Buss, 1968) do not seem to be less productive than other members of the population, but the wet droppings produced cause husbandry problems that may be overcome by eliminating polydipsic individuals from the breeding population. This clearly is a metabolic disease of genetic origin in poultry that may have considerable practical significance.

Similarly, the metabolic disturbance causing tibial dyschondroplasia (Leach and Nesheim, 1972) can be modified by nutrition but seems to have a genetic origin as well. Wise and Jennings (1972) have suggested that this abnormality is associated with selection for rapid growth rate in poultry. Although the causes of tibial dyschondroplasia as yet are not known, present evidence suggests that it has the characteristics of a metabolic disease.

More of these types of conditions have not been discovered in poultry primarily because few metabolic studies are made on large numbers of individuals in diverse populations. Individuals not "metabolically fit" may die young or may not be used as breeders and are therefore selected out of a population. Producers must be alert for those problems that may enter a breeding population, which may not be observed except under certain conditions.

There are likely to be other such hereditary conditions in poultry populations that may be expressed only in certain environments. Fatty liver hemorrhagic problems in laying hens may be an example of such a condition although this has not definitely been shown to be the case (Ivy and Nesheim, 1973).

It is clear that activity of some enzyme systems controlling metabolic processes can be modified by selection. This is true of lysine—ketoglutarate reductase (Wang *et al.*, 1973) and probably also for picolinic carboxylase (DiLorenzo, 1972). It has not been established whether changes in these enzymes have involved genes only concerned with regulation of the amount of enzyme found in the tissue, or whether the changes in tissue enzyme activity are associated with changes in the enzyme structure. The enzyme changes do not seem to be associated with single genes, but the changes in tryptophan and lysine metabolism found appear to be the result of the action of more than one gene.

Not all metabolic processes seem to show as much variation as those affecting tryptophan–niacin conversion and lysine degradation. The response to deficiencies of glycine, choline, and lysine, for example, seem to be subject to relatively little variation (Nesheim, 1970).

Some genetic differences reported between breeds of poultry have involved variation between White Leghorns and the heavy breeds. The riboflavin and thiamin content of eggs and the managanese requirement for prevention of perosis seem to vary between these two basic types of poultry. It would be of interest to determine whether these differences are due to genes directly affecting the metabolism of these nutrients, or whether they may be explained by some other basic genetic difference, such as level of circulating estrogens that may cause the effects observed.

For specific research problems in nutrition, selection of a special population of animals for a characteristic to be studied may be very useful. It can be time-consuming and expensive to approach problems in this way, but often it is the only way to confirm that some apparent nutritional problems may have a genetic origin. In solving biological problems, the compartmentalization of science should not be a bar to using all the tools available to solve the problem. Certainly genetics can be a valuable tool for use in solving many problems related to biology, and nutritionists should not leave all these problems to the geneticist.

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Genetic Variation in Nutrition of Sheep

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Knowledge of sheep nutrition is probably more extensive than for any other aspect of sheep production; however, direct investigation of genetic variation in sheep nutrition has been rare. Little is known of genetic differences among sheep in requirements of specific nutrients. Available information generally comes from research in related areas, such as investigation of environmental effects and studies on relation of feed efficiency to milk production, rate of growth, and body weight. (An exception is the interest in efficiency of feed use for wool growth in Australia.) Still, there may be considerable opportunity to utilize genetic variation in selection to increase the efficiency of production of lamb meat and wool. Turner and Young (1969) list the measurement of efficiency of conversion of feed for wool and other production traits as one of the current problems in sheep breeding. They further mention that no work has been done on the possible genetic variation in a ewe's capacity for turning food into weight of lamb weaned.

Variations in the ability of a sheep to find feed and forage, to select those materials that are more nutritious or easier to digest, to have

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high voluntary feed intake or appetite and to use the feed to produce meat, wool, and lambs, all are involved in *feed efficiency*. Further, a part of the feed consumed is required to maintain body tissues and functions, and a part is needed for growth or the increase in body tissues. The end point of feed use in the sheep is further complicated by the production of two quite different products, meat and wool. Feed efficiency is difficult to measure for it may also vary with age, sex, season, stage of reproduction, behavior and activity, temperature, humidity, and possibly many other factors. Most of the research on genetic variation of nutrition in sheep has been involved with feed efficiency or related factors. Some information is available on genetic variation in mineral metabolism.

HERITABILITY OF FEED EFFICIENCY

Few estimates have been made of heritability of feed efficiency. Botkin (1955) obtained estimates of feed per unit of gain of 0.15 but the estimate for rate of gain was 0.84. Witt *et al.* (1967) found variation of feed efficiency high within and between sire groups of growing lambs. Heritability estimates for feed efficiency were 0.13 from birth to 36 kilograms and 0.17 from 20 to 36 kilograms, but the confidence limits were wide. Vesely and Robison (1968) obtained estimates of heritability of feed efficiency of 0.06 from Rambouillet lambs and 0.16 for Romnelet lambs from a 126-day post-weaning test.

Ercanbrack (1974) estimated heritabilities using various means of evaluating efficiency of post-weaning gain in Targhee lambs. Lambs in the first 2 years were tested late in the 10–80-day post-weaning period for only 28 days. Lambs in the last 2 years were tested earlier for 42 days. Efficiency of gain was evaluated: (1) as the deviate of gain from the curvilinear regression of gain on feed adjusted for body weight, (2) as the deviation of feed from the curvilinear regression of feed on body weight and gain, (3) as the ratio of gain over feed, (4) as the ratio of gain over feed adjusted for body weight, and (5) as the ratio of gain adjusted to standard individual feed over feed adjusted for weight and gain. Heritabilities for all periods were highest for (2) 0.131 ± 0.080 and lowest for (3) 0.023 ± 0.055. Estimates based on only 42-day periods were highest for (1) 0.198 ± 0.141 and lowest for (3) 0.072 ± 0.094. Genetic variability appeared to be revealed better by the 42-day feeding period. None of the evaluations were wholly satisfactory. The author (S. K. Ercanbrack, personal communication, 1974) has since developed an index to use in selecting for feed efficiency, which appears to be better than any of the evaluations used above.

Heritability of body weight and of gain from various ages or weights to slaughter weight are of interest in regard to genetic variation in feed efficiency, but only some of the more recent reports will be cited. Harrington *et al.* (1962) obtained estimates for rate of gain from birth to market weight of 41 kilograms. Heritability to 23 kilograms was 0.09 ± 0.07 to 0.13 ± 0.08; from 23 to 41 kilograms was 0.38 ± 0.13 and from birth to 41 kilograms was 0.34 ± 0.12 to 0.36 ± 0.12. Heritability of weight often increases after maternal effects, such as a varying milk supply, decrease. Butcher *et al.* (1964), Bowman and Broadbent (1966), Vogt *et al.* (1967), Vesely and Robison (1968), Srinivasan (1970), Thrift *et al.* (1971), and Bowman and Hendy (1972) found low to moderate heritability estimates for various measures of preweaning gain.

