SELECTION OF BEEF CATTLE FOR EFFICIENCY OF LEAN GROWTH

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DECLARATION

I declare that this thesis is my own composition, and does not include work submitted for any other degree or professional qualification. The thesis reports my analyses of data collected by myself, or by members of staff of the ARC Animal Breeding Research Organisation.

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ABSTRACT

The aims of this study were: 1) to evaluate measurements for predicting the carcass lean content of live bulls, 2) to assess the importance of different pre-test environmental effects on bull performance, and 3) to compare biological and economic selection indices for use in a terminal sire beef breed.

The data comprised live weight, food intake, ultrasonic and carcass measurements on a total of 235 Hereford bulls, performance tested to 400 days of age on *ad libitum* feeding.

Multiple regression equations using live weight and ultrasonic fat area measurements gave the best prediction of carcass leanness. However, the precision achieved varied depending on the machine, the operator and the group of bulls (R^2 values 0.61 to 0.77).

Artificially reared bulls had low pre-test growth rate, which led to compensatory growth, and increased the variation in performance on test. Bulls weaned at 84 days of age were least affected by environmental factors such as dam age and year-season of birth, and performed as well as bulls weaned at 168 days of age.

There were high phenotypic correlations between growth rate and lean growth rate (0.96) and between food conversion efficiency and lean food conversion efficiency (0.97). Formulae were therefore derived for predicting the phenotypic and genetic relationship between a product trait, such as lean growth rate, and one component trait.

Selection indices were derived which may be suitable for terminal sire breeds in the UK. The indices were insensitive to moderate changes in economic weights and genetic parameters, and were proposed as being superior to the biological indices (product traits) for improving the efficiency of lean meat production.

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ABBREVIATIONS USED IN THE TEXT AND TABLES

* = Probability (P) <0.05
** = $P <0.01$
*** = $P <0.001$
AA = Aberdeen Angus
AFT = anal fold thickness
AI = artificial insemination
BW = birth weight
CPT = central performance test
CV = coefficient of variation
df = degrees of freedom
DFA = fat area estimated from Danscanner ultrasonic scan
DMA = muscle area estimated from Danscanner scan
ECL % = estimated carcass lean %
FA = fat area
FCE = food conversion efficiency (weight gain/food intake)
FCR = food conversion ratio (food intake/weight gain)
FD = fat depth
FF = final feedlot weight
FG = feedlot gain
FI = cumulated food intake
FP = final pasture weight
FW = final weight
G = postweaning gain
GR = growth rate
h^2 = heritability
He = Hereford
HQ = hindquarter
KO % = killing-out %
LFCE = lean food conversion efficiency (lean gain/food intake)
LGR = lean growth rate
LSM = least-squares mean
LW = live weight
MA = muscle area
MD = muscle depth
ME = metabolisable energy
m. long. = *m. longissimus* (*thoracis* or *lumborum*)

n = number of estimates or observations
NS = non-significant
OPR = offspring-parent regression
PG = pasture gain
PHS = paternal half sib
r = correlation coefficient
R = multiple correlation coefficient
RGR = relative growth rate
RSD = residual standard deviation
s.c. fat = subcutaneous fat
SD = standard deviation
SE = standard error
SFA = fat area estimated from Scanogram ultrasonic scan
SFT = skinfold thickness at the 13th rib
SMA = muscle area estimated from Scanogram scan
US = ultrasonic or ultrasound
V = variance
W = preweaning gain
WB = Weighband estimate of live weight
wt = weight (of lean etc.)
WW = weaning weight
Y = yearling weight

CONTENTS

CHAPTER I

Introduction

In the UK over 55% of home-produced beef comes from the dairy herd as cull cows, surplus purebred calves or crossbred beef calves. Most of the remainder comes from suckler herds kept solely for beef production (Allen and Kilkenny, 1980). The dairy and beef industries of many European countries are less distinct than in the UK, with more use of dual-purpose breeds. Deciding on objectives for beef cattle improvement is difficult because the relative importance of different beef traits differs between production systems and from one stage of the production chain to the next (Cunningham, 1981; Kempster, Cuthbertson and Harrington, 1982c). Ease of calving is an important trait in dairy and suckler herds, whereas growth traits are most important to the calf rearer and finisher. The meat trade is concerned with killing-out percentage, fatness, muscle to bone ratio, proportion of high-priced cuts and meat quality. Finally, the consumer is most interested in the price and the eating quality of the beef (Allen and Kilkenny, 1980; Kempster *et al.*, 1982c).

In the past, many improvement programmes have aimed to increase the output of beef, often by within-breed selection for growth rate or by breed substitution. In the UK, for example, there has been considerable substitution of the native terminal sire breeds by large continental European breeds such as the Charolais, Simmental and Limousin. In the European Community, and other nations, many animal products are in surplus. It seems likely, therefore, that the overall objective will change in the future, from increasing output to improving the efficiency of production.

By definition, the efficiency of any process is the ratio of output to input. The major inputs used in animal production are land, feed, fertiliser, labour, capital and water, though these are not independent

(Spedding, Walsingham and Hoxey, 1981). Thus, there are many useful efficiency ratios, but no single ratio is most useful because the relative importance of different inputs varies from one species or production system to the next (see Holmes, 1977). Economic efficiency ratios may be unstable as the value of outputs and the cost of inputs vary over time, and between regions, and are influenced by political decisions. Biological variables such as protein and energy content of some inputs and outputs are often more useful. Comparisons of animals of the same species offered the same diet are usually based on gross food conversion efficiency (weight gain/food intake), or its reciprocal food conversion ratio; these are frequently confused. However, these ratios may be inadequate where the composition of the live weight gain is important.

In most countries *lean* meat is now the most important output from beef production. Kempster and Harrington (1979) estimated that total waste beef fat production in Britain in 1976 was 48 000 tonnes, or 7% of the total carcass weight produced. A more recent survey of slaughterhouses has shown little change in the fatness of beef carcasses (A.J. Kempster, personal communication). Consumers discriminate strongly against fat. In a survey reported by Rhodes (1977), 46% of respondents said they rejected the visible fat on beef. This discrimination may be partly due to an increasing awareness of the health risks of a diet high in animal fat. There is reasonable evidence that saturated fats have a role in coronary heart disease (Department of Health and Social Security, 1974; Royal College of Physicians, 1976). In a recent report, the Royal College of Physicians (1983) highlighted the health risks of obesity; in Britain, 5 to 30% of the adult population in different age groups are overweight. The report recommended government encouragement for the breeding of cattle, sheep and pigs with a lower fat content, and legislation limiting the amount of fat used in the preparation of meat products.

The preference for lean meat therefore seems likely to continue, so the efficient production of lean meat would be a suitable long-term objective for the beef industry in the UK (and other countries). There are many components of beef production systems which affect the efficiency of lean meat production. Growth rate, food conversion efficiency and carcass composition may be influenced by factors such as the quality and quantity of food offered, castration, the use of anti-microbial or anabolic agents, and control of age or weight at slaughter (Blaxter, 1964; Andersen, 1975b; Berg and Butterfield, 1976; Webster, 1977; Béranger, 1978; Geay and Robelin, 1979; Bond, Warwick, Oltjen, Putnam, Hiner, Kotula and Weinland, 1982). Animal scientists must decide which traits can be improved genetically, and whether this is cost-effective. In some cases changes in management may be more desirable than genetic changes, since they tend to be more flexible. In other cases changes in management may augment or interact with genetic change.

In 1976, Fowler, Bichard and Pease discussed objectives in pig breeding, and compared the economic and biological approaches to constructing a selection index. They suggested that:

> *"The elegance, power and complexity of [economic] selection index calculations has served to limit or even break the vital dialogue between geneticists and others, and has led to a view of selection which takes no account of increasing knowledge other than improved estimates of parameters."*

From a consideration of the biological efficiency of production of lean tissue, they proposed the improvement of lean tissue food conversion as a selection objective in pig breeding.

It was suggested that the most important single means of achieving this was increasing the lean tissue growth rate (Fowler *et al.*, 1976; Fowler, 1978). Possible deficiencies of the 'biological index' are: (1) no allowance is made for changes in the relative economic value of lean and feed; (2) the actual weightings on lean and feed, in selection, depend on their coefficients of variation and heritability (Smith, 1967); and (3) no allowance is made for other traits such as meat quality (Smith and Fowler, 1978).

It has been suggested that selection for leanness in cattle may increase the maintenance cost of breeding females, which is a large part of the total costs in suckler herds (Webster, 1977, 1980a). Additionally, Carter (1982) suggested that selection for lean growth in grazing cattle may be detrimental, since fat tissue provides a buffer against fluctuating forage supply. However, it appears that the objectives proposed by Fowler *et al.* (1976) could be important, at least in terminal sire beef breeds.

In 1977, a 200-cow pedigree Hereford herd was established at the Animal Breeding Research Organisation (ABRO), to provide basic information on selection for efficiency of lean meat production, and to allow complementary research on aspects of performance testing. Cows were purchased from many herds and bred, in the first two years, to AI bulls from several sources. Semen was collected from bulls born in the herd in 1977 and 1978 and frozen for later use on control cows. Two replicated selection lines were started, one selected for lean growth rate (LGR) from birth to 400 days, the other selected for lean food conversion efficiency (LFCE) from 200 to 400 days of age. Bulls were selected on their own performance, on a complete diet of dried grass and barley, fed *ad libitum*.

This thesis is based on performance data on 235 bulls tested in the first four years of the experiment.

The *in vivo* estimation of carcass composition is central to selection for lean tissue growth rate and lean tissue food conversion. Danscanner and Scanogram ultrasonic scanners have been used for this purpose in the ABRO experiment. A literature review on the use of ultrasound to assess carcass composition is therefore presented in Chapter II. This is followed by discussion of an experimental evaluation of the accuracy of the two ultrasonic machines, and several other live animal measurements, for predicting carcass composition.

A review on genetic aspects of growth and efficiency is presented in Chapter V. Results are then presented on the effects of pre-test environment on bull performance on test, and the phenotypic relationship between important traits is discussed. Also, results from constant age and constant weight performance testing regimes are compared. The efficacy of selection for product traits, such as lean tissue growth rate and lean tissue food conversion is examined, and compared to economic index selection. Finally, the results are discussed in the context of current beef improvement schemes in the UK, and recommendations are made for future schemes.

CHAPTER II

The Use of Ultrasound to Predict the Carcass Composition of Live Cattle - A Review

2.1 Introduction

The assessment of body or carcass composition is a fundamental problem at all levels of the animal production industry, from the farm to the research station. Many *in vivo* estimation techniques have been tested, varying widely in applicability and accuracy.

On farms, live weight is probably the most commonly used indicator of body composition. Additionally, subjective assessment of subcutaneous fat cover at defined anatomical positions can be a useful aid when selecting animals for slaughter (Meat and Livestock Commission [MLC], 1977). Similar techniques are used to condition score cattle, enabling producers to aim for different target conditions at mating, calving, etc. (East of Scotland College of Agriculture, 1976). Visual appraisal has also been used to assess carcass composition in the live animal, but with variable results (Andersen, 1976).

Skinfold thickness has been examined as an indicator of body composition in humans (e.g. Keys and Brožek, 1953) and cattle (Tulloh, 1961; Charles, 1974; Wright, 1982). For experimental purposes, assessment of animal shape may provide a useful estimation of joint weight (Fisher, 1976). An extension of this technique is the use of photogrammetry (Kallweit, 1982). More precise definition of body composition may be obtained using dilution techniques (e.g. Robelin, 1976, 1982; Kallweit, 1982; Wright, 1982). Estimation of blood and red cell volume and other experimental evaluation techniques were discussed by Wright (1982).

The use of ultrasound to measure carcass traits in live cattle was first reported by Temple, Stonaker, Howry, Posakony and Hazaleus (1956), Price, Pfost, Pearson and Hall (1958), Stouffer, Wallentine and Wellington (1959), and Brinks, Clerk and Kieffer (1962a). Since that time many ultrasonic machines have been developed and tested for use on cattle, sheep and pigs. The development of ultrasonic evaluation techniques was reviewed by Stouffer (1963, 1966a,b), Barton (1967) and Stouffer and Westervelt (1977). There are several recent comparisons of ultrasonic machines (Kempster, Cuthbertson, Jones and Owen, 1981; Andersen, Busk, Chadwick, Cuthbertson, Fursey, Jones, Lewin, Miles and Owen, 1982).

Quite accurate assessment of carcass composition using Computer-aided Tomography (CT) has been reported recently (Vangen, Grønseth, Evensen and Skjervold, 1981). This technique, developed in human medicine, involves computed synthesis of an image from X-ray transmission data. The X-rays pass in many different directions through one plane of the animal or patient. This enables the density of body tissues at different depths to be calculated. The result is a table of 'CT-numbers', each representing the density of tissue at a given point. Skjervold, Grønseth, Vangen and Evensen (1981) predicted the carcass composition of pigs on the basis of the distribution of CT-numbers from one tomographic plane. This method accounted for 89% of the variation in fat content of the carcasses. The technique is very costly, immobile and at present restricted to sheep and pigs because of the dimensions of the machine. Some lesser-known techniques of evaluation were discussed by Miles (1982).

The methods of assessing body composition are numerous. They vary in complexity, and choice of a suitable method will depend on the precision required. Inevitably a compromise between cost and accuracy will result. Ultrasonic machines generally provide such a compromise and this explains their current popularity.

2.2 Physical Principles of Ultrasound Transmission

Ultrasonic examination techniques are widely used in biology - largely because they are non-invasive, non-destructive and painless. The two most widely used techniques are Doppler and pulse-echo techniques.

Doppler techniques are used to study movements of reflecting interfaces such as the opening of the heart valves, the foetal heart beat and blood flow rates in human medicine (Wells, 1969). In animal science, they have been used to detect pregnancy in sheep, goats, cattle, horses and pigs (e.g. Fraser, Nagaratnam and Callicott, 1971; Mitchell, 1973; Deas, 1977; Hanzen, 1980). They have also been used to study foetal behaviour in horses and cattle (Fraser, Hastie, Callicott and Brownlie, 1975; Fraser, 1976).

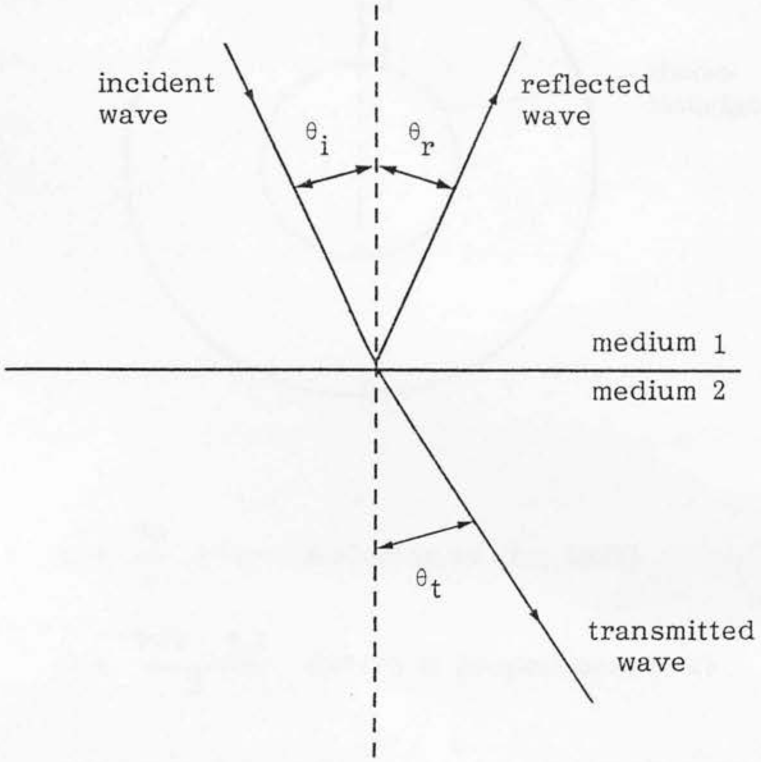
Pulse-echo techniques are used to map tissue boundaries using changes in acoustic impedance (resistance to the transmission of ultrasound). It is pulse-echo techniques which are used in most animal scanners. Pulse-echo techniques have many applications in human medicine including diagnosis of single and multiple pregnancy, diagnosis of malignant tumours and other uses in obstetrics and gynaecology, opthalmology, cardiology, neurology and radiation therapy planning (Wells, 1969, 1977; Hospital Physicists Association, 1976). Parallel to research in human medicine, pulse-echo techniques were developed for use in animal scanners (Stouffer and Westervelt, 1977). Full details of the physical principles of the transmission of ultrasound and their application to scanning machines are given by Wells (1969), Miles (1978) and Andersen *et al*. (1982). Only a brief description is attempted here.

The velocity of ultrasound in a biological medium depends on the temperature and physiological condition of the medium. In most soft tissues and water, the velocity of ultrasound is similar, whilst in air it is much lower and in bone, much higher. When a wave of ultrasound meets an interface between two types of tissue partial reflection may occur. The transmitted wave travels forward at a velocity characteristic of the second tissue and at an angle of refraction governed, as in optics, by Snell's Law (Figure 2.1).

