Impact of Research with Cattle, Pigs, and Sheep on Nutritional Concepts: Body Composition and Growth

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Abstract

Studies with pigs, cattle, and sheep have provided a wealth of information regarding growth and body composition. Most of this information has been obtained using the standard methods for measuring the body composition of meat animals, which consist of dissection and chemical analysis. These methods have been used with meat animals to validate a variety of in vivo techniques that are used in both animal and human body composition studies. Research on the growth and body composition of meat animals has provided important concepts regarding the relation between growth and composition, including chemical maturity, the effects of severe undernutrition, partitioning of nutrients under various physiological conditions, the efficiency of nutrient utilization, and compensatory growth following a period of undernutrition. In addition, several genetic and physiological conditions affecting growth and body composition have been identified in meat animals that serve as important models for both animal and human growth.

Because of their economic importance, the growth and body composition of pigs, cattle, and sheep (referred to collectively as meat animals) have been studied extensively. Over the years, important compositional concepts have been defined and valuable data gathered by those interested in the growth and development of meat animals. Information based on detailed dissection and chemical analysis of meat animals has been available for validating methods of human body composition analysis. Studies of nutritional, pharmacological, and genetic factors affecting the growth and composition of meat animals have provided important information relevant to the growth and composition of animals and humans. In addition, the pig, because of its physiological and genetic similarities to man, has served as an excellent animal model for biomedical research. Studies of the body composition of meat animals have focused primarily on those changes that occur during the growth of the animal up to “market weight,” the point at which they are utilized for meat. Also of concern are changes that occur during pregnancy and lactation. However, because meat animals are not normally kept beyond their productive years, changes that occur as the result of aging have received little attention.

Most of the modern breeds of meat animals were developed over the years by selection for size, shape, and hair color (or wool quality in sheep). It was not until early in the 20th century that serious attention turned to improving growth and body composition. Consequently, through improved nutrition, genetic selection, and advances in techniques for estimating body composition, the meat animals that are produced today grow much faster, more efficiently, and have more lean and less fat.

Fundamental to progress in the study of animal growth and nutrition has been the ability to measure body composition. The most direct method for measuring body composition is to completely dissect it into viscera, skin, bones, muscle, and fatty tissue. In 1859 Lawes and Gilbert (1) used crude dissection and extraction techniques to estimate the composition of the animal body and to study the relative rates of development of the various parts of the body. Even today, dissection and chemical analysis represent the standard for body composition measurement of farm animals. Several studies have involved extensive dissection into fat, muscle, bones, and organs. A classic example of this approach is the study with pigs conducted in 1940 by McMeekan (2). Detailed dissection is extremely labor intensive. A more common method of dissection is based on separation of the carcass into “primal meat cuts” to estimate lean yield. The latter approach is more practical in studies involving a large number of animals because the carcass can then be utilized for meat.

Although growth of the animal is easy to measure, until recent times, estimation of body composition of the live animal...
was accomplished mainly by visual appraisal. In order to facilitate nutritional and genetic improvements in body composition, a suitable means for measuring composition of the live animal was needed. The use of x-ray measurements as an approach to estimate composition of the live animal was developed in Germany in the 1930s. Hogreve (3) used x-ray measurements of the thickness of subcutaneous fat and of belly fat in a study of the process of fat deposition in pigs. Although this approach appeared promising, it was never widely adopted and was subsequently replaced by the use of ultrasound. Research on the use of ultrasonics to measure the body composition of pigs began in the mid-1950s (4). It has become the most commonly used method for estimating live body composition in all 3 species of meat animals and has been validated extensively, especially in pigs. Using real-time ultrasound, measurements are made of subcutaneous fat thickness and the cross-sectional area of the longissimus muscle.

Josef Brožek (5), in discussing the interaction of human and animal research on body composition, noted that “We can expect little help from animal studies regarding the specific quantitative parameters assumed in human body-composition models, such as average mineral content of the body. Nevertheless, various methodological problems can be elucidated on the basis of animal data.” In this regard, studies with meat animals have served as valuable models for validating some of the techniques that are currently used for human body composition measurement. For example, in the 1960s and 1970s there was considerable interest in whole-body $^{40}$K counting as a method for measuring body composition of meat animals. Measurements with live pigs, sheep, and cattle demonstrated a high correlation between total body $^{40}$K measurements and chemical or dissection measurement of total body lean mass. More recently, with the development of sophisticated techniques for body composition analysis such as magnetic resonance imaging, computerized x-ray tomography, and dual x-ray absorptiometry, pig and sheep especially have served as models for validating the accuracy of these new methods.