Heritability of body weight and weight gains tends to increase as weaning age is approached, and is often moderate to high to slaughter weights, as shown by Broadbent and Watson (1967), Vesely and Robison (1968), Radomska (1970), Acharya and Malik (1971), Nawara (1972), Nawara and Duniec (1972), Bowman and Hendy (1972), and Bradford and Spurlock (1972). Ercanbrack and Price (1972) found that heritabilities involving body weights of range lambs tended to increase with time from weaning. Thrift *et al.* (1973) obtained heritabilities of 0.09 ± 0.06 for gain from birth to 70 days, 0.10 ± 0.07 for 70-day weight, 0.23 ± 0.12 for gain from 70 days to market, and 0.21 ± 0.11 for market age. In general, the results indicate that lambs reach their full potential for growth in the period from weaning to market or in the period around 6 months to 1 year of age or both.

Botkin (1964) found that intrasire half-sibling correlations for body weights and gains to slaughter weight were higher for full-siblings than half-siblings. Vogt *et al.* (1967) found the opposite, that heritabilities were higher for singles than for twins. The difference is probably related to conditions under which twins are raised as to whether the difference between individual twin members tends to be increased or decreased by other environmental effects.

Heritability estimates from paternal half-siblings, for both 120-day weights and yearling weights, were higher in a better than in a poorer environment, but realized heritabilities were very similar for the two environments (Osman and Bradford, 1965). Ercanbrack and Price (1972) found that heritabilities of gain under a good nutritive environment were typically at least double those for the less favorable environment during October through December for range lambs. Genetic variation in gains was distinctly higher under the better environment.

RELATIONS OF FEED EFFICIENCY TO OTHER TRAITS

Phenotypic correlations between feed efficiency and rate of gain have generally been high. Botkin (1955) obtained a correlation of -0.72 between rate of gain and the ratio of feed to gain (feed/gain). Relationships between body weight, daily gain, feed consumption and feed efficiency were studied by Frederiksen *et al.* (1959) with post-weaning Rambouillet lambs. Initial body weight was correlated with daily feed consumption (0.59), daily gain (0.18), and feed/gain (0.37). Daily gain was correlated with daily feed intake (0.77) and with feed/gain (-0.63). Broadbent and Watson (1967) obtained estimates of -0.74 when live weight was variable and -0.89 when body weight was held constant. Witt *et al.* (1967) obtained correlations between daily gain and weaning weight of 0.59 and with feed efficiency of 0.58, although the correlation of 0.82 was obtained for 22–36 kilograms of body weight.

Builov (1965) found that, as gain increased from 129, 156, 198, 230, to 294 g/day, feed/gain decreased from 7.4, 6.2, 4.9, 4.6, to 4.2 kilograms. Glimp *et al.* (1968) observed that feed/gain increased from 3.66 when body weight increased from 18.1 to 27.2 kilograms and to 8.08 from 45.3 kilograms. Feed/gain for the entire post-weaning period, with body weight change from 18.1 kilograms to 54.5 kilograms, was 5.50. Obviously heavier lambs require more feed as they eat more and grow faster than lighter lambs, but they also have a higher maintenance requirement. Further, faster growing lambs consume more feed but use it more efficiently.

The relationships between feed efficiency and digestibility were studied on 46 Rambouillet ram lambs in each of three years by Price *et al.* (1965). In digestion trials each year, each lamb was limited to 85 percent of its average *ad libitum* daily feed intake during the last 42 days of the 84-day efficiency of gain tests. In a second trial in the third year, the feed intake was limited to 1.36 kilograms per 45.4 kilograms of body weight. Highly significant correlations between feed efficiency and dry-matter digestibility were found in the first year (-0.68) and with limited feed intake in the third year (-0.70).

Mitic and Kosanovic (1963) found that breeds ranked in the same order for feed efficiency as for rate of gain; the F_1 Hampshire × Tsigai (Cigaja) was highest, followed by the Ile de France × Tsigai, and then the Tsigai. Builov and Dzaparidze (1968) obtained similar results with 5 breeds: The Gorki gained 260 g/day with feed/gain of 4.2, and the Tsigai gained 152 g/day with feed/gain of 7.1 in the period from 5 to 7 months of age.

BODY COMPOSITION AND WEIGHT

Body composition is related to nutritional needs because the body is built from ingredients of feed. Reid *et al.* (1968) have found breed differences in body composition. Hampshires and Suffolks had less fat at 30–50 kilograms than Rambouillet × Columbias, Shropshires, or Corriedales. The Hampshire × Suffolk × Shropshire cross had slightly less fat at 60 kg than the Hampshire. Among the breeds studied, the Suffolks with a heavy mature size had the highest water and protein and the lowest fat content, especially at body weights greater than 30 kg. On the other hand, Corriedales and Shropshires with smaller body size or mature weight had less water and protein and more fat and energy than the other breeds. These differences became greater as body weight increased. Reid *et al.* (1968) further showed that body composition is largely related to weight rather than age. Burton and Reid (1969) also showed that body composition in sheep was not related to prior energy intake, was only slightly associated with age, but was chiefly associated with body weight. Rattray *et al.* (1974d) showed that level of nutrition could influence body composition on both an "as-sampled" basis and on a fat-free basis. Pregnancy appeared to influence empty-body composition in a manner similar to that of lowering the level of nutrition.

Seebeck (1966) found that the crossbred lambs in his study had significantly more dissectible fat than did the Merino. However, when fat content was adjusted for age as well as carcass weight, the genotype difference was removed. Reynolds *et al.* (1968) found significant breed differences in percentage of fat, ranging from 25.0 to 32.8 at 44.4 kilograms of body weight. Vesely and Peters (1972) found a breed effect of 16 percent on total variation of percentage of muscle with Rambouillet, Romnelet, Columbia, Targhee and Suffolk breeds. Rambouillets had the leanest carcasses with 50.5 percent muscle, while Columbias and Romnelets had 46.5 and 47.9 percent, respectively. Glimp *et al.* (1968) found that most of the muscle development of Hampshire-sired lambs occurred before 45.3 kilograms of body weight.

Rattray *et al.* (1973d) compared carcasses and wool-free empty bodies of 15 unselected and 15 weight-selected (10 years' selection for heavy weaning weight) Targhee lambs, 13 half-Finn–half-Targhee lambs, and 17 quarter-Finn–three quarter-Targhee lambs. The quarter-Finn lambs on the average had higher fat and energy but lower water, protein, and ash contents than the other genotypes; while the weight-selected lambs had lower fat and energy but higher water, protein, and ash contents than the other genotypes. Genotypes were not significantly different in any composition parameter on a fat-free basis.

No significant difference due to genotype was found in the regression of carcass ether extract (%) on carcass density. Although the slopes of the regressions were variable, they were not significantly different (Rattray *et al.*, 1973b). Indications of breed differences in chemical composition of fetuses were found in results of Graham (1964), Langlands and Sutherland (1968), and Rattray *et al.* (1974b).

Fat is synthesized more efficiently than protein in the sheep. Orskov and McDonald (1970) using early weaned, rapidly growing lambs on 15 dietary treatments, found the energy cost in both kilocalories per gram and kilocalories per kilocalorie of protein synthesis was higher than that of fat synthesis. Breed differences in feed efficiency appear to be due at least in part to differences in fat content at a specific weight (Reid, 1971). Rattray *et al.* (1974c) found that protein synthesis required 45.6 ± 8.69 kcal ME per gram or 8.14 ± 1.55 kcal ME per kilocalorie of protein deposited. Fat synthesis required 10.2 ± 3.58 kcal ME per gram or 1.10 ± 0.38 kcal ME per kilocalorie of fat deposited.