The intensity of transmitted and reflected waves depends on the incident intensity, the angle of incidence and the acoustic impedance. If the acoustic impedance of the two tissues is approximately equal, a wave of ultrasound at 90° to the interface will be almost perfectly transmitted. If the acoustic impedance differs, most of the energy will be reflected. The acoustic impedance of air is much lower than that of solids or liquids. This is why a coupling agent, such as liquid paraffin, is needed to transmit ultrasound from a scanner to an animal. At body temperature, the acoustic impedance of soft tissues is similar, but that of bone differs. There is, therefore, little reflection from a muscle : fat interface, but much reflection from a muscle : bone interface.

Suppose a wave of ultrasound travels through a tissue, at constant velocity until it is incident at 90° to a tissue boundary. Part of the energy of the wave is then reflected. The time taken for the echo (reflected wave) to reach the original source is proportional to the depth of the boundary (Figure 2.2). It is this principle which underlies most ultrasonic machines used to measure carcass characteristics on live animals.

Pulses of ultrasound are produced by a transducer which also receives reflected waves of ultrasound and converts them to electrical energy. After modification these electrical signals may be displayed on a screen in various ways. In so-called 'A'-mode machines echo amplitude

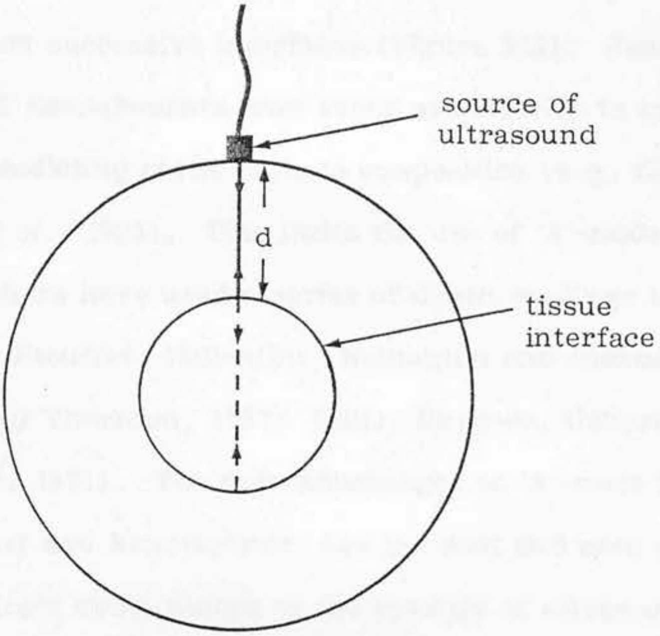


$$\theta_i = \theta_r$$

$$\frac{\mathrm{Sin}\ \theta_i}{\mathrm{Sin}\ \theta_t} = \frac{v_1}{v_2} \quad \text{(Snell's Law)}$$

where v_1 = velocity of ultrasound in medium 1
v_2 = velocity of ultrasound in medium 2

FIGURE 2.1: Reflection and refraction of ultrasound at a plane interface between two media.
(adapted from Wells, 1969 and Andersen *et al*., 1982)



$$t = \frac{2d}{v} + t_0 \quad \text{(Andersen } et\ al.\text{, 1982)}$$

and: $$d = \frac{v(t - t_0)}{2} \quad \text{(which is proportional to t)}$$

where: t = time from emission of the ultrasonic pulse to receipt of the echo.

t_0 = acoustic and electronic delays in the measuring system.

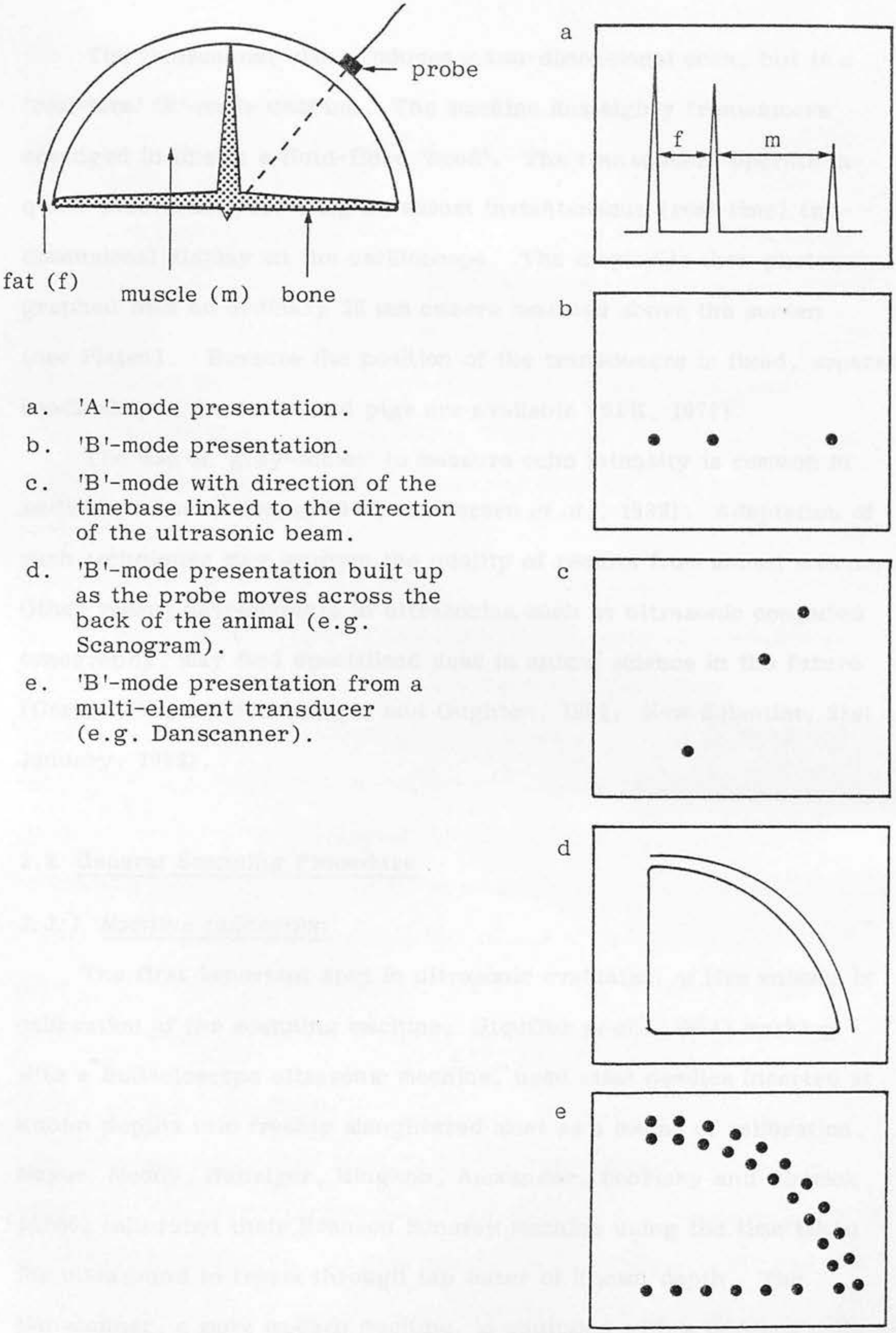
d = depth of the tissue boundary.

v = velocity of ultrasound in the first tissue.

FIGURE 2.2: Schematic diagram illustrating the principle of ultrasonic scanning.

(A) is displayed against time. Echoes appear as spikes on an oscilloscope screen, the distance between successive spikes being related to the distance between successive interfaces (Figure 2.3). Generally fat or muscle depth measurements from scans are inferior to area measurements in predicting cattle carcass composition (e.g. Cuthbertson, 1976; Kempster *et al.*, 1981). This limits the use of 'A'-mode machines, though several authors have used a series of depth readings to estimate muscle areas (e.g. Stouffer, Wallentine, Wellington and Diekmann, 1961; Alsmeyer, Hiner and Thornton, 1963; Gillis, Burgess, Usborne, Greiger and Talbot, 1973). The main advantages of 'A'-mode machines, such as the Sonatest and Krautkrämer, are low cost and ease of operation. Recently, direct measurement of the velocity of ultrasound through the hind limb of cattle has been reported as a method of evaluation (Miles, Woods and Fursey, 1982). In this case, the velocity of ultrasound was measured using a Sonatest machine in conjunction with two transducers and a time interval meter (Miles and Fursey, 1974).

Electrical signals from echoes regulate the brightness (B) of the time base line on a cathode ray tube in 'B'-mode scanners. Here, the distance between successive bright spots represents the distance between successive tissue interfaces (Figure 2.3). Two-dimensional scans can be produced in a number of ways. The Scanogram has a spring-loaded transducer which moves along a track across the animal. The movement of the probe along the track is mechanically coupled to a Polaroid camera aimed at the oscilloscope. The camera moves, in phase with the probe, building up a two-dimensional scan photograph (see plates following Chapter III). The SVC machine also has a single moving transducer, but with this machine the signals from echoes move across the oscilloscope in phase with the transducer. A two-dimensional scan is built up by means of a storage facility on the oscilloscope.



a. 'A'-mode presentation.
b. 'B'-mode presentation.
c. 'B'-mode with direction of the timebase linked to the direction of the ultrasonic beam.
d. 'B'-mode presentation built up as the probe moves across the back of the animal (e.g. Scanogram).
e. 'B'-mode presentation from a multi-element transducer (e.g. Danscanner).

FIGURE 2.3: Schematic diagram of a dorsal cross section through an animal, and different types of ultrasonic scan.

(adapted from Wells, 1969)

The Danscanner also produces a two-dimensional scan, but is a 'real-time' 'B'-mode machine. The machine has eighty transducers arranged in line in a fluid-filled 'head'. The transducers operate in quick succession producing an almost instantaneous (real-time) two-dimensional display on the oscilloscope. The display is then photographed with an ordinary 35 mm camera mounted above the screen (see Plates). Because the position of the transducers is fixed, separate heads shaped for cattle and pigs are available (SFK, 1977).

The use of 'grey-scales' to measure echo intensity is common in medical scanners (Wells, 1977; Andersen *et al.*, 1982). Adaptation of such techniques may improve the quality of results from animal scanners. Other recent developments in ultrasonics, such as ultrasonic computed tomography, may find specialised uses in animal science in the future (Carson, Meyer, Scherzinger and Oughton, 1981; New Scientist, 21st January, 1982).

2.3 General Scanning Procedure

2.3.1 Machine calibration

The first important step in ultrasonic evaluation of live animals is calibration of the scanning machine. Stouffer *et al.* (1961), working with a Reflectoscope ultrasonic machine, used steel needles inserted at known depths into freshly slaughtered meat as a means of calibration. Meyer, Moody, Hunziger, Ringkob, Alexander, Zobrisky and Hedrick (1966) calibrated their Branson Sonoray machine using the time taken for ultrasound to travel through tap water of known depth. The Danscanner, a more modern machine, is equipped with a perspex calibration block in which steel rods are embedded at known depths (SFK, 1977). The transducer head of the machine is placed on the block, with a coupling agent, and the oscilloscope is examined to see whether recalibration is necessary.

2.3.2 *Animal restraint*

Some degree of animal restraint is required to permit scanning. Campbell and Hervé (1971a) tranquillised steers prior to scanning and used a sling to restrain calves. Hervé and Campbell (1971) also found that the sling technique improved the quality of ultrasonic scans of calves. Campbell and Hervé (1971b) conducted a trial using varying degrees of restraint, ranging from a head bail and rigid transducer support to a simple crush. They concluded that whilst the former method improved results, it was still possible to obtain good results under field conditions. Tulloh, Truscott and Lang (1973) found it necessary to tranquillise some steers prior to scanning with a Scanogram. In a trial involving five ultrasonic machines, Andersen *et al*. (1982) found that the machines differed in susceptibility of results to animal movement. Machines which require observation of a screen by the operator are vulnerable to this problem, since attention is diverted from holding the transducer in place. Obviously, the degree of restraint required will depend on whether the animals are used to being handled, the time needed to scan, etc. and will largely be a matter of trial and error.

2.3.3 *Scanning positions*

The vast majority of workers have scanned cattle at positions along the back, over the *mm. longissimi thoracis et lumborum* (formerly called the *m. longissimus dorsi*), usually between the 10th rib and the 5th lumbar vertebra. This is because of the traditional use of muscle area and fat thickness at this location, to assess carcass quality (Hedrick, Miller, Thompson and Freitag, 1965; Stouffer, 1966a).

However, some authors have scanned at other positions, e.g. Davis, Long, Saffle, Warren and Carmon (1964; *biceps femoris*), Campbell and White (1968; *m. infraspinatus*) and Tulloh *et al*. (1973; tuber coxae, scapula and femur) (see Figure 2.4).

2.3.4 Clipping

Stouffer *et al*. (1961) found that clipping the hair of cattle at the point of scanning allowed lower sensitivity settings on the machine. Campbell and Dodd (1965) reported a 35% incidence of failure to detect a particular tissue boundary on ultrasonic scans of unclipped cattle. The incidence of failure fell to 10% when cattle were clipped. Tulloh *et al*. (1973) found that clipping did not necessarily improve Scanogram results at the 10th and 13th rib and 3rd lumbar vertebra of Angus and Friesian steers. However, acceptable scans were more readily obtained on clipped animals. As a result of the differences in muscle area measurements from clipped and unclipped animals, the authors recommended that when animals are being compared they should all be treated in the same way. There is certainly no evidence of a detrimental effect of clipping, and this seems the safest course of action when in doubt.

2.3.5 Coupling agent

Application of a coupling agent ensures transmission of ultrasound from the machine to the animal's body, as previously explained. Early workers used motor oil as a couplant (Stouffer *et al*., 1961; Meyer *et al*., 1966). More recently, liquid paraffin and acoustic gel have been used (e.g. Ernst, Appel and Claus, 1982).

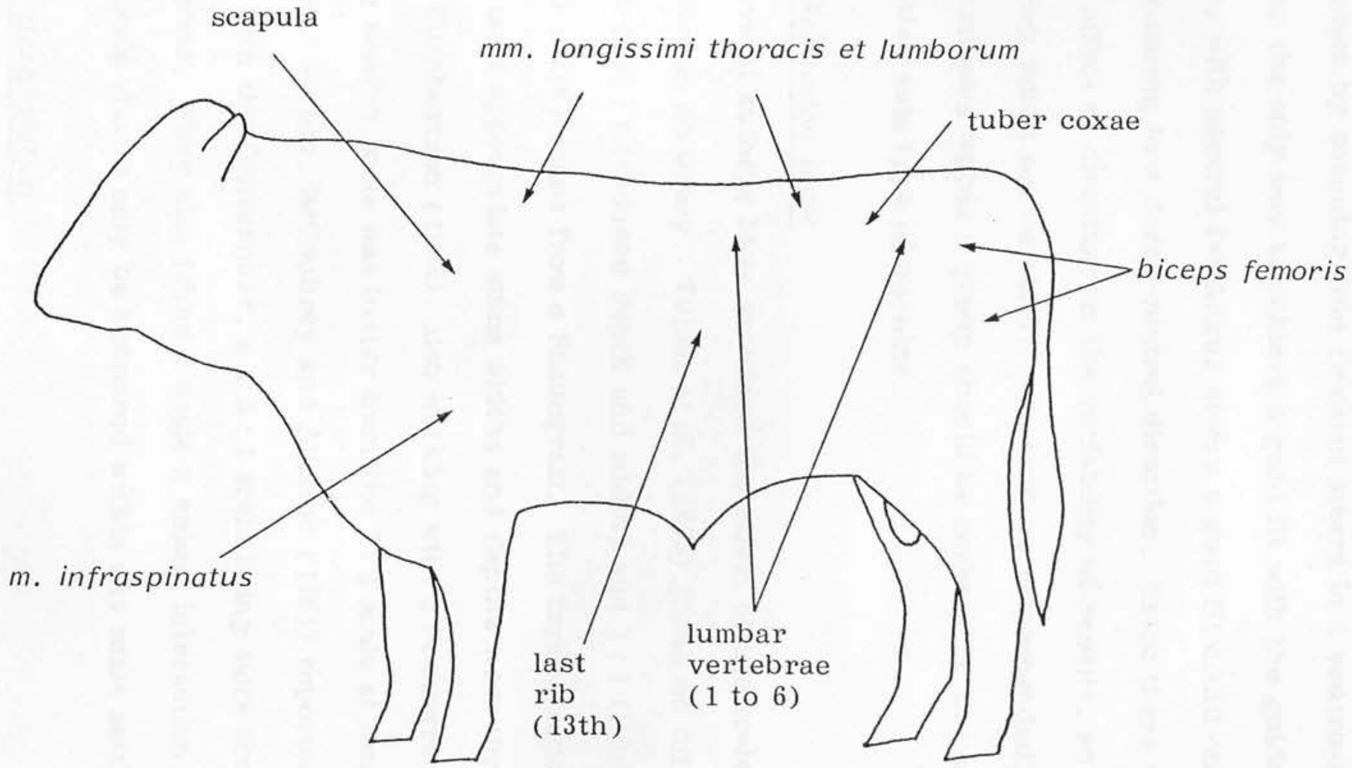


FIGURE 2.4: Schematic diagram showing some sites used for ultrasonic scanning. (For anatomical details see Brown, Coates and Speight, 1978 or Frandson, 1981.)

2.3.6 Direction of scanning

Tulloh *et al*. (1973) found that good Scanogram pictures could only be obtained by scanning thin Friesian steers in a ventro-dorsal direction. This was the only way to achieve a good fit with the guide rail. Conversely, with several fat Angus steers a good fit could only be obtained when scanning in a dorso-ventral direction. Since there was no consistent effect of direction on the variability of results, an overall correction would not be valid. The authors recommended, therefore, that all animals within a group should be scanned in the same direction when using this type of machine.

