THE STRESS SYNDROME AND MEAT QUALITY

SESSION A: GENETICS, GROWTH & DEVELOPMENT

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Genetics, growth and development of meat animals just about cover the complete story of meat production. Any attempt on my part to give a general account of this vast area of research would, I feel, be either too long or too superficial. Perhaps the best way would be the select what appears to me to be key phases or topics and to use these to draw attention to relevant research problems. In doing so, I shall refer to, and present a summary of the submitted papers of my session.

We are today at a threshold in meat science and technology. An era is closing of which it could be said that the overall position of meat production has been largely one where man looked after the animal, while the animal, hopefully, looked after the production of muscle and therefore, meat. This laissez-faire approach is ending, however, and with an increasing understanding of the inter-relations between muscle and meat, a greater and more direct control over the production of muscle and its quality will be exerted in the future.

Meat-animal genetics and studies on the growth and development of tissues in meat animals have as their practical goal the efficient production of muscle containing the attributes of quality meat. The factors relating to or governing the efficient production of meat are many. First, there is the very obvious; more animals mean more meat

SLIDE NO 1

GENETICS AND MEAT PRODUCTION

Factor	Heritability
Reproductive performance	Low
Rate and Level of Growth	Moderate
Carcass Quality	High
Meat Quality	?'s

SLIDE NO 2

NORMAL AND PSE PORK

This slide shows the difference between normal and pale, soft and exudative pork in a very clear way, and so leads us to the subject matter of the next two papers.

(Slide No 1 shown here). Animal numbers are regulated by reproductive performance. Involved are the age of first oestrus, level of fertility, number and frequency of births, and fetal and infant survival rates. Although these are of low heritability, they are significantly effected by husbandry practices.

The second factor is animal growth, its rate and ultimate level. These have been extensively studied. In addition, there have been many detailed studies on the development of bovine (Butterfield and Berg, 1966), porcine (Elsley, et al., 1964) and ovine (Lohse, et al., 1971) musculature, all of which show that muscle growth is allometric. Furthermore, significant major redistributions of muscle mass throughout a carcass does not appear possible for a particular species. Rather, for a more desirable distribution of tissue than, for example, that of our present domestic cattle, the utilization of the water buffalo and deer have been suggested. All growth characteristics are moderately heritable.

The third factor is carcass quality. Lean meat percentage is the most important characteristic of a carcass. Many studies have shown that carcass quality has a high heritability. Not surprising, therefore, is the fact that this factor in meat production receives so much attention and that as a result meatier pigs and double-muscled cattle are with us.

Finally there is the all important factor of meat quality. Its heritability is discussed in two papers of this session, those by McGloughlin and McLoughlin, and by Eikelenboom and Sybesma. Raised in these papers is that most important issue, the compatibility of meat quantity and quality. And, as we shall see anon, there are many problems in this area to be solved and many questions to be answered.

I now return to the question of carcass quality. The formation of fat tissues is an important aspect of this quality factor and so we turn now to Dr Schoen's paper 'The influence of growth factors on quantity and composition of fat tissue in beef carcasses' (A4).

Dr Schoen has studied the formation of different fat tissues, subcutaneous, intermuscular, intramuscular, kidney and pelvic fats. She has shown that these are influenced by age, sex, weight, degree of fattening and breed as well as positions in the carcass. Also characteristiced are the inter-relationships of these different fats. Many of her observations e.g. effects of breed, age, growth rate on fat tissues and the order of growth of these tissues are in agreement with the observations of other investigators. Dr Schoen has correlated various fat parts with total carcass fat and found that the regression coefficients vary with age. In these and other correlations of fat parts to total fat, information, which I feel certain Dr Schoen has, on the standard deviations about regression (s_{xy}), and the regression equations of these relationships would be most valuable in supporting her thesis that the relationships she has established may be of value for selection and for carcass evaluation in meat technology and nutrition. Dr Schoen presents interesting data on the variation of the intramuscular fat which shows a range of 4.6 - 1.3 = 3.3%; with a mean 2.29%. Correlations of individual muscle fat contents with total carcass fat are, however, low suggesting to my mind, that variations in intramuscular fat account but for a small percentage of the variation in total carcass fat. Dr Schoen has produced data on the chemical composition of the various fat tissues and studied their inter-relationships.

I shall now discuss the problem of PSE in pork (Slide No 2 here).