ENERGY REQUIREMENTS

Rattray *et al.* (1973c) have developed a net energy (NE) system for expressing energy requirements and feed values for young sheep. Estimated net energy values were related to metabolizable energy (ME) content of the diet by the following regressions:

$$\begin{aligned} NE_m &= 0.79\ ME - 0.40 \\ NE_g &= 0.58\ ME - 0.52 \\ NE_g &= 0.60\ ME - 0.61 \text{ (wool free)} \end{aligned}$$

where NE_m requirements were derived from fasting heat production and NE_g requirements were derived from the regression of energy gain on body weight gain.

Growing lambs, aged 3–5 months utilized ME for maintenance and gain with efficiencies of 65.7 and 40.8 percent, respectively (Rattray *et al.*, 1973e). Growing ewe lambs utilized ME with efficiencies for maintenance, gain, and pregnancy of 64.9 and 63.0 percent, 47.8 and 40.6 percent, and 17.5 and 16.0 percent, respectively, for high and low-energy diets (Rattray *et al.*, 1973a)

Nonpregnant sheep utilized ME for maintenance and gain with efficiencies of 65.7 and 56.0 percent, respectively (Rattray *et al.*, 1974a).

These authors further showed that efficiency of utilization of ME for pregnancy, conception development, and fetal development was 16.1, 12.5, and 12.2 percent, respectively.

MINERAL REQUIREMENTS

Wiener (1971) has reviewed reports on genetic variation in mineral metabolism of ruminants. Large differences among breeds and among sire progeny groups in the incidence of swayback in lambs were reported by Wiener (1966). Wiener and Field (1966) showed large differences in blood copper concentrations in these breeds. Later work revealed not only that breed differences persisted in spite of copper injections and wide seasonal variation in average copper concentrations in the flock but also that, to a limited extent, seasonal variation was modified by genetic factors (Wiener *et al.*, 1969, 1970). Crossbreds had considerably higher blood concentrations of copper than the mean of their parents even though the crossbreds were more nearly intermediate in incidence of swayback. Seasonal variation in blood copper concentration was lower in groups with relatively high concentrations of blood copper than those with relatively low concentrations. Lamb-mother regressions calculated from one flock indicated that variation in blood copper concentration may be genetically variable within breeds, but information on differences among sire progeny groups is inadequate to predict the response of blood copper to selection (Wiener and Field, 1971).

Concentrations of copper in liver (Wiener and Field, 1969) and in the brain (Wiener and Field, 1970) also show significant breed variation. Crossbreeding appeared to affect liver values differently from blood values, thus indicating some genetic independence in copper concentrations in the blood and liver.

Breed differences in susceptibility to copper poisoning have been observed. There was a significant breed difference in mortality even though risk of death was strongly associated with dose given per unit live weight of sheep (Wiener and Macleod, 1970). Marston (1950) had observed that under experimental conditions, British breeds of sheep usually succumb to the first hemolytic crises; Merino sheep may survive two or three such crises as cited by Wiener (1971).

Significant breed variation based on a single bleeding was found for concentration in whole blood of calcium, phosphorus, magnesium, and chlorine, although the contribution of breed or crossbred group to the total variation was less than 10 percent, except for magnesium, where it was 20 percent (Field *et al.*, 1960; Wiener and Field, 1971). Consistent breed differences in housed sheep were not found for calcium, phosphorus, magnesium, sodium, and potassium (Long *et al.*, 1965) nor for calcium and phosphorus (Becker and Smith, 1950). The influence of breed and Ka genotype on potassium concentrations in plasma of grazing sheep was shown by Eagleton *et al.* (1970). A marked genetic relationship of potassium and sodium exists in whole blood where a gene for high- and low-potassium concentration has been demonstrated by Evans and King (1955). Wiener (1971) suggests that genetic changes in the concentration of one mineral in the blood may well be accompanied by changes in the concentrations of others.

MILK PRODUCTION

Gardner and Hogue (1964b) estimated that lambs utilized 77 percent of the energy of milk consumed and 19.4 percent of supplemental feed energy for body energy gain and maintenance energy. On an energy gain basis only, single and twin lambs utilized milk gross energy with an efficiency of 43.8 and 37.4 percent, respectively. Estimated creep feed utilization was 13.2 percent for single lambs and 8.8 percent for twin lambs. Efficiency values did not differ due to level of intake. Gross energy in the pelleted ration fed to ewes was converted to milk and thence to lamb gain with an average estimated feed efficiency of 8.3 percent. The estimated utilization of milk protein for body protein gain and wool growth was 43.3 percent. Estimated creep ration protein utilization was 19.9 percent. There would seem to be ample room for increasing these efficiencies through genetics and breeding.

LAMB PRODUCTION

Efficiency of feed use for lamb production is involved with the proportion of total feed required to maintain the ewe for the entire year to that consumed directly by the lamb for growth to market weight. Generally, production is more efficient when less feed is used to maintain the ewe and more is used to grow the lambs that are sold (Blaxter, 1968). Large (1970) has defined the efficiency of meat production as the weight of carcass produced per 100 units of digestible organic matter consumed. He concludes that efficiency will be highest from small breeds of ewes producing large litters and crossed with a large breed of ram, leading to a high growth rate and final size in the lamb. He further states that a relatively small increase in litter size in the small breeds of ewe from one to two lambs per year may result in a level of efficiency as high as that achieved by a larger breed with a litter size of three to four lambs per year without having to resort to artificial rearing of lambs.

Body weight has an important relationship to production in utilization of range feed. Terrill and Stoehr (1942) presented data on lifetime lamb and wool production of Columbia, Corriedale, and Rambouillet ewes in relation to yearling body weight while on natural range feed. Weight of lamb weaned per 45.4 kilograms of ewe per year determined from the first 4 lambing years and the average 2–5 year body weights were 20.9, 24.5, and 22.7 kilograms, for light, middle, and heavy groups, respectively, for the Columbia; 25.4, 25.9, and 26.8 kilograms for the Corriedale; and 20.0, 20.9, and 22.7 kilograms, for the Rambouillet. The heaviest group (Columbias) failed to show an advantage over the next lighter group, possibly because the feed requirements of the Columbias exceeded the available supply under range conditions. Fleece weight per unit of body weight was greater for the lighter ewes.

Shelton (1971) showed that efficiency of lamb production increases as the reproductive rate and lamb weight increases but that with higher reproductive rates lighter lambs may be marketed without reducing efficiency. A slaughter weight of 54.5 kilograms might be considered optimum for lambs that are not excessively fat. Hogue (1973) has shown that weight of lamb marketed from the same feed supply can be increased by over 40 percent by increasing the lambs marketed per ewe from one to two where the number of ewes is reduced in relation to the number of lambs marketed. Marketing lambs at 47 kilograms live weight was more efficient than at 37 kilograms.

Lamb production requires extra nutritional demands at various critical stages, such as puberty, ovulation, late pregnancy, and lactation. Genetic variation in these demands has generally not been shown except as they are related to such traits as body weight. Trends in the sheep industry are toward more breeding of ewe lambs to lamb in their first year, more lambs per lambing and more than one lambing per year. All of these trends tend to increase nutritional demands over past practices that generally resulted in one lamb marketed per ewe per year. Even then, nutritional demands were often not met in late pregnancy and lactation, and ewes were often overfed during the long dry period. Basically, increases in lambing rates have been and probably will be obtained by selection. Thus, selection for the capacity to handle the feed necessary to support the extra reproduction demands is automatic.