2.3.7 Reduction scale

Several authors have examined the effect of the scale of the ultrasonic scan on accuracy. Tulloh *et al*. (1973) found no difference between 2.54 : 1 (reduced depth and width) and 1 : 1 (lifesize depth, reduced width) scans from a Scanogram. The former reduction scale seemed most appropriate since widths and depths were then on the same scale. Cuthbertson (1976), also working with a Scanogram, concluded that the smaller scale was better than the 1 : 1 scale at most anatomical positions. Patton, McCoubrey and Alliston (1981) reported similar results with the Danscanner, a 1.5 : 1 scale being more accurate than a 1 : 1 scale. They also found a scale x animal interaction, suggesting that animals should only be compared within one scale setting.

2.3.8 Interpretation

Interpretation of results from 'A'-mode machines involves measurement of the distance between peaks on the oscilloscope, either directly or from a photograph. At the present time results from most 'B'-mode machines require interpretation from a photograph. This usually involves direct measurement of depths of fat and muscle, and tracing of fat and muscle areas followed by planimetry. Computerised systems of planimetry are now available (e.g. Alliston, 1980). Wallace, Stouffer and Westervelt (1977) assessed muscle area from Scanogram pictures either by tracing or using a template. They found little difference between the two methods in the correlation with corresponding carcass measurements (0.58 to 0.77 for tracing, 0.61 to 0.71 for template). Assessing muscle area with a template was, however, much quicker than tracing. Andersen and Ernst (1972) found that tracing muscle areas from photographs was more repeatable than tracing from projected transparencies (Table 2.5). There was little difference between the two methods in correlations with actual muscle area.

Bass (1979) examined the effect of including hide thickness in assessment of fat area from Danscanner pictures. He found that including the hide in interpretation was slightly less repeatable, but correlations with carcass components were as good, or better than those from interpretations excluding the hide. Andersen *et al*. (1982) reported no difference in results whether hide was included or excluded from interpretation. Including hide in the measurement may make interpretation of scans easier, since this boundary is usually better defined than the outer fat boundary. This is especially true in lean animals (H. Busk, personal communication).

The number of photographs obtained at each anatomical position and the number of times each is interpreted will affect the accuracy of ultrasonic evaluation. Increasing the number of photographs taken is better than increasing the number of interpretations, since the former reduces errors of both scanning and interpreting. However, this may not be economically feasible. Tulloh *et al*. (1973) calculated that two photographs per position, each interpreted twice, was a satisfactory compromise between cost and accuracy.

2.4 Trials with Ultrasonic Machines

2.4.1 Assessing results of trials

Investigations into ultrasonic evaluation of live cattle generally examine one or more of the relationships between ultrasonic measurements and (1) corresponding carcass measurements; (2) the weight or proportion of given retail cuts in the carcass; or (3) the weight or proportion of tissue components in a dissected sample joint or half carcass (fat, lean, bone).

It is difficult to compare different trials directly since the machines, scanning locations, operator experience and number, breed, age and weight of cattle vary widely from trial to trial. The most useful information comes from trials where a number of machines or scanning locations are compared on one population of animals.

The vast majority of reports present correlations between ultrasonic measurements and the character concerned. Where authors have not already done so, it may be of interest: (1) to test that coefficients differ from zero; (2) to construct confidence intervals for correlation coefficients; or (3) to test the difference between two coefficients. When the correlation coefficient is not zero, the distribution of estimates becomes skew. Estimates should therefore be transformed to a quantity 'z' (distributed almost normally) before constructing confidence intervals or testing the difference between correlation coefficients (see Snedecor and Cochran [1980] for details). For example, the 99% confidence interval for a correlation coefficient (r) of 0.60 between ultrasonic fat area and % fat in the carcass, estimated on a group of 20 animals is:

$$0.07 \leqslant r \leqslant 0.87$$

(transforming from z back to r). This emphasises the low value of experiments with few animals.

Correlation coefficients can be useful in preliminary investigations within a population of animals, but in some circumstances they can be misleading. If, for example, the correlation between ultrasonic fat area and % fat in the carcass is calculated for a group of animals of very variable carcass composition, an artificially high correlation may result. It is, therefore, unwise to compare correlations across different groups of animals without regard to the variation in the trait being predicted.

This problem can be reduced by using the residual standard deviation as a measure of precision. The residual standard deviation is related to the correlation coefficient, but takes account of the variation in the trait to be predicted (y):

$$\text{Residual } SD_y = SD_y \sqrt{[(1-r^2)\ \frac{n-1}{n-2}\ ]}$$

where SD = standard deviation and n = number of observations (Kempster *et al*., 1982c).

A third variable, such as live weight, can have an important influence on the correlation coefficient. In this case, the partial correlation coefficient between ultrasonic fat area and carcass fat, at constant live weight, is a more useful measure of the predictive value of ultrasonic measurements.

Lists of correlations or residual standard deviations do not necessarily indicate the best combination of measurements for prediction. The ultimate test of a machine is to examine the various combinations of ultrasonic measurements, with live weight, in multiple regression equations for % lean or % fat in the carcass.

2.4.2 Comparison with corresponding carcass measurements

The relationship between ultrasonic measurements and corresponding carcass measurements can provide a useful preliminary evaluation of a machine. However, if the relationship is good, it does not necessarily mean that the relationship with total carcass composition will also be good. Conversely, comparison with actual carcass measurements may be disappointing, due to post-slaughter movement of the soft-tissues relative to the skeleton. Stouffer *et al*. (1961) reported that slaughtering, hanging and splitting affected the shape and size of the muscle and fat at the 12-13th rib. Temple, Ramsey and Patterson (1965) stated that muscle area and fat configuration differed greatly between the live animal and carcass. A shift of 5 cm in relation to the skeleton was observed. The same authors reported that fat removed with the hide produced differences of up to 0.5 cm between estimated and actual fat thickness. Injecting vegetable dye or methylene blue enabled Miles, Pomeroy and Harries (1972) and Watkins, Sherritt and Ziegler (1967) to locate the exact site of scanning *post mortem*. Miles *et al*. (1972) noted that in the extreme thoracic region the soft tissues moved cranially as a result of hanging, splitting and *rigor mortis*. Caudal movement of soft tissues in the lumbar region was also observed, causing soft tissues to stretch along the midline. In the same study, it was noted that the vertebral column became distorted. Because of these carcass changes, it is difficult to evaluate an ultrasonic machine on the relationship with carcass dimensions alone. Andersen *et al*. (1982) found that several ultrasonic machines gave a better prediction of carcass composition than expected from comparison with measurements on carcasses sectioned at the site of scanning. Appel (1980) and Ernst *et al*. (1982) found that although ultrasonic muscle area measurements at the 1st lumbar vertebra were more accurate than those at the 5th lumbar, they were not as highly correlated with yield of retail cuts.

Correlations reported in the literature are presented in Table 2.1. Most results show that muscle areas and fat areas can be measured slightly more accurately than muscle and fat depths, respectively (e.g. Tulloh *et al.*, 1973; Wallace *et al.*, 1977; Patton *et al.*, 1981; Andersen *et al.*, 1982). Gillis *et al.* (1973) noted that muscle area at the 11-12th rib was more accurately measured by a series of 'A'-mode depth measurements (Krautkrämer) than by 'B'-mode scans (Scanogram). There was little difference between the machines in the accuracy of measuring fat depths when experienced interpreters were involved. With an inexperienced interpreter the accuracy of Krautkrämer measurements of fat depths was lower. In another trial involving these two machines, Tong, Newman, Martin and Fredeen (1981) found Scanogram and Krautkrämer measurements of fat depth at the 11-12th rib to be fairly similar in accuracy.

Several authors examined the relationship between ultrasonic measurements at different anatomical locations and measurements on the sectioned carcass. Many authors found that ultrasonic measurements of fat depth or area were most accurate between the 12th rib and 3rd lumbar vertebra. These trials involved a range of animal types and scanning machines (Miles *et al.*, 1972; Tulloh *et al.*, 1973; Wallace *et al.*, 1977 [Scanogram]; Andersen *et al.*, 1982 [Danscanner, Scanogram and three medical scanners]). Scans obtained at more anterior locations may be difficult to interpret because of the muscles overlying the *m. longissimus thoracis* (see Section 2.5.3 and Miles *et al.*, 1972). Most authors found that ultrasonic muscle area measurements are most accurate at locations between the 12th rib and 3rd lumbar vertebra

TABLE 2.1: Correlations between ultrasonic measurements and corresponding carcass measurements.

Source	No. of animals	Machine	Position	Fat depth	Muscle depth	Muscle area	Comments
Stouffer *et al.*, 1961	54,82,16	Sperry Reflectoscope	13th rib	0.32** to 0.54**	0.21* to 0.84**	0.22* to 0.85**	Range of depth readings.
	47,15,64	" " (modified)	13th rib	0.04, 0.42**	0.57* (n=15)	0.42** to 0.58*	(Moving transducer.)
	39	Branson Sonoray	13th rib	-	0.55**	0.42**	
Hedrick *et al.*, 1962	28,47,57, 71	Branson Sonoray 5	12-13th rib	0.11 to 0.63**		0.58** to 0.89**	Both sides of animal.
Lauprecht *et al.*, 1962	54	?	8- 9th rib			0.68***	
Morrow and Wideman, 1962	10-350	A-mode	12th rib			0.85** to 0.94**	
Alsmeyer, *et al.*, 1963	183-256	Curtiss-Wright Echoscope	13th rib	0.46** to 0.61**	-0.13 to 0.20**		Range of depth readings.
Brown *et al.*, 1964	20	Branson Sonoray	rib	0.46		0.78	
Davis *et al.*, 1964	60,10	Branson Sonoray	12-13th rib	0.90**, 0.67*	-	0.87**, 0.93**	
	10		lumbar	-	-	0.82**	
			forearm	-	0.57, 0.55	-	
			B. femoris	-	0.32	-	
Levantin *et al.*, 1964	31	?	13th rib			0.92	
Ritter *et al.*, 1964	41	?	11-12th rib			0.80	
Davis *et al.*, 1965	51	?		0.96**		0.93**	
Ramsey *et al.*, 1965a	25	?	*M. long.*	0.90		0.90	
			B. femoris	-		0.90	
Ramsey *et al.*, 1965b	43	?	*B. femoris*			0.81**	
Davis *et al.*, 1966	27	?	12-13th rib	0.57** to 0.75**		0.84** to 0.92**	Two operators and machines.

TABLE 2.1 (continued): Correlations between ultrasonic measurements and corresponding carcass measurements.

Source	No. of animals	Machine	Position	Fat depth	Muscle depth	Muscle area	Comments
Meyer *et al.*, 1966	24,28,24	Branson Sonoray	12-13th rib			0.82** to 0.94**	
Watkins *et al.*, 1967	40,40,40	Branson Sonoray 510	12-13th rib	0.72** to 0.93**		0.37* to 0.69**	
Campbell and White, 1968	34	Smiths US Grader	*M. infra-spinatus*		0.09 to 0.77***		Different layers of muscle and positions.
			11th and 13th rib			0.87***, 0.85***	
McReynolds and Arthaud, 1970	10	Branson 52	12-13th rib	-		0.95*	Muscle area estimated from 3 depth readings.
	207		12-13th rib	-		0.22* to 0.43**	
	39,24		12-13th rib	0.61**, 0.38		-	
Campbell and Hervé, 1971a	22,25	2D US Echoscope	Ribs 11-13, lumbar 1-5			0.75***to 0.94***	Steers and young calves.
Campbell and Hervé, 1971b	32,(51)	2D US Echoscope	3rd lumbar			0.90*** (0.96***)	(Including 19 steers from 1971a.)
Andersen and Ernst, 1972	213	SVC?	1st and 5th lumbar			0.47***to 0.53***	Two methods of interpretation.
Gillis *et al.*, 1973	107,65	Scanogram	11-12th rib	0.53** to 0.83**		0.17 to 0.56**	Two interpreters.
	39,65	Krautkrämer	11-12th rib	0.47** to 0.67**		(0.32), 0.80**, 0.88**	(Inexperienced interpreter.)
Tulloh *et al.*, 1973	12,13	Scanogram	10th rib	0.89**, 0.93**		0.16 to 0.69*	Two breeds, Angus and Friesian. Two interpreters for muscle area.
	12,13		13th rib	0.94**, 0.88**		0.64* to 0.80**	
	14,15		3rd lumbar	0.79, 0.67***		0.29 to 0.82**	
	14,14		Scapula	0.34, 0.67**		-	
Andersen, 1975a	295	SVC	lumbar			0.61	
Matassino *et al.*, 1976	18,16,16, 22	Scanogram	12-13th rib			0.88***to 0.99***	Analysis within breed (4)
Andersen *et al.*, 1977a	48	Danscanner	1-2nd lumbar			0.64	

TABLE 2.1 (continued): Correlations between ultrasonic measurements and corresponding carcass measurements.

Source	No. of animals	Machine	Position	Fat depth	Fat area	Muscle depth	Muscle area	Comments
Lykke and Andersen, 1977	31	SVC	1-2nd lumbar		0.70, (0.63)		0.89	(Muscle area/fat area.)
Wallace *et al.*, 1977	27	Scanogram	Shoulder	0.70**			–	
			12-13th rib	0.77**			0.58** to 0.77**	2 operators, 2 interpreters.
			2nd lumbar	0.74**			0.28 to 0.45*	
			Rump	0.89*			–	
Harada and Kumazaki, 1980	113,83	Scanogram	5-6th and 7-8th rib	0.96** to 0.97**			0.83** to 0.92**	
Patton *et al.*, 1981	10	Danscanner	10th rib	0.53 to 0.94***	0.74*, 0.92***		0.51, 0.73*	Range of 10 fat depths.
			13th rib	0.29 to 0.66*	0.52 , 0.70*		0.62, 0.63*	Two interpreters.
			3rd lumbar	0.46 to 0.86**	0.49 , 0.72*		0.87***, 0.84**	
Tong *et al.*, 1981	356	Krautkrämer	11-12th rib	0.43** to 0.54**				
	98		11-12th rib	0.41** to C.59**				
	98	Scanogram	11-12th rib	0.43** to 0.61**				
Andersen *et al.*, 1982	30,20	Scanogram [1]	10th rib	0.13 to 0.59	0.22 to 0.47	0.01 to 0.15	0.08 to 0.50	Two interpreters.
	30,20		1st lumbar	0.35 to 0.72	0.51 to 0.81	0.39 to 0.72	0.52 to 0.66	[1]Fat areas 0-15 cm.
	30		3rd lumbar	0.52 to 0.67	0.72 to 0.75	0.32 to 0.58	0.69 to 0.75	
	30,20	Danscanner [1]	10th rib	0.02 to 0.44	0.22 to 0.53	0.23 to 0.30	0.35 to 0.56	
	30,20		1st lumbar	0.45 to 0.65	0.67 to 0.73	0.52 to 0.68	0.66 to 0.80	
	30		3rd lumbar	0.53 to 0.58	0.68 to 0.69	0.35 to 0.41	0.68 to 0.73	
	30,20	Philips [2]	10th rib 1st and 3rd lumbar	0.12 to 0.69	0.19 to 0.76	0.26 to 0.59	0.47 to 0.67	[2]Fat and muscle areas 5-12.5 cm from midline.
	30,20	Ohio [2]	" " "	0.24 to 0.60	0.32 to 0.69	0.07 to 0.55	0.12 to 0.70	
	30,20	Bruel and Kjaer [2]	" " "	-0.10 to 0.60	-	0.13 to 0.61	-	
Busk and Jensen, 1982	132	Danscanner	1st lumbar		(0.79)		0.71	(Includes hide.)
Ernst *et al.*, 1982 (and Appel, 1980)	495,37	Danscanner	1st lumbar				0.47*** to 0.63***	5 different experimental stations.
			5th lumbar				0.31*** to 0.50***	

TABLE 2.2: Correlations between ultrasonic measurements and carcass traits.