In his discussion of the interaction of human and animal body composition research, Brožek (5) went on to say: “But more than method is involved. In the past, important compositional concepts were defined, and valuable data were gathered by individuals concerned with the growth and development of farm animals.”

In 1923 Moulton (6), looking at changes in the chemical composition during the growth of cattle, pigs, and other animals, including man, described 2 basic principles of mammalian development. One was that the percentage of fat was quite variable in the mammalian body. Thus, the composition of animals should be compared on a fat-free basis to make the effects of age and abnormal development apparent. The second principle was that the percentage of water in the fat-free tissue fell rapidly from conception to birth and then more slowly until it reached a constant level. The age at which the relations among protein, water, and total mineral content (fat not included) became stabilized was referred to by Moulton as “chemical maturity.” Although Moulton noted that his reference to chemical maturity should not carry implications of too general a nature, others (7) have pointed out that the age at which chemical maturity occurs in mammals corresponds to ~4.5% of the total life expectancy of the animal.

The cost of feed represents a large proportion of the overall cost of the production of meat animals; thus, the efficiency of feed utilization, commonly referred to as “feed efficiency,” is a very important concept. Feed efficiency is simply the ratio of the amount of growth to the amount of feed consumed. Although it is not clear who reported the first study in which feed efficiency was measured, over the years growth rate (average daily gain) and feed efficiency have been the standard units for evaluating the growth of all 3 species of meat animals in both nutritional and genetic studies. Interestingly, because feed efficiency is correlated with both growth rate and body composition (8), improvements in growth and body composition (more lean and less fat) resulting from either improved nutrition or genetic selection have resulted in substantial improvements in feed efficiency.

One of the goals of meat animal production is to direct or partition as much of the nutrient intake as possible into the growth of skeletal muscle tissue. Based on studies with pigs and sheep, Hammond (9) illustrated the priority of partition of nutrients according to metabolic rate, where the brain and CNS have top priority, followed by bone, muscle, and fat. During pregnancy the placenta and fetal tissues have high priority, but only to a certain point where it does not jeopardize the well-being of the mother. The ability of the animal to partition nutrients according to these priorities involves both homeostatic and homeorhetic mechanisms. From studies with dairy cattle, Bauman and Currie (10) described how homeorhesis comes into play during pregnancy and lactation to support growth of the conceptus, the gravid uterus, the mammary gland, and, with the onset of lactation, the nutrients needed for milk synthesis.

Nutritional approaches to increasing lean growth have involved altering the level of dietary protein or the protein: energy ratio in the diet. Studies with pigs have demonstrated that increasing the level of dietary protein (from suboptimal levels) results not only in faster growth but in also carcasses containing less fat and more lean. As the protein content of the diet increases, growth rate increases until an optimal level of protein is reached, after which growth rate declines (11). As the protein content of the diet increases, the rate of fat deposition continues to decrease, whereas the rate of lean deposition plateaus at the level of protein that is optimal for growth. Thus, growth depression at high levels of protein intake is attributed to the decreased rate of fat deposition (11). These effects are also associated with an increase in heat production and a reduction in the efficiency of energy utilization (12).

Driven by economic reasons, there has long been interest in the potential use of exogenous hormones to improve the growth, body composition, and feed efficiency of meat-producing animals beyond the achievements of improvements in nutrition and genetic selection. As early as 1913 (13) it was demonstrated that hormones could be used to stimulate the growth of animals. The production of synthetic steroidal hormones, initially diethylstilbestrol (DES), was followed by widespread usage, especially in the beef cattle industry. In 1954, Clegg and Cole (14) reported on the effects of DES on the rate of gain and feed efficiency of beef cattle. Subsequently the efficacy of estrogens for improvement of live weight gain and efficiency of feed conversion in finishing cattle has been documented in several hundred studies (15). So wide was the use of DES that it was estimated that in 1974 an additional 135 million kg of animal protein was produced from the same input of dietary protein. Although DES has been banned from use in meat animal production, other steroids are in use to this day, primarily because of their impact on rate of gain and feed efficiency.