Dyrmundsson (1973a,b) has reviewed the factors affecting puberty and early reproductive performance in sheep. Considerable genetic variation exists both among and within breeds of sheep in the attainment of puberty. There is a high relationship between body growth, weight, and sexual development in both sexes. A high plane of nutrition may hasten puberty and a low plane may delay it. Nutrition may be more important in young ewes during pregnancy and lactation because the demands of growth and reproduction must be met at the same time.

Price *et al.* (1973) studied effects of feed levels for 21 days prebreeding, 21 days during breeding, and 42 days prepartum on total weight of lamb produced per ewe. Feed levels were 65, 85, and 105 percent of the National Research Council (NRC) recommendations (National Academy of Sciences, 1968) for each period. Total weight of lamb at 80 days of age produced per ewe was highest (33 ± 2.6 kg) for 85 percent of NRC recommendations for each period, while the poorest (22.3 ± 2.6 kg) was for 105 percent at breeding and 65 percent for the prepartum period.

Huge genetic variation exists in ovulation rate and the ability to produce multiple births in sheep. These variations are often marked by the many environmental influences that occur and their large effects. The literature is too extensive to review here, but nutritional effects are among the important environmental factors that operate. Flushing to increase ovulation and conception rates and effects on embryo and postnatal mortality are prominent.

The increase in lambing rates has increased the need for practical means of raising lambs artificially from birth. Few ewes can raise more than two lambs successfully. Mortality is often reduced with conventional lambing rates if lambs that appear to have a poor chance on their mother are raised artificially. The behavior of lambs is such that artificial raising is more successful and requires less labor if the lambs are transferred during the first day after birth. Colostrum intake is highly desirable. Considerable knowledge of the nutritional requirements of the young lamb has accumulated to produce growth rates of artificially raised lambs equal to or even greater than those of lambs raised by their mothers (Lindahl, 1974). The use of milk replacer for lambs is increasing and its use is quite successful (Frederiksen *et al.*, 1971).

WOOL PRODUCTION

Research on efficiency of feed use for wool production has generally involved comparisons of strains that differed in their ability to produce wool. Ferguson *et al.* (1949) showed that breeds differ in the voluntary intake of feed and the conversion of this feed to tissues. Weston (1959) compared fine and strong-wool Merinos at pasture. The strong-wool strain was 22-percent heavier and produced 39-percent more clean wool.

The strong-wool strain appeared to select feed slightly higher in nutritive value. Differences in digestibility were small and inconsistent. In pens, the strong-wool strain produced 18-percent more clean wool per unit of feed consumed. Wool per unit of body weight was considered a useful criterion for selecting wool-producing sheep on pasture.

Schinckel (1960) concluded that a significant part of the difference in wool production of sheep selected for high, intermediate, and low levels of clean wool per unit of body weight under field grazing was due to differences in feed intake. Dolling and Moore (1960) found an increase in feed efficiency of a strain selected for high clean fleece weight. Hutchinson (1961) found that voluntary feed intake varied with body weight but that feed intake per unit of body weight was significantly associated with wool production. He found significant differences in individual apparent digestibilities, but these did not contribute to differences in gross conversion rates.

Ahmed *et al.* (1963) found a positive genetic association between wool production at pasture and voluntary feed intake in pens. However, Williams and Miller (1965) showed that genetic differences in wool production were not associated with differences in voluntary intake of feed, when intake was corrected for body weight. Williams and Winston (1965) also worked with strains selected for high, random, and low levels of wool production. The relative net efficiencies when there was no change in body weight were 116, 110, and 86.5, respectively, for the three strains. Efficiency varied between levels of nutrition; it decreased from the low to high level in all flocks. There were significant differences in feed efficiency between flocks and ewes within flocks, but the greatest variation was due to levels of nutrition. There was a decrease in feed efficiency with an increase in body weight. Dolling and Piper (1968) compared a strain selected for high wool production with random controls. They observed differences between groups in clean wool per gross energy intake but no significant group-nutrition level interaction. They found a large, positive phenotypic correlation between net efficiency under restricted feeding and gross energy under *ad libitum* feeding, and between net efficiency and clean wool weight under both regimes. No more than 1.5 percent of the energy consumed appeared as energy in the form of wool fiber. Saville and Robards (1972) also found strain differences in efficiency of feed use for wool, which prevailed when strains were fed below maintenance levels.

GENETIC-ENVIRONMENTAL INTERACTIONS

Investigation of genetic–environmental interactions in efficiency of feed use and in nutrition of sheep has attracted considerable interest.

Morley (1956) found that heritabilities of various traits did not vary with the plane of nutrition. Genotype-environment interactions were not found for any fleece trait or for 6-month body weight, but large and highly significant interactions were found for 12 and 17-month body weights.

An extensive experiment in Australia on genetic–environmental interactions involved five strains of Australian Merinos run as breeding groups under natural feed conditions in three wool-growing regions (Dunlop, 1962, 1963). A large number of fleece and body traits and number of weight of lambs born and weaned were studied. Real interactions were found in most of the traits, but they were generally small and accounted for only minor fractions of the variance. Strain differences were only slightly important in lamb production.

Dunlop and Young (1966) estimated interactions between sire and year (age) and sire and drop (year) from the five strains of Merinos at three stations. Interaction terms were generally small and not significant. They concluded that interactions will seldom appreciably hinder genetic progress from individual selection.

Dunlop *et al.* (1966) determined feed efficiency on three strains of Merinos at maintenance and at 1.4-times maintenance. Weight of oven-dry clean wool produced per 100 therms of net energy consumed increased from fine to medium to strong-wool Merinos at each level of nutrition. Interactions of strains and levels were not significant; differences from a digestion experiment were small and not significant. The authors concluded that strain differences in efficiency depend largely on differences in use of nutrients. They suggested that from their results selection of strains and, to a lesser extent, of individuals on a basis of feed efficiency would not be seriously affected by the energy level at which efficiency is measured.

King and Young (1955) compared Blackface, Cheviot, and Wiltshire sheep under good and poor planes of nutrition in warm and cold environments. They found that the breeds reacted differently to the different environments. There was no change in rank, but the Blackface sheep grew faster on a good plane of nutrition and wool production was also greater. The Wiltshire were heaviest and the Blackface lightest. The Wiltshires suffered most on a low plane of nutrition and showed greatest recovery in summer. Interactions were not significant.

King *et al.* (1959) compared the wintering of twin lambs from Blackface and Welsh breeds and five crosses on high (H) and low (L) planes of nutrition from October to January. Twins were both split and distributed in pairs to the two environments. Significant differences were found between crosses and twin pairs of the same cross for body weight and measures and wool production, but not for various blood traits.

There was only one significant cross-plane interaction for nonprotein nitrogen concentration in the blood. At the end of January each plane of nutrition group was subdivided into HH, HL, LH, and LL until May. Again differences were found for body and fleece traits but not for most blood traits. Only one significant interaction of cross and plane was found for weight of cannon bone. The similarity of response of different genotypes to different nutritional environments was notable. Few interactions were found.