Source	No. of animals	Machine	Measurement	Trait	Correlation
Lauprecht *et al.*, 1962	54	?	MA 8- 9th rib	Wt 9-11th rib joint	-0.08
Davis *et al.*, 1964	60	Branson Sonoray	FD 12-13th rib	carcass grade, marbling score	0.70**, 0.65**, 0.73**
			MA 12-13th rib	and killing-out %	0.37**, 0.35**, 0.29**
	10		MA 12-13th rib	trimmed wholesale cuts	0.54 to 0.80**
			MD *biceps femoris*	" " "	0.41 to 0.56
			FD 12-13th rib	" " "	0.23 to 0.52
			MA lumbar	" " "	0.71* to 0.88**
			MD foreleg	" " "	-0.41 to 0.27
Tulloh *et al.*, 1973	25 (approx)	Scanogram	FD 10th, 13th rib, 3rd lumbar, tuber coxae, femur, scapula	% trimmed cuts	-0.52** to -0.33*[1]
				Wt trimmed cuts	0.32 to 0.42*
Matassino *et al.*, 1976	18, 16, 16, 22	Scanogram	MA 12-13th rib	% 1st, 2nd, 3rd quality cuts	-0.56* to 0.66**
Wallace *et al.*, 1977	27	Scanogram	FD shoulder, 12-13th rib,	% primal cuts	-0.52** to -0.77**
				% total yield	-0.50** to -0.72**
			2nd lumbar, rump	primal wt, total yield wt	-0.42* to 0.03
			MA 12-13th rib	primal wt, total retail wt	0.24 to 0.61**, 0.29 to 0.60**
			MA 2nd lumbar	primal wt, total retail wt	0.34 to 0.46*, 0.35 to 0.43*
			MA 12-13th rib, 2nd lumbar	% primal cuts, % total yield	-0.20 to 0.26
Andersen *et al.*, 1982[1]	30, 20	Scanogram	FD 10th rib, 1st, 3rd lumbar	killing-out %	-0.38 to 0.46
			FA 10th rib (0-15 cm)		-0.48 to 0.33
			FA 1st lumbar (0-15 cm)		0.07 to 0.43
			FA 3rd lumbar (0-15 cm)		0.11 to 0.37
			MA 10th rib		-0.07 to 0.39
			MA 1st lumbar		0.33 to 0.57
			MA 3rd lumbar		0.40 to 0.48
		Danscanner	FD 10th rib, 1st, 3rd lumbar	killing-out %	-0.24 to 0.41
			FA 10th rib (0-15 cm)		-0.43 to 0.35
			FA 1st lumbar (0-15 cm)		-0.05 to 0.55
			FA 3rd lumbar (0-15 cm)		-0.07 to 0.51
			MA 10th rib		0.16 to 0.47
			MA 1st lumbar		0.52 to 0.58
			MA 3rd lumbar		0.33 to 0.53

[1] data adjusted to constant live weight.

TABLE 2.2 (continued): Correlations between ultrasonic measurements and carcass traits.

Source	No. of animals	Machine	Measurement	Trait	Correlation
Andersen *et al.*, 1982[1]		Philips	FD 1st lumbar	killing-out %	0.07 to 0.26
			FA 1st lumbar (5-12.5 cm)		0.11 to 0.31
			MA 1st lumbar		0.39 to 0.60
		Ohio	FD 1st lumbar	killing-out %	-0.13 to 0.36
			FA 1st lumbar (5-12.5 cm)		-0.11 to 0.34
			MA 1st lumbar		0.28 to 0.54
		Bruel and Kjaer	FD 1st lumbar	killing-out %	0.30 to 0.44
Ernst *et al.*, 1982	37	Danscanner	MA 1st lumbar	Wt rump and rib, round and pistol joints (bone out)	0.37* to 0.46**
			MA 5th lumbar		0.54***to 0.63***
Rehben, 1982	60	Danscanner	MA 2nd lumbar	saleable lean meat ratio and killing-out %	0.71, 0.73
		R90	MD 3rd lumbar		0.55 to 0.60, 0.69 to 0.77
		Sonic	MD 3rd lumbar		0.65 to 0.69, 0.66 to 0.70

[1] data adjusted to constant live weight.

TABLE 2.3: Correlations between ultrasonic measurements and tissue components in the carcass.

Source	No. of animals	Machine	Measurement	Lean : bone	Lean	Fat[2]	Comments
Lauprecht *et al.*, 1962	54	?	MA 8-9th rib		0.10[1]		Muscle wt.
Alsmeyer *et al.*, 1963	183-256	Curtis-Wright Echoscope	FD 13th rib MD 13th rib		0.23** to 0.30** 0.04 to 0.15	0.40** to 0.68** 0.01 to 0.30**	Separable fat wt and wt of *m. long*. in 9-11th rib joint.
Levantin *et al.*, 1964	31	?	MA 13th rib		0.52		Meat wt in carcass (0.85 with carcass wt).
Campbell and Dodd, 1965		Smiths US grader	FD 10th rib		-0.76* to-0.32 (0.11 to 0.62*)	0.43 to 0.68* (0.42 to 0.46)	Fat (ether extract) % or eye muscle (total protein) % in 9-11 rib cut.
Davis *et al.*, 1965	51	?	MA 11-12th rib		0.83		Estimated wt lean.
Campbell and White, 1968	34,8,5 21	Smiths US grader	MD 1st layer of *m. infraspinatus* MA 11th,13th rib		0.77**,0.83**,0.52 0.34, 0.62		Wt of *m. infraspinatus*. Muscle wt in half carcass (estimated).
Campbell and Hervé, 1971a	22,25	2D US Echoscope	MA ribs 11-13, lumbar 1-5		0.77***to 0.94***		Wt of *m. long*.
Campbell and Hervé, 1971b	32,(51)	2D US Echoscope	MA 3rd lumbar		0.81** (0.88)		(Includes 19 animals from 1971a.)
Hervé and Campbell, 1971	22,9	2D US Echoscope	MA ribs 11-13, lumbar 1-5		0.63** to 0.98*		Estimated muscle wt in half carcass.
Tulloh *et al.*, 1973	~25	Scanogram	FD 10th,13th rib, 3rd lumbar, t. coxae, femur , scapula. MA 10th rib, 13th rib, 3rd lumbar		-0.77** to-0.60** -0.73** to-0.56**[1] -0.36 to-0.19 -0.17 to-0.12[1]	0.75** to 0.88** 0.73** to 0.86**[1] – –	% components.
Andersen, 1975a	295,29	SVC	MA lumbar[1] MA/FA lumbar[1]	0.40**, 0.47** 0.32**, 0.59**	0.31**, 0.21 (0.37**, 0.42*) 0.53**, 0.71** (0.55**,0.78**)	-0.16**, -0.09 -0.47**, -0.64**	% components. ( ) = pistol lean.
Ladan *et al.*, 1976	82	?	MA 13th rib		0.64, 0.42		Meat wt, *m. long*. wt.

[1] data adjusted for live weight.

[2] total fat unless stated otherwise.

TABLE 2.3 (continued): Correlations between ultrasonic measurements and tissue components in the carcass.

Source	No. of animals	Machine	Measurement	Lean : bone	Lean	Fat^2	Comments
Lykke and Andersen, 1977	31	SVC	MA 1-2nd lumbar	0.56	0.31 (0.43)	-0.17	% components. ( ) = pistol lean.
			MA/FA 1-2nd lumbar	0.61	0.72 (0.78)	-0.65	
			FA 1-2nd lumbar	-0.27	-0.66 (-0.65)	0.70	
Bass, 1979	41	Danscanner	FD 13th rib			0.71 (0.83); 0.64 (0.75)	Wt s.c. fat in hindquarter ; or in 10-11th rib cut ( ) = FA+hide, [ ] = FA/MA
			MA 13th rib			0.56 [0.73]; 0.49	
Alliston and Hinks, 1981	45	Danscanner	FD 10th, 13th rib, 3rd lumbar^1		-0.32 to 0.05	0.01 to 0.33	% components in 10th-13th rib joint. Data adjusted LW, sex, scan date.
			FA 10th rib^1		-0.22	0.46**	
			FA 13th rib^1		-0.33	0.43*	
			FA 3rd lumbar^1		-0.43*	0.58***	
			MA 13th rib^1		-0.06	0.04	
			MA 3rd lumbar^1		0.14	0.04	
Miles, 1981 (pers. com.)	20	Velocity US	Hind limb^1		-0.85	0.87	% components.
Tong *et al.*, 1981	356	Krautkrämer	FD 11-12th rib^1		-0.34 to -0.32	0.28 to 0.35	Wt of tissue in primal cuts, left HQ.
	98	Krautkrämer	FD 11-12th rib^1		-0.34 to 0.00	0.21 to 0.48	Wt of tissue in all primal cuts, left side.
		Scanogram	FD 11-12th rib^1		-0.41 to -0.25	0.29 to 0.47	3 depths
Alliston, 1982	50	Danscanner	FD 10th, 13th rib, 3rd lumbar^1		-0.66*** to -0.47***	0.47*** to 0.75***	% components.
			FA 10th rib^1		-0.68***	0.68***	
			FA 13th rib^1		-0.66***	0.71***	
			FA 3rd lumbar^1		-0.66***	0.75***	
			MA 10th rib^1		-0.09	0.11	
			MA 13th rib^1		-0.01	0.06	
			MA 3rd lumbar^1		-0.25	0.37*	
Andersen *et al.*, 1982	30, 20	Scanogram	FD 10th rib, 1st, 3rd lumbar^1	-0.47 to 0.15	-0.71 to -0.12	0.20 to 0.76	% components.
			FA 10th rib (0-15 cm)^1	-0.34 to 0.08	-0.49 to -0.21	0.26 to 0.62	
			FA 1st lumbar (0-15 cm)^1	-0.34 to 0.12	-0.62 to -0.50	0.51 to 0.74	
			FA 3rd lumbar (0-15 cm)^1	-0.44 to 0.08	-0.76 to -0.54	0.58 to 0.84	
			MA 10th rib^1	0.02 to 0.54	-0.07 to 0.25	-0.22 to 0.11	
			MA 1st lumbar^1	0.33 to 0.62	0.03 to 0.45	-0.19 to 0.13	
			MA 3rd lumbar^1	0.28 to 0.62	0.13 to 0.49	-0.31 to -0.03	

[1] data adjusted for live weight.

[2] total fat unless otherwise stated.

TABLE 2.3 (continued): Correlations between ultrasonic measurements and tissue components in the carcass.

Source	No. of animals	Machine	Measurement	Lean : bone	Lean	Fat[2]	Comments
Andersen *et al.*, 1982		Danscanner	FD 10th rib, 1st, 3rd lumbar[1]	-0.32 to 0.16	-0.58 to -0.10	0.10 to 0.65	% components
			FA 10th rib (0-15 cm)[1]	-0.31 to 0.06	-0.33 to -0.19	0.19 to 0.42	
			FA 1st lumbar (0-15 cm)[1]	-0.47 to 0.01	-0.69 to -0.41	0.54 to 0.72	
			FA 3rd lumbar (0-15 cm)[1]	-0.32 to 0.24	-0.58 to -0.34	0.55 to 0.64	
			MA 10th rib[1]	-0.04 to 0.62	-0.08 to 0.31	0.04 to 0.15	
			MA 1st lumbar[1]	0.43 to 0.75	0.23 to 0.54	-0.24 to -0.07	
			MA 3rd lumbar[1]	0.37 to 0.63	0.23 to 0.57	-0.33 to -0.12	
		Philips	FD 1st lumbar[1]	-0.33 to -0.06	-0.60 to -0.47	0.54 to 0.65	
			FA 1st lumbar (5-12.5 cm)[1]	-0.43 to 0.04	-0.72 to -0.43	0.52 to 0.78	
			MA 1st lumbar (5-12.5 cm)[1]	0.11 to 0.57	-0.14 to 0.44	-0.23 to 0.20	
		Ohio	FD 1st lumbar[1]	-0.44 to 0.14	-0.65 to -0.44	0.56 to 0.68	
			FA 1st lumbar (5-12.5 cm)[1]	-0.44 to 0.05	-0.69 to -0.48	0.57 to 0.73	
			MA 1st lumbar (5-12.5 cm)[1]	0.48 to 0.67	0.24 to 0.39	-0.14 to -0.04	
		Bruel and Kjaer	FD 1st lumbar[1]	-0.21 to 0.17	-0.44 to 0.13	-0.09 to 0.51	
Busk and Jensen, 1982	?	Danscanner	MA 1st lumbar[1]	0.47	0.21 (0.42)	-0.09	% components.
			MA/FA 1st lumbar[1]	0.59	0.71 (0.78)	-0.64	( ) = pistol lean.
Rehben, 1982	60	Danscanner	MA 2nd lumbar			-0.31	% components
		R90	MD 3rd lumbar			-0.21 to -0.04	
		Sonic	MD 3rd lumbar			-0.27 to -0.18	

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[1] data adjusted for live weight.

[2] total fat unless otherwise stated.

TABLE 2.4: Precision of prediction of carcass traits from ultrasonic measurements.

Source	No. of animals	Machine	Predict	Measurements	R^2	RSD	Comments
Davis *et al.*, 1965	51		Estimated wt lean	MA + FA, 11-12th rib; off test LW	0.95		
Ramsey *et al.*, 1965b	43		Trimmed round wt; round muscle wt	*B. femoris* area + LW	0.87, 0.86		[1]only significant equation
Campbell and Hervé, 1971a	25	2D US Echoscope	Wt *m. long.*	MA 3rd lumbar + empty LW	0.89		
Hervé and Campbell, 1971	9	2D US Echoscope	Dissected muscle wt in half carcass	MA 2,3,4 or 5 lumbar + (LW)	0.92 to 0.96		
Tulloh *et al.*, 1973	24-28	Scanogram	Wt dissected fat	FD tuber coxae + LW	0.86	2.88 kg	
			% dissected fat	FD tuber coxae, 10th rib + LW	0.82	1.7% (2.10 kg)	
			Wt dissected muscle	MA 13th rib x length 10th rib - tuber coxae + LW	0.86	3.09 kg	
			% dissected muscle	FD femur + 10th rib	0.69 (0.88, 0.60)	1.6%	(Friesian, Angus)
			Wt trimmed retail cuts	MA 13th rib + LW	0.86	3.18 kg	
			% trimmed retail cuts	FD 10th rib + MD 3rd lumbar + LW	0.61	1.4% (1.69 kg)	
Cuthbertson, 1976	31	Scanogram	% lean, (% s.c. fat)	FA 0-15 cm 10th rib (2 : 1 scale)		2.02%, (1.12%)	Best single predictors
			(% lean), % s.c. fat	FA 0-15 cm 13th rib (1 : 1 scale)		(2.29%), 1.05%	
			% lean, % s.c. fat	FA 10th rib (2 : 1) + FA 13th rib (1 : 1)		1.89%, 0.95%	Best pairs of measurements
			% lean, % s.c. fat	FA 10th rib (2 : 1) + FA 13th rib (2 : 1)		1.98%, 0.98%	
			% lean, % s.c. fat	FA 10th rib (2 : 1) + FD 3rd lumbar, 10 cm (2 : 1)		1.84%, 1.07%	
Lykke and Andersen, 1977	31	SVC	% lean, % fat	MA/FA 1-2nd lumbar + av. b MA/FA from 6 monthly readings	0.61, 0.52		Better than separate MA + FA's b= regression on age.
			% pistol lean, lean : bone		0.67, 0.41		
	60+70		% fat	MA or FA, or MA/FA	0, 0.29 to 0.41, 0.38 to 0.44		2 yrs data.
Wallace *et al.*, 1977	27	Scanogram	wt primal cuts	FD 2nd lumbar + LW (+MA 2nd lumbar)	0.67** (0.73**)	5.18 kg (4.78 kg)	(only equation where MA increased R^2)
			wt total retail cuts	FD 12-13th rib + LW	0.63**	8.53 kg	
			% primal cuts	FD 12-13th rib	0.60**	1.79%	
			% total retail cuts	FD 12-13th rib	0.51**	2.97%	

TABLE 2.4 (continued): Precision of prediction of carcass traits from ultrasonic measurements.

Source	No. of animals	Machine	Predict	Measurements	RSD	Comments
Kempster *et al.*, 1979a	313	Scanogram	% s.c. fat	FA 10th and 13th rib	1.18%	Pooled within breed and production system.
Alliston and Hinks, 1981	45	Danscanner	% s.c. fat in sample joint	FD 3rd lumbar (10 cm)	1.32%	Data adjusted for LW, sex, date of scanning, diet.
			% total fat in sample joint	FA 3rd lumbar	2.51%	Best single predictor of fat.
			% lean in sample joint	FA 3rd lumbar	2.31%	
			% lean, % fat in sample joint	FA 3rd lumbar + 2 depths 3rd lumbar (7.5, 10 cm)	2.30%, 2.38%	Best combination.
Kempster *et al.*, 1981	83	Sonatest	% lean, % s.c. fat	FD 10th rib (10 cm) + LW	2.56%, 1.22%	Best depth. Data pooled within sex and feeding regime.
	31	Scanogram	% lean, % s.c. fat	FA 13th rib (0-15 cm)(1 : 1)	2.29%, 1.05%	Best of single predictors.
				FA 10th rib (0-15 cm) (2 : 1)	2.09%, 1.12%	
				MA 3rd lumbar (2 : 1)	2.90%, 1.63%	Best MA.
				FA 10th rib (2 : 1) and 13th rib (1 : 1) (0-15 cm)	1.89%, 0.95%	Best pair measurements for s.c. fat and lean,
				FA 10th rib (0-15 cm) (2 : 1) + FD 3rd lumbar (10 cm) (2 : 1)	1.84%, 1.07%	no effect LW or breed in either case.
	46	Sonatest	% lean, % s.c. fat	FD 3rd lumbar (10 cm) + LW	3.88%, 2.29%	Best fat depths.
	50			FD 13th rib (10 cm) + LW	2.68%, 1.60%	
	46	Scanogram	% lean, % s.c. fat	FA 13th rib (0-15 cm) + LW	2.91%, 1.76%	Best single measurement.
				FD 13th rib (5 cm) + LW	2.97%, 1.87%	Best depth.
				MA 3rd lumbar + LW	4.74%, 3.30%	Best MA.
				FD 10th rib (5 cm) + FD 3rd lumbar (5 cm) + LW	- 1.54%	Best pair measurements for % s.c. fat.
				FA 13th rib + FA 10th rib + LW	2.63% -	Best pair measurements for % lean.
	50			FA 10th rib (0-15 cm) + LW	2.08%, 1.19%	Best single.
				FD 10th rib (5 cm) + LW	2.38%, 1.39%	Best depth.
				MA 3rd lumbar + LW	2.85%, 1.88%	Best MA.
				FA 10th rib and 13th rib + LW	- 1.06%	Best pair for % s.c. fat.
				FA 10th rib + FA 3rd lumbar + LW	1.97% -	Best pair for % lean.