Further advances in the partitioning of nutrients into muscle growth came in the 1980s. The availability of recombinant somatotropin (ST) and the development of a number β-adrenergic agonist (β-AA) compounds prompted a renewed interest in studies of the growth and development of meat animals and, as a result, provided

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2 Abbreviations used: β-AA, β-adrenergic agonist; DES, diethylstilbestrol; MH, malignant hyperthermia; PSS, porcine stress syndrome; ST, somatotropin.
a wealth of information about the basic effects of these compounds on physiological processes related to growth and body composition. These effects have been summarized in a number of reviews on the subject (16,17). In general, administration of ST to growing animals leads to accelerated weight gain consisting of more muscle and visceral organ growth, but with little decrease in fat deposition. Likewise, certain β-AA compounds stimulate growth, increasing muscle growth, decreasing fat deposition, but having little effect on visceral organ growth. In the course of these studies, it was found that an adequate level of protein in the diet was needed to realize the increase in lean deposition in response to either β-AA or ST. When the level of protein in the diet is increased from 11% to 16%, the addition of β-AA increased nitrogen retention and protein deposition, resulting in an improvement in both leanness and growth rate (18). Both dietary energy and protein intake influence the rates of protein and lipid deposition in response to the ST treatment of pigs (19). Nossaman et al. (20) suggested that a feeding strategy for ST-treated pigs with low genetic potential for lean gain should include energy restriction, although an increased energy intake would be desirable for pigs with a high genetic potential for lean gain. Smith and Kasson (21) concluded that the level of protein in the diet had to be >14% in order for ST to improve the growth of pigs from 55 to 110 kg.

Detailed studies of severe undernutrition in humans have been confined primarily to adults, whereas with meat animals, much work has been with the growing animal. A series of studies by McCance and Widdowson and coworkers examined the effects of severe prolonged undernutrition in young growing pigs (22,23). Pigs were maintained at slightly more than their birth weight for as long as 3 y. After 1 y, undernourished pigs weighed only 27% of well-nourished pigs; muscle was 2%, the heart was 6.3%, small intestines were 13%, and the cerebellum was 88%.

Studies of the runt pig have provided insight into the importance of intrauterine nutrition on birth weight and subsequent growth potential. Frequently within a litter of pigs, 1 or more individuals, referred to as runts, have significantly lower body weights (as much as one-half or one-third) compared with their littermates. Prenatal runting is thought to be caused by a placental insufficiency of the fetus in the uterine horn that results in decreased transport of oxygen and nutrients to the fetus (24). Results obtained by Widdowson (25) indicate that runting results in the greatest reduction in the weight of the small intestines, liver, and skeletal muscle, with the least effect being on the weight of the brain.

The lower birth weight of the runt pig has 2 major implications: lower rates of survival and postnatal growth. Of the runts that survive the neonatal period, growth rate is reduced (25,26). The results of Powell and Aberle (26) suggest that runts weighing <1.0 kg not only grow more slowly but also grow less efficiently and are more likely to produce a carcass containing more fat and less muscle than larger-birth-weight pigs slaughtered at the same weight. When allowed to grow to maturity (3 y old), severely runted pigs (450-g birth weight) never achieve the body weight or body composition of their littermates. Prenatal runting results in the greatest reduction in the weight of the small intestines, liver, and skeletal muscle, with the least effect being on the weight of the brain.

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Compensatory growth, i.e., “catch-up growth,” following a period of undernutrition is a common feature among higher animals, including humans. The first report on the subject was in 1908 by Waters (28), who noted that beef steers that had been undernourished subsequently recovered to reach normal mature weight and height. Similar findings have been recorded for children (29). The term “compensatory growth” was first used by Bohman (30) to describe the effects of diet on the growth of beef cattle. Because of its impact on growth rate, body composition, and feed efficiency, compensatory growth has been studied extensively in meat animals; for example, cattle, swine, and sheep (31). These and other studies have shown that the animals’ ability to compensate for prior undernutrition is affected by severity and duration of the period of undernutrition, stage of development of the animal (effects on cellular proliferation relative to differentiation of each tissue), genotype, sex, level of feed intake during realimentation, period of refeeding, and composition of the diet during realimentation. In the examples cited above, neither the severely undernourished nor the runt pig is able to adequately compensate to achieve the body weight of adequately nourished pigs.