The phenomena, Porcine Stress Syndrome (PSS), Malignant Hyperthermia Syndrome (MHS), and Pale, Soft and Exudative (PSE) pork are nowadays regarded as expressions of the same muscular condition. Indeed, the paper (A1) by Eikelenboom & Sybesma in this session again underlines the close relationship between MHS in pigs and PSE pork, but more about this paper later and the important significance of their observations on selection for meat quality in pigs. With regard to PSE meat it appears that it is most likely to develop in a lean, rapidly growing type of pig, suggesting that meat quantity and quality may not be compatible in pork. In their paper 'The inheritance of meat quality in pigs' (A3), McGloughlin and McLoughlin describe the results of their studies on the Irish Landrace and Large White pigs. They found that breed, and test station for 1 year only, significantly affected M. L. dorsi pH_1 values, an index of PSE. Sex had no effect. The heritability of pH_1 was equal and moderate in both breeds. They also found that genetic correlations between pH_1 and daily gain, food conversion efficiency and backfat were low with high standard errors, and inferred therefore, that there was no strong relationship between pH_1 and these performance traits. Because of a lack of agreement between the same correlations for the two breeds, the authors suggest that there may be a real difference in the two populations. They further found a low correlation between pH_1 and eye muscle area and conclude that there was no antagonism between meatiness and quality in the breeds they used. McGloughlin and McLoughlin state that pH_1, an index of meat quality, will respond to selection.

Following the view of McGloughlin and McLoughlin that PSE will respond to selection and, that meatiness and quality may not be incompatible, the review of methods for the prediction of PSE pork by Eikelenboom and Sybesma (A1) is particularly opportune. Their paper contains a distillate of their experience with three methods:-

1. Analyses of blood serum enzymes. Of the various enzymes, creatine phosphokinase (CPK) is the most specific indicator of PSE. At

present, neither the accuracy of the test nor its relationship with ultimate meat quality are sufficient for pig performance testing.

2. Muscle biopsy analyses. The levels of various metabolites e.g. energy-rich phosphate compounds, lactate, pyruvate and glucose-6-phosphate have been analysed in muscle biopsy samples, and correlated with ultimate meat quality.

3. The non-destructive testing of young pigs for sensitivity to the malignant hyperthermia syndrome. When stress susceptible (SS) pigs are anaesthesized with halothane they develop severe muscle rigidity and progressive hyperthermia. In an evaluation of the relationship between the reaction of SS Dutch Landrace pigs to halothane anaesthesia and the occurrance of PSE meat; considerable differences in growth and carcass composition traits were observed between susceptible and non-susceptible pigs. Susceptible pigs were leaner than the others and their ham and loin muslce had a significantly lower pH_1 and a significantly higher temperature. This incompatibility of meat quantity and quality is in contrast to the findings of McGloughlin and McLoughlin in the previous paper. Perhaps Irish pigs differ in this respect from the Dutch.

The ease, cheapness and obvious promise of this non-destructive test will surely hasten its evaluation in commercial pig testing and breeding schemes for meat quality.

I shall now review, very briefly, cellular aspects of muscle growth development and differentiation. (Slide No 3 here).

At a cellular level there are two main developments during muscle growth. These are morphological changes in all muscle cells, together with a differentiation of myofibers into their various biochemical and physiological types.

SLIDE NO 3

Muscle mass increases by:-

1. Elongation of (a) continuous myofibers, and
   (b) intrafascicularly terminating myofibers
2. Myofiber hyperplasia
3. Myofiber hypertrophy, and
4. Development of intramuscular adipose and connective tissue

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SLIDE NO 4

MYOFIBER TYPES

(a) Biochemical Characteristics

Type I or Red:	Aerobic glycolysis	R
Type II or White:	Anaerobic glycolysis	W
Type III or Intermediate:	Combined	I

(b) Physiological Characteristics

Speed of Contraction:	Fast	α
	Slow	β
Resistance to Fatigue:	High	R
	Low	W

Dr Schoen, in her paper (A4) discusses the factors which significantly effect the formation of intramuscular fat. However, because myofibers constitute up to 90%, on a moisture free basis, of muscle mass, any change in their shape, size and mass will have a far greater effect on muscle mass than changes in intramuscular adipose and connective tissues.