TABLE 2.4 (continued): Precision of prediction of carcass traits from ultrasonic measurements.

Source	No. of animals	Machine	Predict	Measurements	R^2	RSD	Comments
Miles, 1981 (pers. com.)	20	Velocity US	% lean, % fat	Velocity US (hind limb) + LW		1.34%, 1.77%	
	42	Velocity US	% fat	Velocity US (hind limb) + LW		2.78%	6-20 months of age.
Tong *et al* ., 1981	98	Krautkrämer	wt muscle, fat	FD 11-12th rib + line + LW	0.75, 0.67	2.71 kg, 1.66 kg	
		Scanogram	wt muscle, fat	FD 11-12th rib + line + LW	0.76, 0.69	2.66 kg, 1.61 kg	
Alliston, 1982	50	Danscanner	% lean, % fat	FA 10th rib		2.06%, (2.40%)	Best singles for lean, fat.
				FA 3rd lumbar		(2.11%), 2.18%	
				FD 13th rib + FD 3rd lumbar		2.05%, 2.10%	Best pair FD; best pair FA Data adjusted for LW and day of slaughter.
				FA 13th rib + FA 3rd lumbar		2.06%, 2.14%	
Rehben, 1982	60	Sonic (A-mode?)	Killing-out %, slmr^1, % fat	MD 3rd lumbar	0.52, 0.50, 0.18	2.40%, 2.70%, 2.90%	^{1}Saleable lean meat ratio.
		R90 (A-mode?)		MD 3rd lumbar	0.59, 0.37, NS	2.20%, 3.00% –	
		Danscanner		MA 2nd lumbar	0.67, 0.61, 0.40	2.00%, 2.40%, 2.50%	
Wright, 1982	73	Scanogram	Wt chemical fat	$\sqrt{FD}$ 12-13th rib + LW	0.94	16.3 kg	Wide range in body condition, several breeds.
			Wt chemical protein	MA 12-13th rib + MA 3rd lumbar	0.77	5.43 kg	

(e.g. Tulloh *et al.*, 1973; Patton *et al.*, 1981; Andersen *et al.*, 1982). Disparity between results may be due to differences in the breed and maturity of the animals scanned, differences between machines and differences in operator and interpeter experience.

2.4.3 Comparison with carcass traits

Some authors have examined the correlation between ultrasonic measurements and killing-out % or yield of retail joints. Others have used ultrasonic measurements in multiple regression to predict these traits. The results of these studies are summarised in Tables 2.2 and 2.4.

(1) Killing-out %

Relatively few authors have examined correlations between ultrasonic measurements and killing-out %. The most recent evidence indicates that ultrasonic muscle area measurements are more highly correlated than ultrasonic fat measurements with killing-out %. Andersen *et al.* (1982) scanned animals at the 10th rib and 1st and 3rd lumbar vertebrae with Scanogram and Danscanner machines. Muscle areas in the lumbar region were more highly correlated than those at the 10th rib with killing-out %. The same authors examined the relationship between direct measurement of fat or muscle on the sectioned carcass and killing-out %. Muscle area measurements were superior to fat measurements and produced correlations similar to those from ultrasonic muscle areas. Rehben (1982) also found good correlations between muscle area in the lumbar region and killing-out %, though Danscanner measurements were not quite as good as direct carcass measurements. Contrary to these results, Davis *et al.* (1964) reported ultrasonic fat depths at the 12-13th rib to be more highly correlated than ultrasonic muscle areas with killing-out %, carcass grade and marbling score. Muscle areas were accurately measured in this study (see Table 2.1), so this does not explain the disparity between these and more recent results.

Rehben (1982) found Danscanner muscle areas to be better than muscle depths (measured by two other machines) in multiple regression equations to predict killing-out %. However, neither method was as good as visual appraisal, though the animals used were of a range of weights and breeds.

In general muscle areas are most highly correlated with killing-out %, though animal breed, live weight and level of fatness are likely to affect accuracy.

(2) Yield of retail joints

One limitation of studies comparing ultrasonic measurements with yield of retail joints is that cutting techniques vary from area to area, and from country to country. This makes comparison of different trials difficult. Live weight of the animal has an important effect on the percentage and, especially, the weight of certain cuts in the carcass. Tulloh *et al*. (1973) reported a correlation of 0.91 between live weight and yield of trimmed retail cuts.

Results of trials reported are summarised in Tables 2.2 and 2.4. Generally, ultrasonic muscle areas show a moderate or good relationship with weight of carcass cuts (Davis *et al*., 1964; Tulloh *et al*., 1973; Wallace *et al*., 1977; Ernst *et al*., 1982). However, when data are adjusted for live weight or examined on a percentage basis the relationship becomes much weaker. Fat depths are generally more highly correlated that muscle depths or areas with % retail cuts (Tulloh *et al*., 1973; Wallace *et al*., 1977). In multiple regression equations, fat measurements and live weight are usually the best predictors of % retail or primal cuts. Addition of muscle depth or area measurements may increase precision on occasions (e.g. Tulloh *et al.*, 1973; Wallace *et al.*, 1977).

2.4.4 Comparison with tissue components in the carcass

The composition of sample joints has been used by several authors to evaluate ultrasonic machines. However, the relationship between sample joint composition and total carcass composition is not always strong. If animals are scanned directly over the site of the sample joint, it seems likely that the relationship with joint composition will be stronger than the relationship with total carcass composition. For these reasons, it may be unwise to compare results from trials involving sample joint dissection with those involving half-carcass dissection. Tables 2.3 and 2.4 show results from the literature.

(1) Lean : bone ratio

Andersen *et al.* (1982) reported that ultrasonic measurements of muscle area (with several scanners) produced higher correlations than fat measurements with lean : bone ratio. The same was true for direct measurements on the sectioned carcass. Measurements in the lumbar region were, in both cases, better than those at the 10th rib.

Lean : bone ratio was more accurately estimated from ultrasonic muscle area than from ultrasonic muscle area/fat area in one group of animals examined by Andersen (1975a). The reverse was true in a smaller group of animals examined by Andersen and in other trials reported by Lykke and Andersen (1977) using a similar machine (SVC), and Busk and Jensen (1982) using a Danscanner. It appears that muscle area measurements are the best single measurements for estimating lean : bone ratio. However, using muscle area/fat area may increase accuracy in some cases.

(2) Lean content

Several authors have examined the relationship between ultrasonic measurements and weight of dissectible muscle or chemical protein. Tulloh *et al*. (1973) found Scanogram muscle depths and areas but not fat depths to be significantly correlated with weight of dissectible muscle. After adjusting ultrasonic measurements for live weight, virtually all correlations become low. Muscle area at the 13th rib, length from the 10th rib to the tuber coxae, and live weight gave the best prediction equation for weight of muscle. Tong *et al*. (1981) measured three fat depths at the 11-12th rib on two groups of cattle, using Krautkrämer and Scanogram machines. Scanogram fat depths had higher correlations than Krautkrämer depths with weight of muscle. Prediction equations for weight of muscle were also slightly more precise using Scanogram depths than using Krautkrämer depths. Using the sum of the three depths failed to increase precision above that achieved with the best single depth. Wright (1982) used Scanogram muscle areas at the 12-13th rib and 3rd lumbar vertebra as predictors of the weight of chemical protein in the body of suckler cows. Combining both muscle areas gave more precise prediction than using the best single area (12-13th rib). However, ultrasonic measurements failed to increase precision significantly above that achieved using live weight alone.

Most authors have examined correlations between ultrasonic measurements and % lean or % dissectible muscle in the carcass. Generally, fat measurements are better than muscle measurements as estimators of % lean (Tulloh *et al*., 1973; Alliston and Hinks, 1981; Kempster *et al*., 1981; Alliston, 1982; Andersen *et al*., 1982). Also, fat areas are usually superior to fat depths (Cuthbertson, 1976; Alliston and Hinks, 1981; Kempster *et al*., 1981; Alliston, 1982; Andersen *et al*., 1982).

Andersen (1975a) reported that muscle area/fat area was more highly correlated than muscle area, with % lean. Similarly, Lykke and Andersen (1977) found that muscle area/fat area was better than fat area which, in turn, was better than muscle area as an estimator of % lean.

Prediction equations for % lean were evaluated by Cuthbertson (1976) using Scanogram fat depths and areas at the 6th, 10th and 13th rib and 3rd lumbar vertebra. Fat area at the 10th rib was the best single predictor of % lean. Precision was improved by using pairs of fat measurements at the 10th and 13th rib and 3rd lumbar. Kempster *et al*. (1981) conducted an extensive trial involving Sonatest and Scanogram machines. The best measurement position varied from one group of animals to another, and addition of live weight to prediction equations did not always improve precision. Alliston (1982) found little difference in accuracy between fat measurements at the 10th rib, 13th rib and 3rd lumbar vertebra. Combining pairs of fat depths or areas with live weight increased precision of predicting % lean. The variability of results regarding the best ultrasonic measurements for prediction equations illustrates that new equations should be evaluated for each breed and type of animal.

Quite precise prediction of % lean has been achieved by measuring the velocity of ultrasound through the hind limb of bulls (C.A. Miles, personal communication). The results compare very favourably with those from other more complicated techniques (see Table 2.3).

Precision achieved in predicting lean content of cattle carcasses compares quite favourably with results for pigs. Busk (1979) reported an R^2 value of 0.80 for *in vivo* prediction of % lean in pig carcasses. Kempster, Cuthbertson, Owen and Alliston (1979b) achieved residual standard deviations ranging from 2.08 to 2.72% lean, for four machines.

(3) Fat content

The authors who examined correlations with weight of muscle also examined weights of dissectible fat or chemical fat. Tulloh *et al.* (1973) found that fat depths at the 10th and 13th ribs, 3rd lumbar vertebra, tuber coxae, femur and scapula were all significantly correlated with both weight and % fat (before and after data were adjusted for live weight). Fat depth at the tuber coxae was the best measurement, and combined with live weight gave the most precise prediction equation for weight of fat. Tong *et al.* (1981) found that Scanogram fat depth measurements were more highly correlated than Krautkrämer measurements with weight of fat, though neither ultrasonic measurement was as good an estimator as actual carcass fat depth. Scanogram measurements also produced slightly more precise prediction equations. Precision of predicting weight of fat was not improved by summing three fat depths. Wright (1982) used the square root of Scanogram fat depths at the 12-13th rib, 3rd lumbar, scapula, femur and hind leg to predict the weight of chemical fat in suckler cows. Fat depth at the 12-13th rib was the best single predictor, and increased precision above that achieved with live weight alone.

Other authors examined correlations between ultrasonic measurements and % subcutaneous or total fat in the carcass. Generally, fat measurements were better estimators than muscle measurements (e.g. Tulloh *et al.*, 1973; Lykke and Andersen, 1977; Alliston and Hinks, 1981; Kempster *et al.*, 1981; Alliston, 1982; Andersen *et al.*, 1982). Fat areas were usually better estimators of carcass fat than depths (e.g. Cuthbertson, 1976; Alliston and Hinks, 1981; Kempster *et al.*, 1981; Andersen *et al.*, 1982).

In several trials, Scanogram measurements produced better correlations with % fat than either 'A'-mode machines (Kempster *et al.*, 1981; Tong *et al.*, 1981) or Danscanner (Andersen *et al.*, 1982). This indicates that there may be some advantage in selecting a particular machine to measure a given carcass trait.

The best anatomical position for scanning, judged on the precision of predicting % fat, varied between trials (Cuthbertson, 1976; Kempster *et al.*, 1981; Alliston, 1982). The velocity of ultrasound technique produced relatively precise prediction of % fat.

In the early stages of the development of ultrasonic scanning techniques, some workers (cited by Andersen, 1975a) reported that there was no relationship between ultrasonic measurements and carcass composition. Since that time most reports indicate a reasonable relationship. Most workers have found that muscle area is a useful predictor of killing-out % and lean : bone ratio. However, most reports indicate that fat depths or areas are superior for prediction of % lean and fat in the carcass.

The best positions for measurement vary from trial to trial. It may therefore be inaccurate to apply prediction equations constructed in one circumstance to animals of different breed, age or sex. Adjustment of ultrasonic data for live weight may have a marked effect on correlations with tissue components. It seems sensible to evaluate ultrasonic measurements in terms of the extra precision achieved when they are added to live weight in prediction equations (see Kempster *et al.*, 1981). Target residual standard deviations for prediction equations should be below 2.0% for % lean and below 2.5% for predicting % total fat (assuming reasonable variation in carcass composition).

2.5 Factors Affecting Accuracy and Repeatability

Some general factors affecting accuracy, such as animal restraint, measuring site, clipping, direction of scanning and type of interpretation have already been discussed. In addition, the type of animal being scanned, repeating measurements and differences between operators and interpreters can affect accuracy.

2.5.1 Animals

The type of animals being examined can have a marked effect on the accuracy of ultrasonic evaluation. Temple *et al.* (1965) reported that fat animals were difficult to scan. Similarly, Tulloh *et al.* (1973) found that a good fit with the guide rail of their Scanogram machine could only be obtained by scanning very fat steers dorso-ventrally and very thin steers ventro-dorsally. Busk (1982) proposed that breed differences in difficulty of scanning could be due to a poor fit with the transducer head, differences between breeds in velocity of ultrasound in various tissues, or different amounts of intramuscular fat. Experience with the Danscanner in Denmark has shown that, in general, good scans are more readily obtained from dairy or dual-purpose breeds than from beef breeds (H. Busk, personal communication).

2.5.2 Repeated measurements

Table 2.5 shows correlations between repeated measurements by the same operator on the same animals. Generally, repeatabilities were quite high, though there does not seem to have been any improvement with the use of more sophisticated machines. There were quite large differences in repeatability between the different machines examined by Andersen *et al.* (1982). The Scanogram had the highest repeatability of measurement of fat depths and areas, whilst the Danscanner was most

TABLE 2.5: Correlations between repeated measurements by the same machine operator.

Source	No. of animals	Machine	Position	Correlation between observations			Comments
				Fat depth	Fat area	Muscle area	
Stouffer *et al.*, 1961	15	Sperry Reflectoscope	13th rib	0.67***		0.89**	1 interpreter.
	10	Branson Sonoray	13th rib	0.90**		0.71**	2 interpreters.
				0.75**		0.90**	
Davis *et al.*, 1966	27	Branson Sonoray	12-13th rib	0.85**		0.91**	
Andersen and Ernst, 1972	50	SVC	1st, 5th lumbar		0.57***, 0.35**	0.49***, 0.37**	Method A (tracing from projected transparency).
	62				0.69***, 0.68***	0.76***, 0.59***	
	101				0.46***, 0.57***	0.71***, 0.67***	
	50					0.82***, 0.82***	Method B (tracing from photograph).
	62					0.83***, 0.82***	
	101					0.83***, 0.85***	
Andersen, 1975a	295	SVC	Lumbar			0.76 to 0.89	
Wallace *et al.*, 1977	27	Scanogram				0.80 to 0.89	
Bass, 1979	20	Danscanner	13th rib	0.95 (0.95)			(Includes hide.)
Andersen *et al.*, 1982	30	Scanogram [1]	10th rib	0.85, 0.71	0.77, 0.83	0.40, 0.49	UK then DK animals
	20		1st lumbar	0.74, 0.79	0.82, 0.76	0.45, 0.64	[1] Fat areas 0-15 cm.
		Danscanner	10th rib	0.26, 0.68	0.34, 0.70	0.67, 0.41	
			1st lumbar	0.47, 0.57	0.59, 0.51	0.85, 0.82	
		Philips [2]	10th rib	0.44, 0.54	0.54, 0.60	0.47, 0.45	[2] Muscle and fat areas 5-12 cm
			1st lumbar	0.71, 0.23	0.69, 0.67	0.45, 0.78	
		Ohio [2]	10th rib	0.49, 0.54	0.67, 0.55	0.10, 0.09	
			1st lumbar	0.75, 0.63	0.81, 0.78	0.77, 0.74	
		Bruel and Kjaer	10th rib	0.36, 0.00	-	-	
			1st lumbar	0.25, 0.35	-	-	
Busk and Jensen, 1982	50	Danscanner	1st lumbar?	(0.84)		0.97	(Includes hide.)
Ernst *et al.*, 1982	737	Danscanner	1st lumbar			0.96	
			5th lumbar			0.96	

repeatable for muscle area. The Philips and Ohio medical machines compared favourably with the purpose-built animal scanners, but the Bruel and Kjaer machine did not produce repeatable measurements.

Campbell and Hervé (1971b) reported correlations of 0.72 to 0.84 between repeated interpretations of the same scan. Accuracy of prediction of carcass traits can be improved by using mean values from repeat observations and interpretations, as already mentioned.