Osman and Bradford (1965) selected Targhee-type sheep for 120-day weight at two locations. They found that both phenotypic variation and selection differential were higher in a good than in a poor environment. These differences were found for traits in which the means did not differ. There was no evidence of large genotypic interactions. The same authors (Osman and Bradford, 1967) found significant sire–plane of nutrition interactions in only 5 of 38 comparisons, suggesting that this interaction is not a major source of variation even when the nutritional treatment effect is large. There were no side differences in compensatory growth. Bowman and Broadbent (1966) found evidence of ram–breed of ewe interactions in growth rate of lambs.

Blaxter *et al.* (1966) found that breeds differed markedly in their resistance to environmental stresses caused by wind and rain and that these largely reflected the characteristic fleece types of the breeds concerned.

Significant breed–environment interactions among noninbred lambs were observed under managerial–nutritional treatments by Ercanbrack and Price (1969). However, Dhaliwal *et al.* (1963) observed no important interactions between weight and size of ewe with level of nutrition as affecting rate of lambing. Carter *et al.* (1971a) found a strong suggestion of location–breed interaction in body weight of ewes. Significant location–breed cross interactions were found in percentage of ewes lambing and in weight of lamb weaned per ewe mated. The same authors (Carter *et al.*, 1971b) found significant ewe breed cross–location interaction for birth weight and adjusted 120-day weight, but not for average daily gain from birth to weaning. Breed–location interactions were fairly small and unimportant economically. However, when the differential response in lamb performance was added to the much more important difference in ewe production, they concluded that local adaptation of ewe breeds or breed crosses is considerably important to total production.

There are some other reports of significant or important genetic–environmental interactions. Ch'ang (1963) found that Romney Marsh singles were lower in fertility on an estrogenic red clover pasture than twins, but the difference was not found in the control pasture. Masri *et al.* (1967) found significant breed–location interactions in blood traits. Burdukovskaya (1971) found a difference in genotypic variability of weight at 1 year of age, but not in birth weights at high nutritional levels. Elemesov (1971) found that nutritional differences between years affected the inheritance of pelt type in Karakuls.

BREED DIFFERENCES

Breed differences in feed efficiency might be expected, but Blaxter (1962) did not find such differences in metabolism. His comparison of results in Australia and America did not reveal any racial differences. Breed differences found by Daley and Carter (1955) in wool production were small when compared in terms of clean wool per kilogram of feed intake. Price (1967) generally found nonsignificant breed differences for body weight gains from early to late weaning. However, Kromann and Ray (1967) found significant breed group differences in energy gain. Olson *et al.* (1968) found breed differences in gastrointestinal pH values among Hampshire, Romney, Rambouillet, and Merino lambs. They attributed differences to adaptation of breeds to climate or the faster growth of the Hampshire breed. Balaine *et al.* (1971) did not find significant differences in efficiency of feed use of Lohi and Nali lambs and their cross. Gains and feed efficiency tended to be related to initial weights, with the exception of the pure Nali lambs.

Breed differences and other genetic variations in efficiency of utilization of ME are indicated in comparisons of results of Blaxter *et al.* (1966), Doney (1967), Graham (1967), and Reid *et al.* (1968). Blaxter *et al.* (1966) concluded that metabolic differences between different breeds of sheep differing widely in size were quite small.

Doney and Russel (1968) compared Romney, Scottish Blackface, and Tasmanian fine-wool Merinos when individually penned. Comparable values for maintenance requirements were 8.4, 9.2, and 14.0 g digestible organic matter/kg/day, respectively. The Merino value was significantly higher than those for the other breeds. Estimated requirements per unit change in live weight after allowing for maintenance were 5.1, 4.6, and 3.0 g digestible organic matter/g live-weight change, respectively. Wool was included as a character of live-weight gain rather than maintenance.

Significant breed differences in utilizing either gross or digestible energy for milk production were found by Gardner and Hogue (1966). Hampshire ewes produced significantly more milk and milk calories and were more efficient for milk production than Corriedales. Gardner and Hogue (1964a) showed that ewes suckling twin lambs were more efficient in coverting feed energy into milk energy than those suckling single lambs.

Glimp (1971) studied lambs from eight breeds to determine the effect of breed and ration energy level on rate and efficiency of lamb growth. Suffolks and Hampshires gained faster and Navajo lambs gained slower than the other breeds; a significant breed–ration concentrate level interaction was observed. When the ration energy level was increased, Suffolk and Hampshire lambs gained faster; but there was no such effect on the other breeds. Feed efficiency improved as the ration energy concentration increased.

Searle and Graham (1972) compared energy utilization between Merino and halfbred (Border Leicester × Merino) wethers. The halfbreds ate more and grew faster. Merinos grew progressively fatter, weight for weight, than halfbreds, but fatness was not affected by diet per se. No detectable difference between breeds was found in energetic efficiency.

Kellaway (1973) studied the effects of plane of nutrition, genotype, and sex on growth, body composition, and wool production in grazing sheep. The two genotypes consisted of the South Australian Merino and the Dorset Horn × Border Leicester–Merino cross. The crossbred lambs grew faster and were fatter at weaning than the Merinos. Post-weaning growth rates were higher for the crossbreds at both levels of nutrition. Merinos grew more wool on both planes of nutrition. The empty body of the crossbred sheep contained more fat and protein and less ash than that of the Merinos.

McClelland *et al.* (1973) compared Soay, Southdown, Finnsheep, and Oxford dam breeds on growth, efficiency of food use, and body fat. Breed differences in growth rate were large, but these differences were removed when growth rate was considered as a percentage of mature body weight. Efficiency of food utilization did not differ between breeds over the range of 40–76 percent of estimated mature body weight. At each stage of maturity the percentage fat in the fleece-free empty body was lowest in the Soay and greatest in the Oxford; the Finnish Landrace and Southdown values were nearer to that of the Oxford. When the fat-free empty body weight was expressed as a percentage of mature body weight, the rate of chemical fat deposition was similar for all breeds from weaning to 76 percent maturity.

The Agricultural Research Council (1965) presented data on the minimum requirements of sheep for available protein for maintenance and wool production for different breed groups. Requirements range from 16 g/day of available protein for hill breeds of 30-kg live weight to 34 g/day for long-wool lowland breeds of 70 kg live weight. Hill breeds have the lowest requirements, long-wool lowland breeds have the highest, and short-wool lowland breeds are intermediate but closer to the hill breeds. Likewise, crosses are intermediate between short- and long-wool lowland breeds but are closer to the short-wool lowland breeds. Crosses appear to have slightly lower requirements than the average of all groups.

Various other breed differences have been reported. Mitic *et al.* (1964) found that feed consumed per kilogram of weight gain was lowest for the F_1 Blackfaced German × Tsigai, followed by the F_1 Merino Precoce × Tsigai; feed efficiency was poorest for the pure Tsigai. Kruger *et al.* (1966) found no significant differences in gain and feed efficiency between Merino-landschaf, Duetsches schwarzkopfiges Fleischaf, Fleischaf, Rhon and a cross of the first two breeds. Allden (1970) compared Merino and Dorset Horn × Merino lambs. The crossbred lambs were heavier and grew more rapidly to 200 days, and used feed more efficiently than Merinos during the summer drought. Jacobsz *et al.* (1971) compared German Merinos, Dohne Merinos, and Merinos under intensive feeding for 6–42 months. Gains from 6 to 18 months were greatest for the German Merinos, followed by the Dohne Merinos, and then the Merinos. Merinos needed more digestible energy and nitrogen from 6 to 18 months for weight gain than did the other two breeds. Frederiksen *et al.* (1971) did not find breed difference in gains of orphan lambs of Rambouillet, Targhee, Columbia, Suffolk-cross, and Dorset-cross breeds reared artificially from birth to 12–14 kilograms and then on dry diets to 26 kilograms.