The selection of animals for lean tissue growth has resulted in some extreme conditions that present interesting models of animal growth and also demonstrate how genetic selection can be used to direct the partitioning of nutrients for tissue growth.

In the late 1800s, long before the discovery of myostatin, a highly muscled breed of cattle was being developed in Belgium. In cattle this condition of extreme muscling is also referred to as double muscling. These animals are characterized by skeletal muscle hyperplasia, resulting in an increase in muscle mass of ~20%. Soon after the identification of the novel TGF-β member called GDF8/myostatin as a negative regulator of muscle growth, it was found that a mutation in the bovine myostatin was associated with the double muscle trait (32). With the loss of function of myostatin, an increase in muscle fiber numbers occurs in utero, resulting in the production of a larger and more muscular fetus. Muscle fiber number could be controlled through fetal myoblast proliferation or through terminal differentiation. Of possible significance is the observation that low-birth-weight pigs were found to have elevated myostatin expression in the longissimus muscle (33). In sheep the callipyge gene is a mutation that results in pronounced muscle hypertrophy, primarily in certain muscles of the pelvic limb (34). In this case the hypertrophy is not present at birth and does not appear to involve myostatin.

Another example of how selection for “leanness” can alter metabolism to affect nutrient partitioning was the emergence of the halothane (HAL) gene in swine. Pigs carrying the HAL gene have less fat and more lean than pigs without the gene. Unfortunately, the presence of the HAL gene is also linked to porcine stress syndrome (PSS), which is characterized by sudden death resulting from malignant hyperthermia (MH) and by meat that is pale, soft, and exudative. After PSS was first described in 1968 (35), there have been numerous investigations regarding the genetics and physiology responsible for the condition [see review by Kathirvel and Archibald (36)]. Humans are also afflicted by MH, and although the porcine and human forms of the disorder are not identical, there are many similarities. Mutations in the gene encoding the skeletal muscle sarcoplasmic reticulum calcium release channel (ryanodine receptor, RYR1) are responsible for predisposition to MH in both pigs and humans. There is also evidence that humans susceptible to MH are leaner and possibly more muscular. It has been suggested that calcium leaking from the defective calcium release channel could cause muscle contractions, thereby leading to greater muscle and less fat in pigs.

The pig offers an excellent model for the study of nutrition-related obesity. The modern pig grown commercially for meat is a fairly lean individual. Nevertheless, it will respond to a low-protein or high-fat diet by depositing more fat. Certain breeds
such as the Chinese Meischan, the Gottingen minipig, and the feral Ossabaw have a much greater propensity for obesity. Obese lines of pigs have been developed by genetic selection for obesity-related traits such as maximal backfat thickness (37). There are several reports where these breeds or genetic lines of obese pigs have been utilized as models for studies related to human obesity [see review by Mersmann (38)]. Examples include insulin sensitivity and growth hormone profile, feeding behavior, leptin levels, lipid metabolism, and glucose turnover.

Although relatively uncommon, anorexia-like symptoms have been observed in pigs. The condition is more prevalent among pigs that have been bred for extreme leanness and can result in irreversible self-starvation and emaciation. Anorexia in pigs develops mainly postweaning as the “wasting pig syndrome” or after farrowing as the “thin sow syndrome” (39). In both cases diet and social interactions with other pigs may be contributing factors.

In summary, research on the growth and body composition of meat animals has contributed significantly to the knowledge regarding body composition methodology, the effects of severe undernutrition, compensatory growth following a period of undernutrition, and factors that influence the partitioning of nutrients into various tissues. This has resulted in improvements in the growth, body composition, and feed efficiency of meat-producing animals, to the benefit of both the producers and consumers.

Literature Cited

1. Lawes JB, Gilbert JH. Experimental inquiry into the composition of some of the animals fed and slaughtered as human food. Philosophical Transactions of the Royal Society of London - Part II; 1859, p. 494-680.