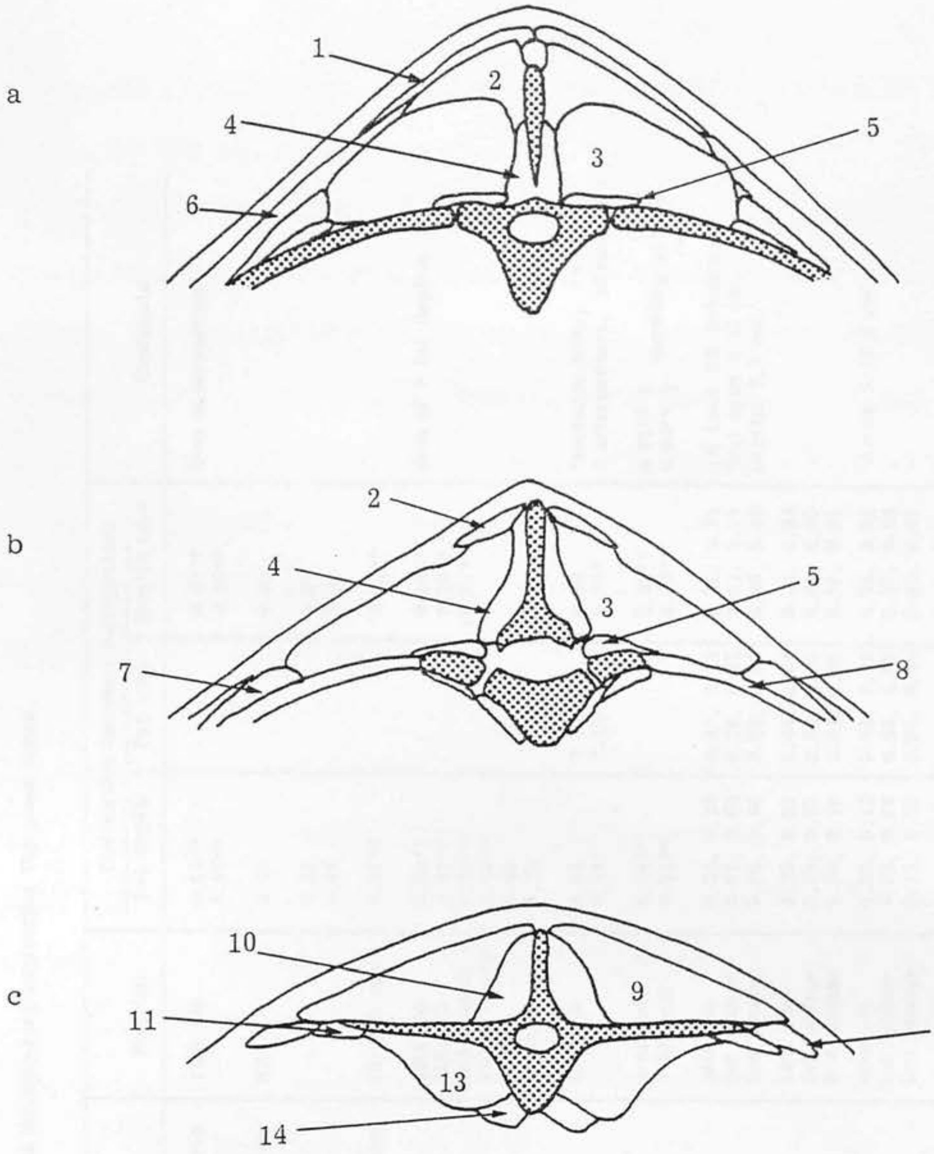
2.5.3 Differences between operators and interpeters

Campbell and Hervé (1971b) found no significant differences between ultrasonic measurements made by two machine operators. Tulloh *et al*. (1973) formed the same conclusion and suggested that provided operators were trained in the use of the machine and the anatomy of the animal, comparisons of a group of animals need not be restricted to one operator. Wallace *et al*. (1977) also found no significant difference between operators.

On the contrary, most workers have reported important differences between interpreters (Davis, Temple and McCormick, 1966; Campbell and Hervé, 1971b; Miles *et al*., 1972; Gillis *et al*., 1973; Tulloh *et al*., 1973; Wallace *et al*., 1977; Patton *et al*., 1981). Gillis *et al*. (1973) found that interpreter experience was especially important when an 'A'-mode machine was used. Correlations between ultrasonic measurements of muscle area and the corresponding carcass measurements were 0.80 and 0.32, respectively, for experienced and less experienced interpreters. Patton *et al*. (1981) measured fat depths and areas and muscle areas with a Danscanner, and found differences between interpreters, but not consistently in favour of the most experienced interpreter.

Miles *et al*. (1972) made a thorough examination of factors affecting repeatability of ultrasonic scanning.

Six steers of varying fatness were scanned with a Scanogram, in parallel planes perpendicular to the spine at the level of each vertebra, from the 9th rib to the 3rd-4th lumbar vertebrae. At each position, fat thickness and *mm. longissimi thoracis et lumborum* depth, width and area were measured. Two analyses of the bias between ultrasonic and carcass measurements were conducted. The first analysis involved interpretation of all pictures of all animals, by two judges. The second analysis involved five repeated interpretations of each of five scans, by nine judges. Fat thickness was most accurately measured in the region of the 13th rib and 1st lumbar. At this position fat cover is relatively thin and there is less chance of confusing the boundary between fat layers with the boundary between fat and muscle. Scans in the anterior thoracic region were found to be difficult to interpret due to the presence of the *m. trapezius* and *m. spinalis et semi spinalis* overlying the *mm. longissimi thoracis et lumborum* (Figure 2.5). Subjective errors of interpretation arose due to: (1) misidentifying discontinuities in acoustic impedance as anatomical boundaries; (2) inability to recognise multiple reflection artefacts consistently; and (3) omission of data on the scan where the ultrasonic beam was not perpendicular to an anatomical boundary. (The latter source of error was also reported by Stouffer *et al*. (1961) and Hedrick *et al*. (1962)). Different judges were found to interpret scans in a different way, and accuracy varied at different positions. There appeared to be no effect of judges' previous experience on bias values. It was concluded that although interpreters may themselves be relatively consistent, in general they differed significantly from each other. For this reason, it was recommended



1. *pars thoracica mi. trapezii*
2. *m. spinalis et semispinalis thoracis et cervicis*
3. *m. longissimus thoracis*
4. *m. multifidus thoracis*
5. *m. levator costae*
6. *m. latissimus dorsi*
7. *m. iliocostalis thoracis*
8. *mm. intercostales*
9. *m. longissimus lumborum*
10. *m. multifidus lumborum*
11. *m. quadratus lumborum*
12. *m. iliocostalis lumborum*
13. *m. psoas major*
14. *m. psoas minor*

FIGURE 2.5: Dorsal cross section of the bovine at the level of the tenth rib (a), thirteenth rib (b) or third lumbar vertebra (c).

(after Popesko, 1977)

TABLE 2.6: Correlations between results of two interpreters evaluating the same scans.

Source	No. of animals	Machine	Position	Correlation between interpreters Fat depth	Fat area	Muscle area	Comments
Stouffer *et al.*, 1961	10	Branson Sonoray	13th rib	0.81**		0.67**	Two observations.
				0.87**		0.81**	
Brown *et al.*, 1964	20	Branson Sonoray	Rib	0.94		0.91	
Temple *et al.*, 1965	49			0.61		0.61	
	20			0.94		0.91	
Davis *et al.*, 1966	27	Branson Sonoray	12-13th rib	0.81**		0.91**	
Tulloh *et al.*, 1973	25	Scanogram	10th rib	0.80**		0.88**	Sum of 3 fat depths.
	25		13th rib	0.99**		0.87**	
	29 (25)		3rd lumbar	0.98**		(0.81**)	
	29		Tuber coxae	0.98**		-	
	28		Femur	0.93		-	
	28		Scapula	0.75		-	
Bass, 1979	12	Danscanner	13th rib	0.81	0.70	0.60	^{1}Includes hide; ^{2}FA/MA.
				0.51^1	0.19^1	0.85^2	3 interpreters, intraclass r.
Harada and Kumazaki, 1979	55	Scanogram	5-6th rib	0.98**		0.89**	0.90**) marbling score.
			7-8th rib	0.91**		0.85**	0.94**)
Andersen *et al.*, 1982	20	Scanogram ^{1}	10th rib	0.34, 0.25	0.33, 0.11	0.38, 0.58	UK then DK animals.
			1st lumbar	0.81, 0.65	0.78, 0.65	0.81, 0.72	^{1}Fat area 0-15 cm.
			3rd lumbar	0.69, 0.58	0.82, 0.66	0.86, 0.68	Depths 7.5 cm.
		Danscanner ^{1}	10th rib	0.25, 0.62	0.45, 0.51	0.89, 0.84	
			1st lumbar	0.86, 0.77	0.84, 0.85	0.91, 0.96	
			3rd lumbar	0.84, 0.76	0.91, 0.89	0.79, 0.93	
		Philips ^{2}	10th rib	0.33, 0.22	0.49, 0.50	0.54, 0.81	^{2}Areas 5-12.5 cm
			1st lumbar	0.75, 0.84	0.80, 0.83	0.90, 0.92	
			3rd lumbar	0.75, 0.76	0.86, 0.85	0.90, 0.84	
		Ohio ^{2}	10th rib	0.46, 0.49	0.33, 0.41	0.57, -0.01	
			1st lumbar	0.75, 0.66	0.77, 0.80	0.97, 0.93	
			3rd lumbar	0.85, 0.72	0.82, 0.83	0.90, 0.91	
		Bruel and Kjaer	10th rib	0.41, 0.02	-	-	
			1st lumbar	0.86, 0.69	-	-	
			3rd lumbar	0.91, 0.87	-	-	

that scans from a group of animals being compared should all be interpreted by the same judge.

Tulloh *et al*. (1973) reported significant animal x interpreter interactions at all sites measured for muscle area, and at all sites except the 13th rib for total fat depth. In spite of the fact that both interpreters trained on the same practice material, each had developed his own pattern of interpretation. Patton *et al*. (1981) also observed interactions between interpreters and various traits, and once again suggested that comparison of animals should be made within one interpreter.

Table 2.6 shows correlations between interpreters reported in the literature. Andersen *et al*. (1982) found that correlations between interpreters were higher at the 1st and 3rd lumbar vertebrae than at the 10th rib. Correlations between interpreters for scans at the lumbar sites ranged from about 0.6 to 0.9. There was little difference in correlations between interpreters for scans from the different machines.

From the preceding results, it appears that more than one experienced machine operator may be used in a comparison, without affecting results. The same is not true of interpreters.

2.6 Future Developments

To be of wide practical use, ultrasonic scanning machines must be mobile, robust and relatively simple to operate (King, 1982). Busk (1982) expected future development of ultrasonic machines to be aimed at two goals. The first was ultrasonic machines for measuring a few simple carcass traits under farm conditions; the second was more specialised machines to study organ development, etc. on research stations.

The use of velocity of ultrasound transmission to predict carcass composition has given very promising results (C.A. Miles, personal communication). This relatively simple method of evaluation has several advantages over more complex scanning machines. The technique gives a digital reading; no subjective interpretation or lengthy analysis is needed. It also responds to intramuscular, intermuscular and subcutaneous fat alike. This is of special benefit in scanning cattle, since they are less fat in absolute terms than pigs, and less of the fat in cattle is in subcutaneous depots (Miles *et al.*, 1982). Development of this technique for on-farm use could prove useful in the future.

Preliminary investigations have shown that some medical scanners can be used effectively to scan live cattle (Andersen *et al.*, 1982). Such machines would need modification for use on farms, but have useful features like grey-scales and frame-freeze oscilloscopes. Other developments in the field of medical ultrasonics may have applications in animal science (Carson *et al.*, 1981; Lewin, 1982).

King (1982) suggested that for animal breeding purposes money may be more effectively spent in opening up new techniques rather than refining existing *in vivo* estimation procedures. By splitting embryos it should be possible in the near future to obtain clones of animals of identical genotype. This would enable selection of breeding animals based on carcass dissection of an identical animal. Such techniques could also be useful in other fields of animal science where ultrasonic evaluation is currently used. To find wide application, *in vivo* techniques must be relatively quick and cheap to operate. Should the cost of computerised tomography fall in the future, much use could be made of this method.

2.7 Conclusions

Ultrasonic scanning techniques are useful in several areas of animal science and practical agriculture. Since the early use of simple 'A'-mode machines much research effort has been directed towards development of more sophisticated machines. Generally, these 'B'-mode machines are slightly more accurate for measuring carcass traits than 'A'-mode machines. Whether the extra purchase cost and running cost of these machines are justified is less clear. Cost-benefit analysis of ultrasonic evaluation techniques has recently been identified by the Commission of the European Community as an area needing more work (Andersen, 1982).

The most informative investigations have combined ultrasonic measurements and live weight to predict tissue components as determined by carcass dissection. Ultrasonically measured muscle areas are useful predictors of killing-out %, lean : bone ratio and weight of retail cuts. Fat measurements are the best predictors of % lean and % fat in the carcass. Selection of a suitable machine will depend on the trait being investigated. Choice of suitable scanning sites should, however, be based on a pilot trial with animals representative of the population to be studied. In several trials the correlation between ultrasonic measurements and carcass traits was as high as the correlation between measurements on the sectioned carcass and the trait concerned. In such cases, it is unlikely that accuracy can be substantially improved.

The accuracy of measurement with existing machines can be maximised by following a rigorous scanning procedure. Comparison of animals should be made within one interpeter and animals should be treated in the same way with regard to clipping, direction of scanning, etc. Operators and interpeters should have some knowledge of anatomy, and be well trained in the use of the equipment (including calibration). A good machine-servicing facility and periodic checks with carcass data or other machines are essential (Andersen *et al.*, 1982; Busk and Jensen, 1982). Statistical corrections for breed, live weight and day of measuring may also improve accuracy (e.g. Busk and Jensen, 1982).

CHAPTER III

Repeatability of Live Animal Measurements and Correlations with Carcass Composition

3.1 Introduction

Two ultrasonic scanners, the Danscanner and the Scanogram, have been used to predict the carcass composition of bulls for selection in the ABRO Hereford experiment. Between 1977 and 1980, half-carcasses of 54 bulls were dissected following routine scanning, to allow evaluation of the ultrasonic machines. During 1981 and 1982 a further 46 bulls were dissected to allow a more comprehensive comparison of the scanners, and to assess other live animal measurements as predictors of carcass composition. The experiments and analyses reported in this and the following chapter were designed to examine the repeatability of live animal measurements, their correlations with carcass composition, and their value in prediction equations. The effect of operator/interpreter experience on the precision of Danscanner measurements was also assessed.

3.2 Materials and Methods

3.2.1 *Animals*

A total of 235 bulls, in ten groups, were involved in this study. Carcass dissection data were available for 100 of these animals, the remainder were used only to assess the repeatability of live animal measurements. All bulls were performance tested from 200 to 400 days of age on a complete grass/barley pelleted diet, offered *ad libitum*. A small amount of hay was also provided to promote rumination. Between 400 days of age and slaughter, bulls were fed either the grass/barley diet or a straw/barley complete diet *ad libitum*, or they grazed pasture. Nutritional information on the grass/barley diet is shown in Table A3.1 (all tables prefixed by the letter A appear in the Appendix).

3.2.2 Live animal measurements

A description of the Danscanner and Scanogram ultrasonic machines was given in Section 2.2. The machines were manufactured by SFK, Copenhagen and Ithaco Inc., New York, respectively. On each measuring occasion, bulls were weighed then restrained in a handling crate for scanning. Measurements were made over the *mm. longissimus thoracis et lumborum* at the level of the 10th rib, 13th rib, 1st or 3rd lumbar vertebra. Bulls were clipped at the appropriate site, and liquid paraffin was used as an acoustic couplant. Different combinations of measurements were made in 1978 to 1980, which complicated data analysis.

On each measuring occasion, two acceptable Danscanner scans were obtained per location, using the 1.5 : 1 reduction scale (Plates 1, 2 and 3). Danscanner fat areas (DFA) and muscle areas (DMA) were traced from transparencies, then digitised with a planimeter linked to a computer. The method of interpreting scans varied from trial to trial and is described later. Three Danscanner operators/interpreters were involved in the study. Operators 1 (GS) and 3 had several months experience with the machine, whilst operator 2 had five years experience.

A single acceptable Scanogram scan was obtained at each anatomical site by one of two experienced operators, from MLC (Plates 5 and 6). In each trial scans were obtained using the 2.54 : 1 reduction scale. Scanogram fat areas (SFA) were measured from the mid-vertebra to a point 15 cm ventral from it. (All measurements refer to the live animal; scans were on a reduced scale).

On bulls in groups 6 to 9 additional estimates of live weight (LW) were obtained from girth measurements using a 'Weighband' (Dalton Supplies Ltd, Henley-on-Thames). Estimating live weight in this way may reduce the effects of gut fill, and thus may provide more precise prediction of carcass composition. The band was placed around the bull's chest, immediately posterior to the fore-limbs. Five kilograms tension was applied to the band before reading the measurement. Skinfold thickness was measured with calipers at two sites, on the same bulls. The first site (SFT) was at the distal end of the 13th rib. The second site (AFT) was the anal fold, the fold of skin and subcutaneous fat at the tail head. In each case, a fold was made by pinching together skin and loose tissue (subcutaneous fat). The fold was pinched and measured repeatedly, until one measurement was obtained several times (after Charles, 1974).