Blaxter *et al.* (1961) suggest that the between-sheep variation in voluntary feed intake is so small that it negates the possibility of breeding sheep for increased feed intake. However, numerous reports from Australia indicate that sheep selected for clean-fleece weight have higher efficiency of feed use, although feed intake is related to the gain.

Little information is available on the effect of crossbreeding on feed efficiency, although the positive effects of crossbreeding on rate of gain indicates that effects on feed efficiency would be favorable. Doney (1967) found that outbred sheep consumed 17-percent more feed than inbred (25%) sheep, and that daily rates of live-weight gain were 33- and 27-percent higher for outbred than inbred groups. Intake per unit of body weight was not different between groups. Estimated maintenance requirements of 20.1 ± 0.59 g/kg live weight for outbred groups and 21.9 ± 0.6 g/kg live weight for inbred groups did differ significantly. The growth rate of inbred sheep is depressed in the post-weaning stage, partly because of increased requirements for maintenance and partly because of reduction in total intake.

Langlands (1973) found that crossbred lambs consumed more milk and more grass and grew more rapidly than Merino lambs. The greatest intakes and growth rates were observed for Border Leicester and Dorset Horn crosses with Merinos, but Corriedale and Southdown crosses also grew more rapidly than Merinos.

SUMMARY AND RECOMMENDATIONS

Heritability of feed efficiency and related traits in sheep is generally low to moderate, but some related traits such as body weight and carcass components may have fairly high heritability. A general lack of large genetic differences may be partly due to the complexity of the traits, especially feed efficiency, and may indicate that improvement will be difficult rather than futile. Feed efficiency is so important to economical production that selection experiments for its component parts, as well as for overall efficiency, should be undertaken in a number of breeds.

Body weight and composition are important in nutritional requirements and feed efficiency because these determine feed use. Fat is synthesized more efficiently than protein in sheep so that increasing the efficient production of meat with relatively low fat content will require an increase in efficiency of producing protein. Further, body composition or a reduction in fatness at heavier weights must also be considered in selection because relatively low fat meat is desired by the consumer.

Genetic differences in energy requirements have not been demonstrated, but the actual requirements are such that improvement seems feasible. Mineral requirements are related to genetic differences and genetic changes in the concentration of one mineral in the blood may well be accompanied by changes in the concentrations of others. There seems to be ample room for increasing the efficiency of utilization of both energy and protein by the lamb from both milk and creep feed through genetics and breeding.

Efficiency of feed use for lamb production is dependent on the proportion of total feed required to maintain the ewe for the entire year to feed consumed directly by the lamb for growth to market weight. Thus, less total feed is consumed in maintaining the ewe and more in growing the lamb, if the number of lambs marketed per ewe per year is increased. There is important, although sometimes low, genetic variation in almost all aspects of lamb production per ewe or per weight of ewe. Lamb production requires extra nutritional demands at various critical stages, such as puberty, ovulation, late pregnancy, and lactation. Genetic variation in these demands has generally not been shown, except as it is related to such traits as body weight. Trends in the sheep industry toward breeding more ewe lambs to lamb in their first year, more lambs per lambing, and more than one lambing per year, all tend to increase nutritional demands over past practices. Selection for improvement of these traits under limited feed intakes will automatically select for more efficient feed use in meeting these extra reproductive demands.

Genetic differences in efficiency of feed use for wool production have been well demonstrated. Selection was effective in obtaining increased efficiency of wool growth. Further increases in efficiency seem quite feasible even on low levels of feed intake.

Genetic environmental interactions were generally small and unimportant for body and fleece traits. However, such interactions may be important for lamb production and survival. Breed differences in lamb production and in mortality need to be tested under different environments.

Breed comparisons, realized heritabilities, and genetic correlations are needed for the feed requirements of various phases of production because of the importance of feed cost in production. Increased efficiency using low-quality feeds and natural forages is especially important. Some genetic variability independent of mature size or weight gains probably exists. Well-designed selection experiments are needed to test the extent of this genetic variability. Crossbreeding is expected to have beneficial effects on feed efficiency because of the effects of inbreeding and its effect on rate of gain. However, more information is needed on the actual relationships of crossbreeding and feed efficiency of sheep.

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Genetic Variation in Nutritional Requirements of Swine

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Swine producers make many assumptions regarding the roles of inheritance and environment in the performance and behavior of swine. They reach conclusions based on their experiences and those of their peers. For example, a breeder of purebreds who sells several bred gilts to each of five producers learns at a later date that offspring from those gilts on two farms exhibit Porcine Stress Syndrome (PSS). As there are no signs of the problem on the other three farms, he is convinced that the problem is solely environmental and surely not genetic. On the other hand, a feeder who buys pigs from two sources and observes that the red ones gain faster than the black ones assumes that the difference is entirely genetic. Whenever variable genetic groups and variable environments are brought together, there is a possibility of interaction; but there is insufficient research information to predict the regularity and incidence of occurrence.

The swine industry could make good use of "predictors" that will allow more refinement in formulating diets according to known genetic parameters. Hogmen who are raising longer and more upstanding animals are asking if the genetic change in body dimensions is causing a concomitant change in nutrient requirements.

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Investigators have commonly observed that when growing-finishing (GF) swine are fed a "borderline level" of a single nutrient in an otherwise nutritionally complete diet, some individuals thrive, whereas others are markedly retarded. Yet rarely have studies been conducted to determine the effect of genetic variance and pre-environmental treatment.

BREEDS AND TYPE

Breed comparisons have usually been comprised of information gathered from several sources over a period of several years. Performance data in sufficient numbers for all breeds can be collected in no other way; yet the validity of most breed comparisons can be challenged because of variable sampling practices, variable management practices, variable geographical sources, etc. Comprehensive studies of breeds and their nutrient requirements have not been conducted—the undertaking is impractical, if not impossible—and the results would probably have little, if any, applied value in individual herds or within a few years after the study was conducted.

Nevertheless, breed variations in economically important and heritable characteristics as shown by averages should not be totally ignored. For example, a study by Self (1959) found that the extremes in average litter size among nine breeds were 8.07 and 11.13. This dramatic difference poses at least two questions: (1) Do these two breeds have the same nutrient requirements during pregnancy, and (2) might the two breeds have differential nutrient needs for optimum ovulation, and—if such were known—could the difference be narrowed by differential feeding?

Comparisons of other traits (Self, 1959; Bruner and Swiger, 1968) have shown that breeds vary in rate of gain, carcass excellence, and feed conversion, but it is not known whether these variables cause a need for differential ratios or amounts of nutrients.