Hyperplasia, which is genetically controlled with high heritability (Staun, 1972) appears to be fixed about the time of birth in meat animals. It has a significant effect on ultimate muscle yield. Meatier animals are said to have a greater number of myofibers per muscle.

The post-natal growth of skeletal muscle is due to both hypertrophy and elongation of myofibers. Two types of myofiber elongation viz. that of the continuous and of the intrafascicularly terminating types are recognised. According to Swatland and Cassens (1972) intrafascicularly terminating myofibers in both bovine and porcine muscles grow at a slower rate than those with completely tendinous insertions. Swatland, (1973, 1974) has more recently elaborated on the importance of the growth of intrafascicularly terminating myofibers during the fetal and neofetal period. With regard to the contribution of hypertrophy and hyperplasia to variation in muscle mass, we can only guess very imperfectly from the work of Staun (1963) that they may, respectively, account for about 40% and 35% of the total variation in muscle mass. Others regard double muscling in cattle as a combination of heritable hypertrophy and hyperplasia.

When we come to consider that very question, which is basic to muscle mass increase; how is protein biosynthesised in myofibers? We can only hypothesise in answer. We do not know for sure.

SLIDE NO 5

MYOFIBER HISTOCHEMISTRY

Myofiber Type	Indicator Enzyme
R	NADH-TR, SDH, α-GPDH
W	GPase, LDH
I	SDH + GPase
α	MATPase, Heavy
β	MATPase, Light

NADH-TR:	Nicotinamide adenine dinucleotide tetrazolium reductase
SDH:	Succinate dehydrogenase
α - GPDH:	α-Glycerophosphate dehydrogenase
GPase:	Glycogen phosphorylase
LDH:	Lactate dehydrogenase
MATPase:	Myofibrillar adenosine triphosphatase

Verily, there is much to learn concerning the control of muscle mass in meat animals.

Simultaneous with muscle enlargement by the processes I have just outlined, differentiation of myofibers takes place (Slide No 4 here).

This slide contains a scheme for classifying myofibers. The problem of myofiber classification is confounded by the fact that there are almost as many schemes of nomenclature as there are investigators in the field. Nonetheless, it is possible to find much that is common to many investigators and the following scheme is the outcome of such a comparison. Two main characteristics biochemical and physiological are recognised. In the biochemical group there exist three myofiber types; the Red or Type I with a high capacity for aerobic glycolysis; the White or Type II with a high capacity for anaerobic glycolysis, and the Intermediate or Type III having a capacity for both aerobic and anaerobic glycolysis, ie. a combined metabolism. In the physiological grouping there are the α or fast contracting myofibers, and the β or slow contracting myofibers. These 3 types are indicated in Slide No 4 by the symbols R, W and I respectively. In addition, myofibers differ in their resistance to fatigue. Those with a high resistance are rich in oxidative enzymes and are thus designated Red. The fatigue-sensitive myofibers appear to have little oxidative capacity and to depend primarily on anaerobic glycolysis (Burke & Tsairis, 1974). The biochemical and physiological characteristics are inter-related so that six myofiber types are possible.

Investigators encounter mostly five types, however, namely, αR, αW, αI, βR and βI. Histochemistry is now widely used in myofiber typing, and the next slide (Slide No 5 here) relates myofiber characteristics to the enzymes most frequently used. Many assumptions have and continue to be made, which means that there are some drawbacks to the histochemical approach. These drawbacks stem from ambiguous methods, lack of controls, unsatisfactory definitions, and an inadequate knowledge of the basal metabolism of skeletal muscle. What associations that exist between myofiber histochemistry and the biochemical and physiological characteristics of myofibers, have been deduced by comparing myofiber aggregates with muscles. There is, therefore, an urgent need to establish, especially for meat animals, a correlation between the physiology, biochemistry, and histochemistry of individual myofibers. Time may not permit a satisfactory discussion of the material on Slide No 5, but one or two points may serve to illustrate the criticisms which can be made. For example, α-glycerophosphate dehydrogenase is used by some investigators to identify anaerobic or white myofibers. In reality this enzyme is part of the glycerophosphate shunt for producing nicotinamide adenine dinucleodide (NAD) and is intimately involved with mitochondrial activity. This method of producing NAD does in fact cease when anaerobic conditions pertain. α-Glycerophosphate dehydrogenase activity is oxidative and is therefore more correctly associated with Red myofibers.