3.2.3 Carcass evaluation

Between 1977 and 1982 eight groups of bulls were slaughtered after measurements had been taken. Within each group, bulls were slaughtered in batches over a period of several days. One side of each carcass was then dissected by the carcass evaluation units of MLC, the Edinburgh School of Agriculture (ESA) or the ARC Meat Research Institute (MRI). At MLC and ESA, half-carcasses were divided into 14 joints and then into lean, subcutaneous fat, bone and waste (after Kempster, Cook and Smith, 1980). At MRI, half-carcasses were divided by anatomical region and then into individual muscle groups, subcutaneous fat, intermuscular fat, bone and waste (after Williams and Bergström, 1980). Weights of perinephric and retroperitoneal fat, scrotal fat and thoracic fat were available for all except two bulls (in group 6). Data on these two bulls were excluded from analyses in Chapter IV.

3.2.4 Statistical methods

In each trial the mean DFA of the pair of scans obtained at each position was used in analysis. Data were analysed by least-squares analysis of variance (Harvey, 1977). Repeatability of live animal measurements was calculated as the unadjusted correlation between measurements on consecutive occasions, one day or more apart. Correlations with carcass data were adjusted for live weight and, where appropriate, dissection agency.

3.3 Details and Results of Trials

3.3.1 Ultrasonics trial 1

This trial involved 40 bulls in groups 6 and 7. At the time of scanning, bulls averaged about 450 days of age and 430 kg live weight. Scans were obtained at the 10th and 13th ribs and at the 3rd lumbar vertebra with Danscanner (operator 1, GS) and Scanogram ultrasonic machines. In this trial, DFAs were measured between points ±6 cm from the middle of the *m. longissimus*, as the vertebral column was not easily distinguished on scans. Danscanner measurements were repeated on all bulls 18 days after the first measuring occasion. No direct measure of the repeatability of SFA measurements was available but results were compared to SFAs measured for the routine selection of bulls, two months before this trial.

Correlations between SFA and DFA measurements were lower than expected, especially at the 10th rib and 3rd lumbar vertebra (Table 3.1). Repeatability of DFAs was also very low. Repeatability of SFA measurements at the 13th rib was reasonable considering the time interval between measurements, that for SFAs at the 10th rib was low (Table 3.2). Correlations between repeat DFA and SFA measurements taken

TABLE 3.1: Correlations between Danscanner and Scanogram fat area measurements at three anatomical positions - trial 1 (40 animals).

Position	Correlation
10th rib	0.26
13th rib	0.68
3rd lumbar	0.20

Correlations >0.31 are significantly different from zero (P <0.05).

TABLE 3.2: Correlations between repeat Danscanner and Scanogram fat area measurements - trial 1 (40 animals).

	DFA	SFA
Interval between measurements (days)	18	60
Position	Correlation	
10th rib	0.24	0.22
13th rib	0.22	0.67
3rd lumbar	0.11	-

Correlations >0.31 are significantly different from zero (P <0.05).

TABLE 3.3: Correlations between ultrasonic measurements on two occasions, one month apart[1].

	Group[2] 9	Group[2] 10
No. of animals	56	69
Measurement:		
Danscanner fat area	0.25	0.25
Scanogram fat area	0.77	0.83

[1] Mean of correlation at 2 or 3 anatomical locations (10th rib, 13th rib and 3rd lumbar vertebra).

[2] See Table 4.1 for additional information on bulls.

Correlations >0.26 (n=56) or >0.24 (n=69) are significantly different from zero ($P < 0.05$).

one month apart for routine bull selection are shown in Table 3.3. Even with an experienced Danscanner operator (2) repeatability of DFA measurements was very low. Repeatability of SFA measurements was quite high.

Assessment of DFAs involves tracing the two lines of signals on scans which mark the boundary of the subcutaneous fat layer with the hide and with the *m. longissimus* (see Plate 3). On many of the Danscanner scans in this trial a fourth line of signals was present (Plate 4). These extra signals may be due to: (1) a split in the subcutaneous fat layer; (2) multiple echoes caused by poor acoustic contact with the animal; or (3) machine error. At the time of scanning, an attempt was made to eliminate 'extra' signals by repositioning the transducer head, adding more couplant, or adjusting the machine controls slightly. Further subjective judgement was made when interpreting scans, based on the continuity and intensity of these signals and their position on the scan.

To examine the effect of this subjective interpretation on repeatability of DFA measurements, each scan from the trial was scored as 'difficult' or 'easy' to interpret. The difference between DFAs measured on the first occasion, and the corresponding DFA measured 18 days later was then calculated for each animal. Differences of more than 2 cm^2 were scored as discordant. A Chi-squared test showed that scans which were difficult to interpret contributed significantly to the low repeatability of measurement (Table A3.2). Animals which had 'difficult' scans on the first measuring occasion did not necessarily have 'difficult' repeat scans. To investigate the problem further a second trial was planned.

3.3.2 Ultrasonics trial 2

This trial involved 30 of the bulls in groups 6 and 7 immediately prior to slaughter. Dissection data are shown in Table 3.4. On day 1 Scanogram measurements were obtained on all 30 bulls. DFAs were obtained by operator 1 three days later, and repeat DFA measurements were made on the following day. Danscanner scan quality was again poor in this trial, with many scans having extra lines of signals. Scans at the 10th rib were particularly difficult to interpret, perhaps because of the *m. trapezius* and *mm. spinalis et semi spinalis* overlying the *m. longissimus thoracis* at this position (Figure 2.5 and Plate 7). Analysis of Danscanner results was therefore confined to scans at the 13th rib and 3rd lumbar vertebra on both measuring occasions, for a sample of 20 bulls. The boundary of the vertebral column and the *m. longissimus* was clearer on scans in this trial, so DFA was measured from this boundary to a point 12 cm ventral from it. For comparison DFAs were also measured from the vertebra/muscle boundary to a point 15 cm ventral from it. Each scan was interpreted twice by each of these methods. Repeatability of interpretation was slightly higher when DFAs were measured over a distance of 15 cm rather than 12 cm (0.79 versus 0.74), and this method of interpretation was adopted in all following work. A second more experienced Danscanner operator/ interpreter (2) also interpreted the sample of scans described.

Correlations between repeat interpretations of the same scans were lower than expected. Correlations between DFA measurements on the same animal on consecutive days were rather low, especially for the less experienced interpreter (1) (Table 3.5). The error involved in repeat interpretations of Danscanner scans may be due to: (1) tracing different signals on the scan on two occasions; or (2) erratic digitising

TABLE 3.4: Data on dissected bulls - trial 2.

Groups		6 and 7	
No. of animals		30	
		Mean	SD
Age	(days)	503	19
Live weight	(kg)	494	40
Carcass lean	(%)	61.1	3.0
Carcass fat	(%)[1]	23.6	3.7

[1] Total dissectible fat excluding perinephric and retroperitoneal fat, scrotal fat and thoracic fat.

TABLE 3.5: Correlations between repeat interpretations of the same Danscanner scans and between DFA measurements on consecutive days - trial 2 (20 scans per position).

Interpreter	Scan	Position	Correlation
1	day 1, repeat	13th rib	0.85
1	day 1, repeat	3rd lumbar	0.76
1	day 1, day 2	13th rib	0.42
1	day 1, day 2	3rd lumbar	0.36
2	day 1, day 2	13th rib	0.60
2	day 1, day 2	3rd lumbar	0.77

Correlations >0.43 are significantly different from zero (P <0.05).

of the fat area after tracing it onto paper. To evaluate these sources of error, DFAs were traced from 40 scans. Each tracing was digitised twice in a random order. The correlation between repeated digitising of each tracing was 0.99, so low repeatability of interpretation and differences between interpreters must have been due to subjective decisions on which signals represented tissue interfaces.

To investigate this problem further, both interpreters measured DFAs on scans at the 13th rib and 3rd lumbar vertebra for 14 bulls, in three ways:

1. measuring the area between the second line of signals (hide/subcutaneous fat interface) and the third line of signals on all scans;
2. measuring the area between the second and fourth lines of signals on all scans;
3. subjective interpretation using either method 1 or 2.

Correlations between DFAs and carcass lean and fat percentages (excluding internal fat in this trial) were generally higher for the more experienced interpreter (Table 3.6). However, the first method of interpretation always produced the highest correlations. All previous Danscanner work at ABRO had involved subjective interpretation (method 3). Discrepancies between the two interpreters were due to disagreement on which was the true third line of signals on scans which showed multiple echoes. This indicates that even when strict rules are applied, interpeters will differ when the quality of scans is poor. Scatter diagrams showed that the fatness of one outlying bull was consistently underestimated by DFA measurements obtained by method 1. In this case, the extra signals on scans were probably true signals.

TABLE 3.6: Correlations between ultrasonic measurements and carcass composition - trial 2 (14 animals for DFA, 30 animals for SFA).

Measurement	Position	Interpretation method	Correlation with % lean interpreter 1	Correlation with % lean interpreter 2	Correlation with % fat [1] interpreter 1	Correlation with % fat [1] interpreter 2
DFA	13	1	-0.54	-0.63	0.54	0.63
DFA	13	2	-0.26	-0.21	0.24	0.22
DFA	13	3	-0.44	-0.56	0.48	0.55
DFA	3	1	-0.22	-0.82	0.28	0.79
DFA	3	2	-0.02	-0.39	0.00	0.42
DFA	3	3	-0.11	-0.67	0.21	0.63
SFA	10		-0.44		0.62	
SFA	13		-0.39		0.65	
SFA	3		-0.31		0.56	

[1] Total dissectible fat excluding perinephric and retroperitoneal fat, scrotal and thoracic fat.

Correlations >0.51 or <-0.51 (n=14) and >0.36 or <-0.36 (n=30) are significantly different from zero (P <0.05).

Neither interpreter had included these signals in subjective interpretation of scans from this bull, which indicates the difficulty in distinguishing true signals from multiple echoes.

Correlations between SFAs and % lean were fairly low and not as good as those for the best DFA measurements. Correlations between SFAs and % fat were reasonable, and similar to those for the best DFAs (Table 3.6).

Because of the poor Danscanner scan quality the machine was taken for examination to the Medicotechnical Institute, Copenhagen. Discussions were also held with ultrasonics experts at the National Institute of Animal Science, Copenhagen. Several major faults in the scanner and flaws in the scanning techniques were identified. It was suggested that:

1. Defects with the scanner probably contributed to difficulty in learning to use the machine (GS) and to differences between results of the two interpreters.
2. Fourth lines of signals are rarely seen on cattle Danscanner scans. Most of these were due to machine error in the trials discussed.
3. Acoustic gel should always be used after applying liquid paraffin at the scanning position.
4. Including the hide in measurement of DFA makes interpretation of scans easier, especially when animals are young or lean.
5. Danish workers have found that scans at the 1st and 3rd lumbar vertebrae are of higher quality and produce more satisfactory results than scans at the 10th or 13th rib.

A third trial was conducted to evaluate the repaired Danscanner.

3.3.3 Ultrasonics trial 3

This trial involved 16 bulls in group 8. One animal in the group was much older than the rest, but its carcass composition was within the range of the younger bulls. Results were not affected by including data from this animal.

Bulls were scanned with the Scanogram and by two Danscanner operators (1 and 3) of similar experience. Repeat measurements were obtained by both Danscanner operators, either later on the same day (operator 3) or on the following day. Acoustic gel was used before scanning with the Danscanner. SFA measurements were taken at the 10th rib and both SFAs and SMAs were measured at the 13th rib, 1st and 3rd lumbar vertebrae. DFAs and DMAs were measured at the 13th rib, 1st and 3rd lumbar vertebrae. DFA measurements included the hide in this trial.

Danscanner scan quality was much better in this trial than in previous trials. However, virtually all scans had one extra row of signals in the region of the fat/muscle boundary. It was found, using a template, that these signals were in the same position on each scan, so they were ignored during interpretation. Scans were sent to Denmark for examination, from which it was suggested that the chemical composition of both the transducer head fluid and the acoustic gel should be modified.

Bulls in this trial had been selected for lean growth rate (LGR) or lean food conversion efficiency (LFCE) at 400 days of age, so the variation in carcass composition was lower than in trial 2 (Table 3.7). Internal fat weights were included in calculating tissue proportions in this trial. This is unlikely to lead to different results since % fat, including internal fat, was very highly correlated with % fat excluding

TABLE 3.7: Data on dissected bulls - trial 3.

Group	8	
No. of animals	16	
	Mean	SD
Age (days)	636	97
Live weight (kg)	517	67
Carcass lean (%)	64.6	1.5
Carcass fat (%)[1]	17.6	1.8
Lean : bone ratio	3.6	0.2

[1] Total dissectible fat including perinephric and retroperitoneal fat, scrotal fat and thoracic fat.

TABLE 3.8: Correlations between repeat Danscanner measurements - trial 3 (16 animals).

Measurement	Correlation operator 1	operator 3
DFA 13th rib	0.69	0.39
DFA 1st lumbar	0.68	0.41
DFA 3rd lumbar	0.60	0.44
DMA 13th rib	0.46	0.07
DMA 1st lumbar	0.77	0.08
DMA 3rd lumbar	0.75	0.32

Correlations >0.48 are significantly different from zero ($P < 0.05$).

internal fat (0.99 in a sample of 80 bulls). Bulls in this trial were older than in trial 2, but comparison of results of the two machines should still provide a measure of the improvements made to the Danscanner.

Correlations between Danscanner measurements on consecutive occasions were higher for operator 1 than operator 3. Repeatability of DMA measurements was highest in the lumbar region where the *m. longissimus* is clearly defined and of regular shape (Table 3.8 and Plate 8).

Correlations between ultrasonic measurements and carcass composition were rather low, partly because of the low variation in composition. However, mean Danscanner measurements from the two scanning occasions generally showed higher correlations than Scanogram measurements. DFAs were more highly correlated with % lean than % fat, while the reverse was true for SFAs (as noted in trial 2). Correlations between DFAs and carcass traits were fairly similar for the two operators. The measurement giving highest correlations with a given carcass trait varied with machine and operator. Ignoring the poor results for DMAs measured by operator 3, fat areas tended to be more highly correlated than muscle areas with % lean and % fat, while muscle areas showed highest correlations with lean : bone ratio (Table 3.9).

3.3.4 Additional live animal measurements

Weighband (WB) and skinfold thickness measurements (SFT and AFT) were taken on all bulls in trials 2 and 3 and on 56 bulls in group 9. Mean values of these measurements on two consecutive days are shown in Table 3.10. Differences in mean skinfold thickness between groups of bulls, and between measuring sites within each group, may

TABLE 3.9: Correlations between ultrasonic measurements and carcass composition - trial 3 (16 animals; mean DFA and DMA on two occasions).

			Correlation with		
Measurement	Position	Operator	% lean	% fat[1]	lean : bone
DFA	13	1	-0.48	0.43	-0.24
DFA	1	1	-0.55	0.51	-0.25
DFA	3	1	-0.36	0.30	-0.22
DMA	13	1	0.16	0.13	0.50
DMA	1	1	0.37	-0.19	0.39
DMA	3	1	0.27	-0.14	0.27
DFA	13	3	-0.65	0.58	-0.34
DFA	1	3	-0.24	0.15	-0.25
DFA	3	3	-0.43	0.28	-0.39
DMA	13	3	0.10	-0.18	-0.11
DMA	1	3	0.07	0.09	0.27
DMA	3	3	0.11	-0.15	-0.06
SFA	10[2]		-0.29	0.28	-0.11
SFA	13		-0.11	0.17	0.03
SFA	1		-0.27	0.50	0.29
SFA	3		-0.28	0.31	-0.03
SMA	13		0.19	0.01	0.36
SMA	1		-0.05	0.31	0.36
SMA	3		0.19	0.13	0.54

[1] Total dissectible fat including perinephric and retroperitoneal fat, scrotal fat and thoracic fat.

[2] 15 animals only.

Correlations >0.48 or <-0.48 are significantly different from zero (P <0.05).

TABLE 3.10: Mean Weighband and skinfold thickness measurements on two consecutive days.

No. of animals	Weighband (kg)		Skinfold 13th rib (cm)		Anal fold (cm)	
	mean	SD	mean	SD	mean	SD
40 (Trial 2)	485	51	35.3	1.8	23.5	1.4
16 (Trial 3)	513	74	17.6	2.6	22.3	4.5
56 (Group 9)	369	42	15.7	2.0	18.1	2.4

TABLE 3.11: Correlations between live animal measurements on two consecutive days.

No. of animals	Live weight	Weighband	Skinfold 13th rib	Anal fold
40	1.00	0.94	0.45	0.14
16	0.99	0.94	0.79	-0.46
56	0.99	0.93	0.67	0.41

Correlations >0.48 (n=16), >0.31 (n=40), >0.26 (n=56) or <-0.48 (n=16) are significantly different from zero (P <0.05).

TABLE 3.12: Correlations between mean live animal measurements on two days and carcass composition (42 animals).

Measurement	Correlation with % lean	% fat [1]
Age	-0.14	0.14
Live weight	-0.10	0.17
Weighband	-0.33	0.38
Skinfold 13th rib	-0.18	0.13
Anal fold thickness	0.04	-0.06

[1] Total dissectible fat including perinephric and retroperitoneal fat, scrotal fat and thoracic fat.

Correlations >0.30 or <-0.30 are significantly different from zero (P <0.05).

be due to the differences in age, live weight and carcass composition. Repeatability of live weight (LW) and WB measurements was high in each group of bulls. The repeatability of SFT varied from group to group; that for AFT was not significantly different from zero (Table 3.11).

Correlations between live animal measurements and carcass data for 42 bulls from groups 6 to 8 are shown in Table 3.12. Correlations between age, live weight or SFT and carcass data were similar and rather low. Correlations between WB measurements and carcass traits were considerably higher. There was virtually no correlation between AFT and carcass composition.