The performance of samples of breeds are sometimes compared as a by-product of nutritional studies. Usually the sample is far too small to represent a breed and is, therefore, a variable genotype that may or may not represent the breed. Yet some of these observations are of interest because they suggest a genotype-nutrition interaction. Galloway (1974) observed what appeared to be a dramatic breed and nutritional treatment interaction as characterized by low serum calcium values followed by mortality from PSS. The time of onset of symptoms and the severity of symptoms differed markedly among breeds.

Hetzer and Miller (1972a) reported that, based on data collected through 13 and 11 generations of selection for high and low backfat, respectively, Durocs and Yorkshires differed in the correlated responses as shown by pre- and post-weaning growth measures. Again, the nutritional significance of this apparent breed difference is unknown.

Additional examples of breed differences are reported elsewhere in this manuscript (such as Weniger, 1952; Plank and Berg, 1963). Breeds have undergone periodic "type" changes, and at the present time the show ring standards for body shape are undergoing an alteration. Do radical changes in conformation affect nutrient requirements? Bruner (1967) concluded from a summary of records of the Ohio Swine Improvement Program that the meat-type hog was more efficient than the fat or over-finished type. A wide variety of genetic backgrounds was represented among the swine in this program, and they were divided into two groups: those that did and those that did not meet the meat-type certification standards. The group that qualified had, on the average, about 0.3-inches less backfat, about 0.7-square inches more loin eye, and required 20 fewer pounds of feed per hundredweight of gain. This observation of a positive relationship between leanness and efficiency appears to be in conflict with the findings of Dickerson (1947), in which he observed an association of rapid fat deposition with low feed requirement. The apparent discrepancy between these two reports may be explained by one or more of the several differences in the information that led to the two conclusions (e.g., the latter was a genetic study, whereas the former was not, and the populations studied were probably quite different genetically because of the breeds represented and the effects of selection practices occurring during the time gap between the two studies).

Nevertheless, the genetic relationship between meatiness and other traits is important to swine producers, and the degree of meatiness is related to nutrient requirement as discussed in another section.

SEX

Whether the male and female represent different genotypes is debatable; nevertheless, it is well established that the sexes differ in phenotype, especially if castrate males are included in the comparison (Bruner, 1957; Plank and Berg, 1963, Berruecos *et al.,* 1970; Friend and MacIntyre, 1970). The three sex classes differ markedly in rate of gain and leanness of carcass. Wallace (1968) reported that gilts and barrows responded differentially to varying levels of dietary protein. Barrows that gain faster but produce fatter carcasses than gilts showed a greater advantage in gain and a lesser disadvantage in lean cuts at lower than at higher protein levels. Wallace also showed that gilts fared somewhat better in terms of gain under restricted feeding when the dietary protein level was high.

Giesler *et al.* (1972) observed that barrows and gilts grew differently when a corn diet was compared with a 25-percent oats diet. The gilts gained comparatively better on the oats diet, which supplied a more favorable amino acid spectrum; thus, it is suggested that gilts, having a leaner carcass, have a different protein (amino acid) requirement. On the other hand, Christian (1971) failed to show that gilts and barrows respond differentially to variable levels of dietary protein.

Jonsson (1959) observed that gilts outgained castrates when fed individually, whereas the reverse happened under group feeding conditions. He found this difference to be highly significant statistically and that the sex–feeding system interaction occurred at all Danish testing stations. Feeding system did not interact with body length and backfat thickness between sexes. This study involved several hundred test groups composed of more than 2,500 animals, the progeny of nearly 500 sires.

PROTEIN

Historically, percent crude protein has been the criterion used to determine the protein needs of swine. Levels recommended by experiment stations have varied for swine of similar weights and ages. In recent years, studies have shown that variation in the fat to lean ratio has an effect on the protein needs of growing–finishing swine. Christian (1971) compared two strains of swine (lean and fat strains). The strains differed in carcass characteristics, growth pattern, and efficiency of feed utilization. The two strains were fed two levels of crude protein, 12 and 16 percent, and each responded in growth to the higher level during the initial phase of the trial. During the latter two phases, only the lean strain responded. The lean strain converted the 16-percent diet more efficiently until a slaughter weight of 260 pounds, whereas the fat strain did not differentiate between the two levels after they reached 200 pounds.

Davey and Morgan (1969) found a significant line–diet interaction among GF hogs for weight of carcass lean. Duroc and Yorkshire lines selected for high and low fatness were fed diets containing 12- and 20-percent crude protein, and they yielded amounts (kg) of lean in the carcass as follows.

	12-percent crude protein	20-percent crude protein
Low-fat pigs	15.7	21.4
High-fat pigs	14.8	16.3

The same study revealed no significant interaction between genotype and protein level for rate of gain.

Weniger (1952), observing four German breeds of swine fed a normal and a protein deficient diet, found that the breeds changed rank between treatments when measured for daily gain and feed efficiency. This suggested an interaction of breeds, protein level, and performance.

Three genetic groups, resulting from Yorkshire sows mated to either a Yorkshire, Wessex Saddleback, or Landrace boar, were fed two diets that varied in levels of protein and energy (King, 1963). The one diet, designed to promote rapid growth, increased rate of gain by 34 percent and feed conversion by 26 percent. However, no significant genotype–environment interactions were found except for streak thickness, a carcass measurement taken from the middle of the flank.

Aunan *et al.* (1961) compared Durocs and Yorkshires on three levels of dietary protein and found a highly significant effect of breed on all measures of carcass leanness and fat, but carcass differences due to level of protein were not significant statistically. Although they did not examine the data for interactions, it is fairly obvious from the means that were presented that there would not have been significant genotype–protein level interactions.

PLANE OF NUTRITION OR ENERGY LEVEL AND MANAGEMENT SYSTEM

Studies dealing with energy level are usually confounded with the ratio of protein to energy and possibly with the ratio of energy to other nutrients. Investigators are faced with the decision of adjusting protein and other nutrients as energy level is varied. Regardless of the kind of diet formulation, the performance responses to variable energy intake may be a function of altered nutrient ratios as well as energy per se.

As early as 1932, Lingren *et al.* observed the performance of two genotypes of growing-finishing swine when fed two levels of feed intake. A big-type and chunky-type Chester White were self-fed or restricted to about 75-percent full-feed during the GF period. Although the data were not analyzed for interactions, the researchers concluded that the findings tended to show that breeding or heredity had more to do with the type of market hog than the amount of feed given or management used, and that the diets apparently did not exert a differential effect of type on market desirability.

Kuhlers *et al.* (1972) using Poland Chinas, Yorkshires, and their reciprocal crosses, failed to show significant interaction between breed and feeding regime when progeny were fed two diets containing a high and low level of total digestible nutrients (TDN). Rate of gain, efficiency, and certain carcass traits were measured during and/or at the conclusion of the GF period. They concluded that selection for those traits observed should be equally effective when growing–finishing hogs are fed either a 88-percent TDN or a 74-percent TDN diet.

Fowler and Ensminger (1960), with a common reservoir of genetic variability beginning after six generations of selection for rate of gain on two planes (full feed and 70% of full feed) of nutrition, found a definite genotype–environment interaction. They postulated that superior gains in the low plane group may be due to superior feed efficiency as a result of lower thyroid activity, whereas superior gains in the high plane may be due to genes conditioning appetite, metabolic rate, etc.