In summary the situation which at present pertains in the usage of histochemistry for myofiber typing is one where hypotheses have not been critically tested and much of our approaches are intuitive. However, it is well to remember that intuition is the means by which great leaps forward are made in science. Let us now turn to the final paper (A2) of this session. This paper 'The effect of body size and selection on skeletal muscle fiber types in mammals' by Gunn and Davies is concerned generally with muscle composition, in terms of myofiber types, as related to function and body size. They report the results of three investigations:-

1. In studies on the diaphgram of 10 species of animals, ranging in size from the shrew to the horse, they found that the proportion of fast contracting myofibers increased with decreasing body size. There was no apparent variation in muscle oxidative capacity with body size. The larger the animal the more myofibers rich in anaerobic capacity were observed. Taken with the evidence from ATPase staining this indicates a preponderance of αW (fast-white) myofibers in larger animals. It would appear that with the inclusion of the author's data on red myofibers, there are indications of a greater amount of αI (fast-intermediate) myofibers in the diaphragm of larger animals.

   In relating the myofiber composition of the M. semitendinosus to animal size, the authors observe that with increasing body size the proportion of slow-twitch myofibers increased. They suggest that the speed of movement of the diaphragm and the limbs decrease with increasing body size.

2. Of special interest to meat research workers is the observation of Gunn & Davies that the transverse area of porcine M. longissimus dorsi increased with increasing body weight in a relationship to the $\frac{2}{3}$ power of the body weight. They also found that the mean myofiber transverse area was directly proportional to the whole muscle transverse area. Gunn & Davies have also observed a most interesting point that the proportion of myofibers with low ATPase activity increased throughout growth and that the area of muscle occupied by these slow myofibers bears a linear relationship to body weight.

3. Dr Gunn has told me that he has long been interested in finding an answer to the question; why do racehorses and greyhounds run so fast? This curiosity has led him to the observation that breeds which have been selected to run quickly have a lower proportion of slow-twitch myofibers in their muscles.

Finally, Gunn & Davies generalise that the ratio of slow-contracting to fast-contracting myofibers can be related to speed of limb movement and muscular function.

I stated at the outset of my review that I was going to be selective. There are therefore, many aspects e.g. the significance of innervation of muscle in meat animals, not discussed. There are however, two further points I would like to refer to before finishing.

In looking to the future one may expect a major emphasis in increasing the efficiency of conversion of feed to meat. A prerequisite to this is the need to discern the real mechanisms which regulate growth and development in meat animals. A corollary here is (a) the establishment of means for identifying which myofibers are actively synthesising protein, and (b) the charting of the pattern of myofiber differentiation during the growth of meat animals. One may expect a quantification of the heritability of these traits and the exploitation of such knowledge in selecting the superior meat producing animals.

The second point concerns excercise and muscle composition. We are aware of some of the effects of excercise on muscle composition. Hypertrophy of myofibers occurs and fast-white, αW, myofibers are said to change into slow-red, βR types. About the converse, lack of excercise, our knowledge is much more meagre. In times when intensive beef production units are increasing in size and in number, there is a

SLIDE NO 6

Red and White Muscle

R.G. Cassens & C.C. Cooper. Adv. Fd. Res. 19: 1-74, 1971

Postembryonic Growth and Differentiation of Striated Muscle

G. Goldspink. In: The Structure and Function of Muscle, Vol 1 (2nd Ed) 179-236, 1972. New York & London: Academic Press

Selected Topics in Skeletal Myogenesis

H. Holtzer et al. In: Cold Spring Harbor Symposia on Quantitative Biology, 37: 549-566, 1973

Myogenesis: Differentiation of Skeletal Muscle Fibers.

T.L. Lentz. In: Development Regulation (Ed. S.J. Coward), 169-192, 1973. New York & London: Academic Press

Cellular Regulations of Growth and Development in Skeletal Muscle

J.G. Burleigh. Biol. Rev. 49: 267-320, 1974

Symposium on Protein Synthesis and Muscle Growth

65th Ann. Meet. Amer. Soc. Lincon. Neb. 1973, J. Anim. Sci. 38: 1050-1175, 1974

need to research what are the effects such a sedentary existence has on beef muscle composition. Are undesirable combinations of myofiber types being produced in such circumstances?

My final slide (Slide No 6 here) contains a selection of reviews and articles, relevant to our Session, which have appeared within the last three years.