Davey *et al.* (1969), using the Beltsville low- and high-fat lines of Durocs and Yorkshires, fed littermate pairs of barrows two levels of feed intake. One mate was fed a certain percentage of body weight and the other approximately 75-percent that amount. Daily intake of the major nutrients except for carbohydrate was about the same for each member of the pair. Results led to these conclusions: (1) that a critical point related to the plane of nutrition exists beyond which any further lowering may affect the formation of muscle tissue, and (2) that the low-fat Yorkshire line, which appears to have the greatest potential for muscle tissue formation, may be especially sensitive to limiting factors in the diet.

Salmela *et al.* (1960) fed three kinds of crossbred pigs three levels of energy, and significant breeding–treatment interactions were found in average daily gains and in age at 200 pounds live weight.

Omtvedt *et al.* (1962) used swine of three lines of breeding to study genotype–environment interactions. Two feeding methods were imposed upon two management systems, namely confinement and pasture, and the study involved a total of 240 GF swine. Interactions of line of breeding with management system were generally nonsignificant for the traits investigated, which indicated that the genotypes used responded in a similar manner to both confinement and pasture management systems.

Gregory and Dickerson (1952) reported that line-cross and top-cross swine grew faster and more efficiently than the parent-inbred lines when fed at two different levels (full fed and about 87%). They concluded from the results of digestion trials and growth performance that heterosis does not affect digestibility of feed, but that greater efficiency may be ascribed to reduced energy losses because of "Specific Dynamic Action" or lower maintenance requirement.

In a study in which swine were selected for thinner backfat, Zoellner *et al.* (1963), after two years of selection, concluded that genetic environmental interactions were not significant for backfat thickness, rate of gain, litter weaning weight, and feed efficiency.

Bowland and Berg (1959) varied both energy and protein levels for different genetic strains and found strain–sex interactions in rate of gain during both the growing and finishing periods, whereas a strain–ration interaction was present during the growing period only. The strains differed in carcass characteristics, but no appreciable strain–ration interactions were noted.

Offspring from Yorkshire females that were mated to Yorkshire, Lacombe, or Landrace males were studied by Plank and Berg (1963) for genotype–plane of nutrition interactions. Three levels of feeding, ranging from 75 percent of NRC recommendations to *ad libitum* feeding, were offered to growing–finishing swine. Genotype–plane of nutrition interactions were significant for average daily feed consumed ($P < 0.05$), average daily gain ($P < 0.01$), length ($P < 0.05$), and total Registry of Performance (ROP) score ($P < 0.01$).

Lucas *et al.* (1960) compared two breed types that were fed three levels of TDN, which was intended to furnish variable energy intake. In each of three experiments, there were examples of significant interactions between feeding and breeding, which included growth rate, feed conversion, fat measurements, and percentage "fore" in the carcass.

Most studies of genotype-nutrition interactions involved genotypes that were radically different, such as breeds or crossbreds of different breeds. Hale and Coey (1963) made intrastrain comparisons of bacon pigs under full and restricted levels of feeding and found no significant interactions between litters and feeding treatments when measuring live-weight gains, feed efficiency, and a number of carcass measurements. Likewise, Jonsson (1959) could not demonstrate a significant interaction between genotype and feeding system when the experimental animals were selected from within a single breed. The two systems were individual feeding and group feeding. On the other hand, Kristjansson (1957) studied sire groups of the Canadian Yorkshire breed that were fed in confinement or on pasture. He found that sire–treatment interaction for loin area was significant ($P = < 0.05$) and approached significance for rate of gain ($P = 0.09$), carcass score ($P = 0.13$), and average backfat thickness ($P = 0.08$).

HORMONES AND ENZYMES

Expression of the economically important trait, whether it be growth or reproduction, is determined by genetics, environment, and the interaction of the two. Genotype variability in physiological functions is probably due largely to variation in endocrine gland activity and the hormonal control of many physiological systems, which in part includes enzyme activity.

Baird *et al.* (1952), using two genetically different (rate of gain) lines of Hampshires, found that the rapid-line pigs differed significantly from the slow-line in daily feed consumption (2.5 *vs.* 1.1 lb), daily gain (0.94 *vs.* 0.31 lb), and efficiency (2.76 *vs.* 3.64 lb), respectively. In spite of the difference in feed conversion, the investigators found no differences between the lines in digestibility of all nutrients, ability to metabolize gross energy, amount of heat production per unit of body surface, or amount of metabolic nitrogen excreted per kilogram of ration. Pituitary and thyroid weights, in relation to body weight, were not significantly different; however, the rapid line consistently secreted larger amounts of growth hormone at all ages.

In a study of the Beltsville low- and high-fat lines of Yorkshires, Benevenga *et al.* (1971) observed a differential adaptation to an elevation of protein in the diet as measured by feed consumption and blood amino nitrogen patterns. The high-fat pigs consumed more high-protein feed, had less blood amino nitrogen, and had blood levels that returned to normal more quickly than did the low-fat line. These results suggest that the lines differed in intermediary metabolism and activity of certain enzymes. Steele *et al.* 1972) studied the Beltsville low- and high-fat lines of Durocs for genetic influence on various parameters of lipid metabolism. They monitored the activity of four lipogenic enzymes found in subcutaneous adipose tissue and the serum levels of glucose and cholesterol, which are commonly employed as measurements of lipid metabolism. They concluded that lipid metabolism was influenced by genetic composition.

CONCLUSION

There are numerous reports on estimated heritabilities of traits, genetic correlation of traits, and the relative importance of inheritance and environment as related to swine, but a paucity of information on *genetic variability and nutrition* that is based on research designed specifically to determine the presence of interactions between genetic groups and individual nutrients or combinations of nutrients.

Swine breeders have historically changed the type or shape of the hog in pendulum fashion going from one extreme to the other. Zeller and Hetzer (1944) recorded some of these changes and also reported the findings of a comparison of small-type, intermediate-type, and large-type Poland Chinas with respect to prolificacy, viability, rate of growth, economy of gain, and dressing percentage. They concluded that the intermediate-type hogs in general were superior to those of small or large types from the standpoint of the swine producer.

Hetzer and Miller (1972b) showed that, as thickness of backfat was changed by selection in Durocs and Yorkshires, there was a change in body shape as measured by length, width, height, and circumference. Such information leads to possible associations between shape and nutrient requirements.

In a study of the relationship of growth rate and carcass quality in bacon pigs, Donald (1940) arrived at the following conclusion:

> Since the influence of growth rate on carcass measurements appears to have been expressed in a variable way according to type of pig concerned, it may be unwise to make detailed predictions of the relation between growth rate and carcass quality. The difficulty of establishing effects of growth rate after weaning on carcass measurements suggests that within a limited range of variation in growth rate, these effects tend to be small, inconsistent, and relatively less important than individual type.

The extent of interactions between genotype and nutrition among swine is not clear. The literature both supports and refutes their existence. Yet there is sufficient evidence to support a hypothesis that there are genetic lines of swine that perform differentially as nutrition is varied and that the variable responses may include the more economically important characteristics.

In-depth investigations are necessary to relate measurable and highly heritable characteristics, such as length of body or fat-to-lean ratio or to nutritional requirements. Heritable blood factors may be useful to predict variable nutrient requirements. Experimental design should be refined to better isolate and characterize both the swine genotype and the nutritional factors that are to be studied.

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