3.4 Discussion and Conclusions

The repeatability of DFA measurements by operator 1 increased steadily throughout the study, from 0.11 to 0.24 in trial 1 up to 0.60 to 0.69 in trial 3. This may be due to improvements made to the machine and the measuring technique and to increasing experience. Correction of the faults identified in this study and adoption of a more rigorous scanning and interpreting routine for the Danscanner has led to improved scan quality and more promising results.

Andersen *et al*. (1982) reported correlations of 0.34 to 0.70 between repeat DFA measurements at the 10th rib and 1st lumbar vertebra. As in this chapter, these authors found SFA measurements to be more repeatable than DFA measurements (mean repeatability of SFAs 0.80). Comparison with repeatability measurements in the literature suggests that further improvement could be made with the Danscanner (Table 2.5). Repeatability of SFA measurements in this study compare favourably with literature results.

Correlations between SFA and carcass traits were generally more consistent from one trial to the next than correlations between DFAs and carcass composition. Literature results are extremely variable but further improvements in accuracy could be made with both machines (Table 2.3). Animals involved in this study were, however, of the same breed and within each trial were fairly closely matched in age and live weight. This is not always true for published experiments, so comparison may be unfair.

Generally, DFAs and SFAs were more highly correlated than DMAs or SMAs with % lean and % fat in this study. Muscle areas were superior predictors of lean : bone ratio. The best position for scanning varied depending on the machine, the operator/interpreter and the group of animals. These observations agree with published results discussed in Section 2.4.4.

In both trials involving carcass dissection, SFA measurements were more highly correlated with % fat than % lean. DFA measurements were more highly correlated with % lean or correlated to the same extent with % lean and % fat. This difference between machines is difficult to explain since, in theory, both are measuring the same fat area. However, similar observations have been reported in the literature (Section 2.4.4).

The poor predictive value of skinfold thickness at the 13th rib confirms the findings of Tulloh (1961). He measured skinfold at the 11th rib and concluded that it was of no value in predicting subcutaneous fat depth, though it was highly repeatable. Similarly, Wright (1982) found skinfold thickness measurements at the 13th rib of no value in predicting the weight of chemical fat in the body of suckler cows.

The low predictive value of AFT measurements in this study is at variance with the results of Charles (1974). He reported correlations of -0.92 and 0.94 between AFT and % muscle and % fat in the carcass. However, his trial involved four breeds of cattle with a large range in carcass fatness (14.7 to 40.9%). From this preliminary study it appears that WB measurements may be more valuable than live weight as a predictor of carcass composition.

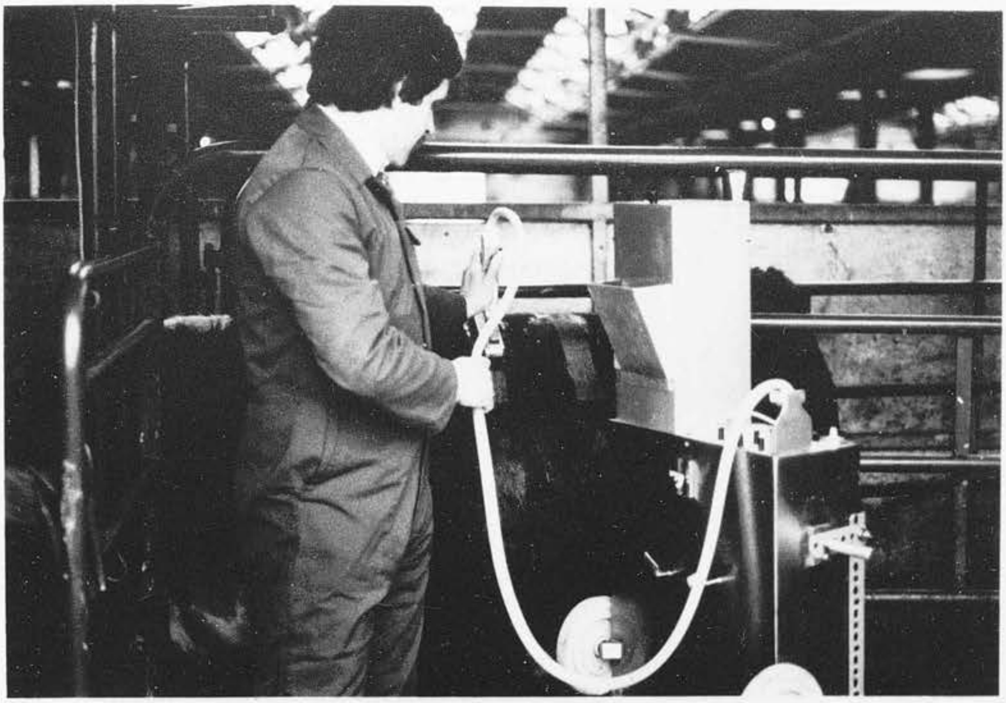


PLATE 1: The Danscanner in operation.

PLATE 2: The Danscanner transducer head.

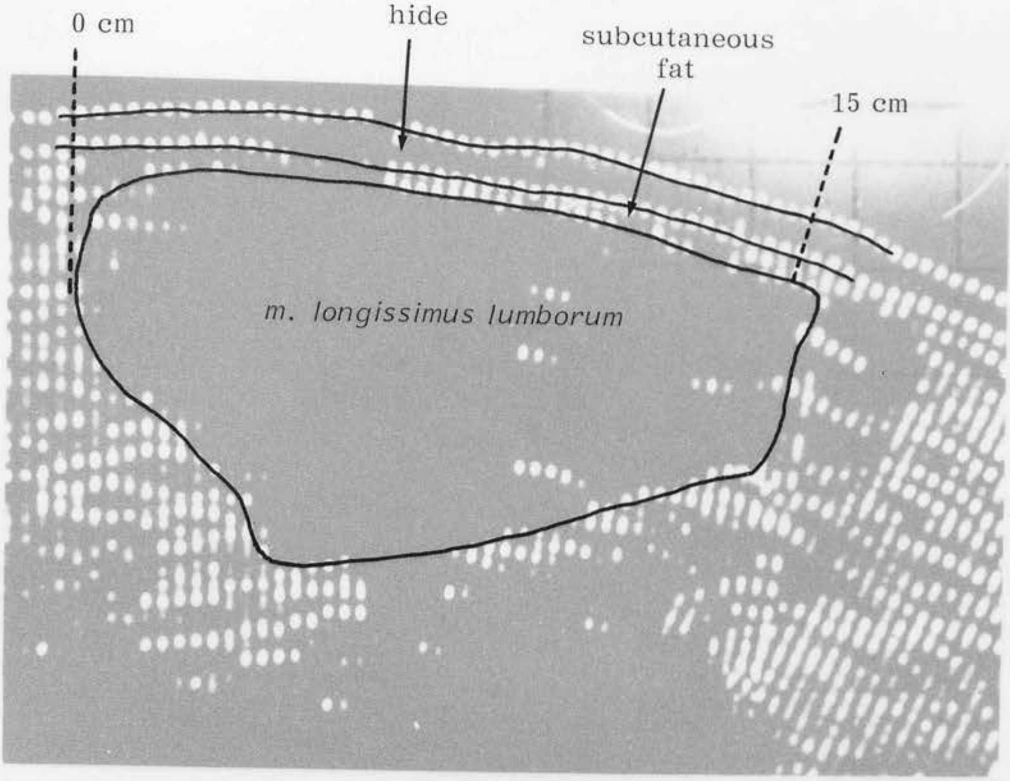


PLATE 3: A Danscanner scan at the 3rd lumbar vertebra.

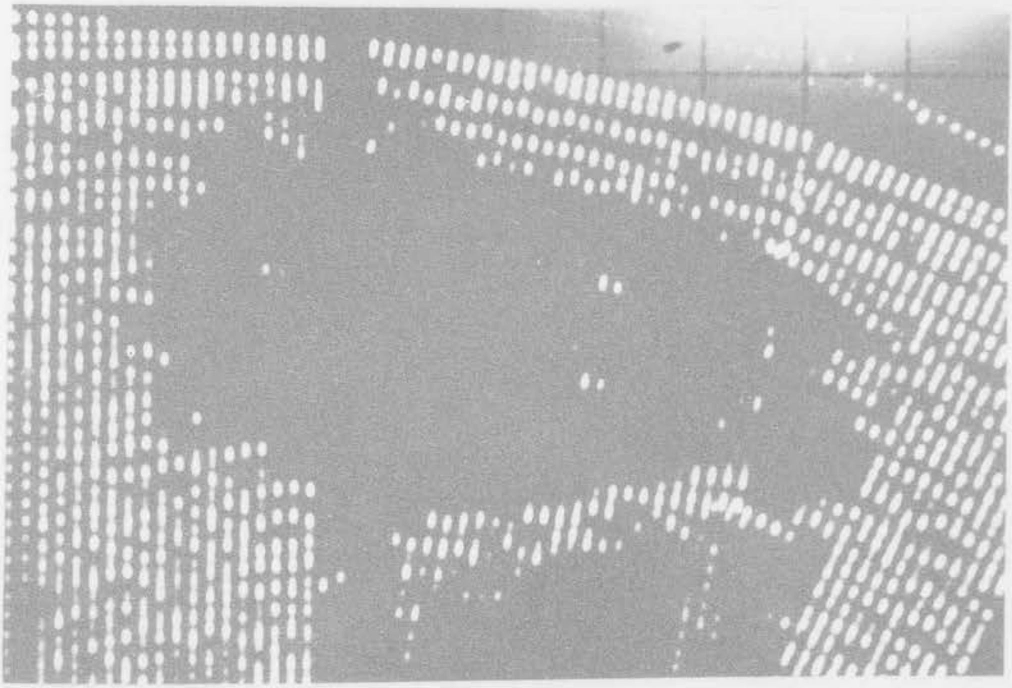


PLATE 4: A Danscanner scan showing multiple signals.

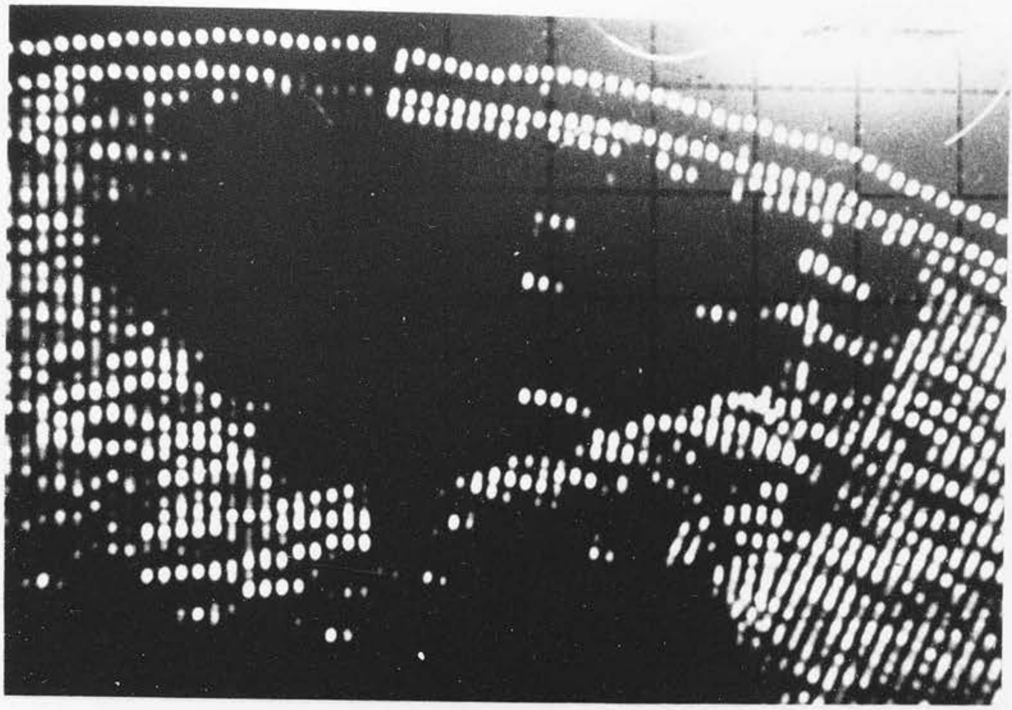


PLATE 3: A Danscanner scan at the 3rd lumbar vertebra.

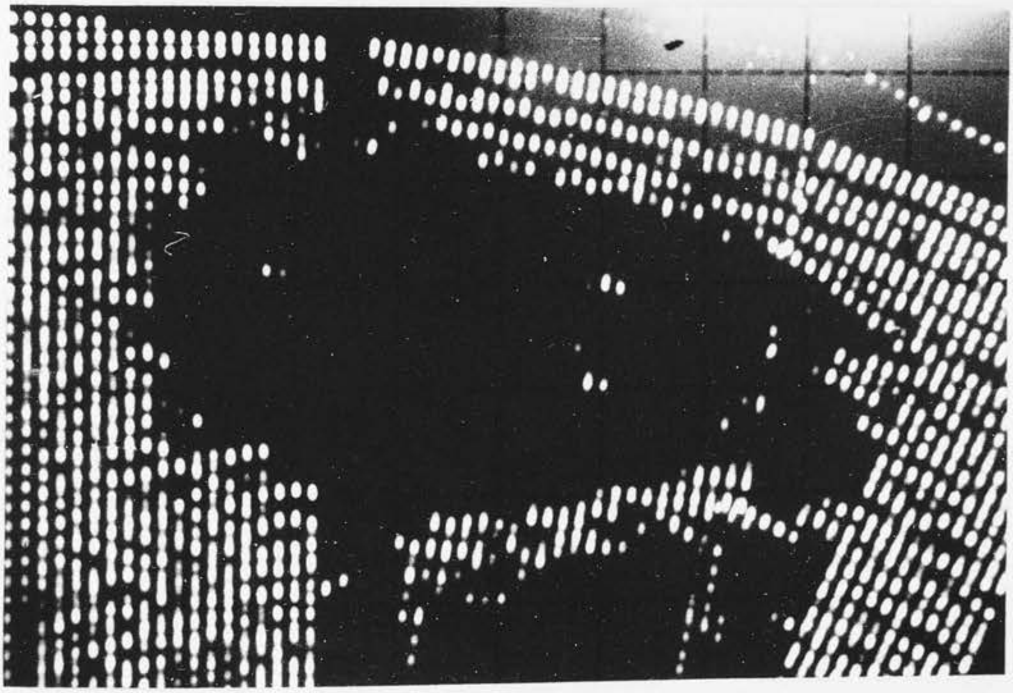


PLATE 4: A Danscanner scan showing multiple signals.

PLATE 5: The Scanogram in operation at an MLC central test station (courtesy of MLC).

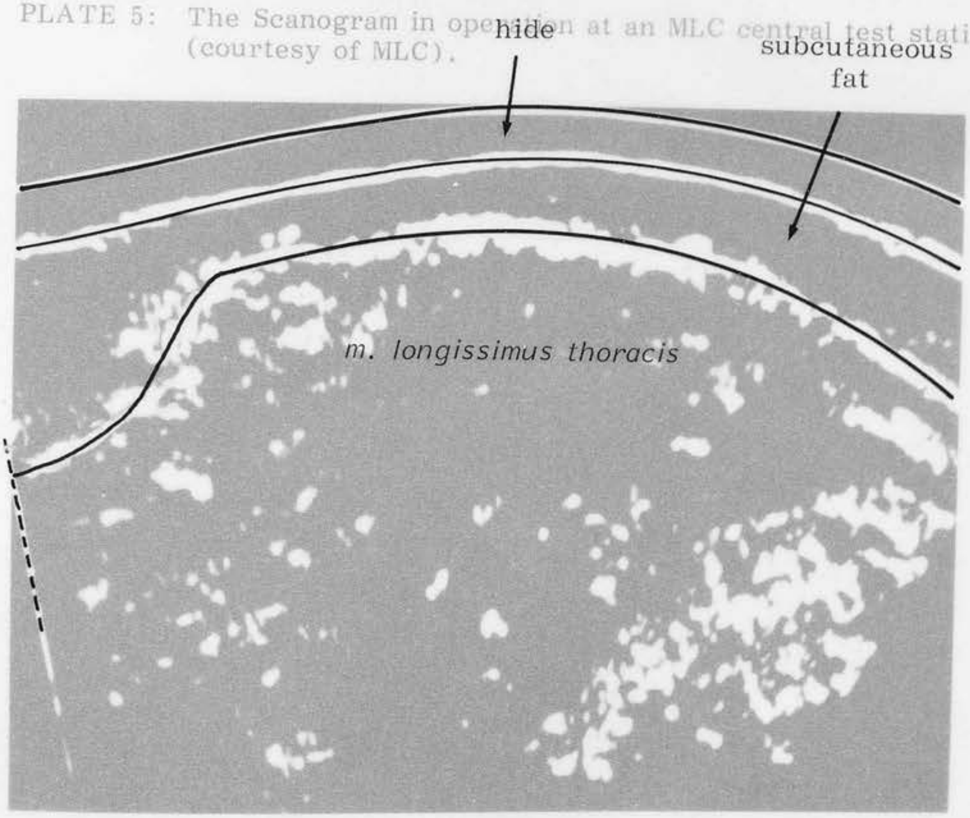


PLATE 6: A Scanogram scan at the 13th rib (courtesy of MLC).

PLATE 5: The Scanogram in operation at an MLC central test station (courtesy of MLC).

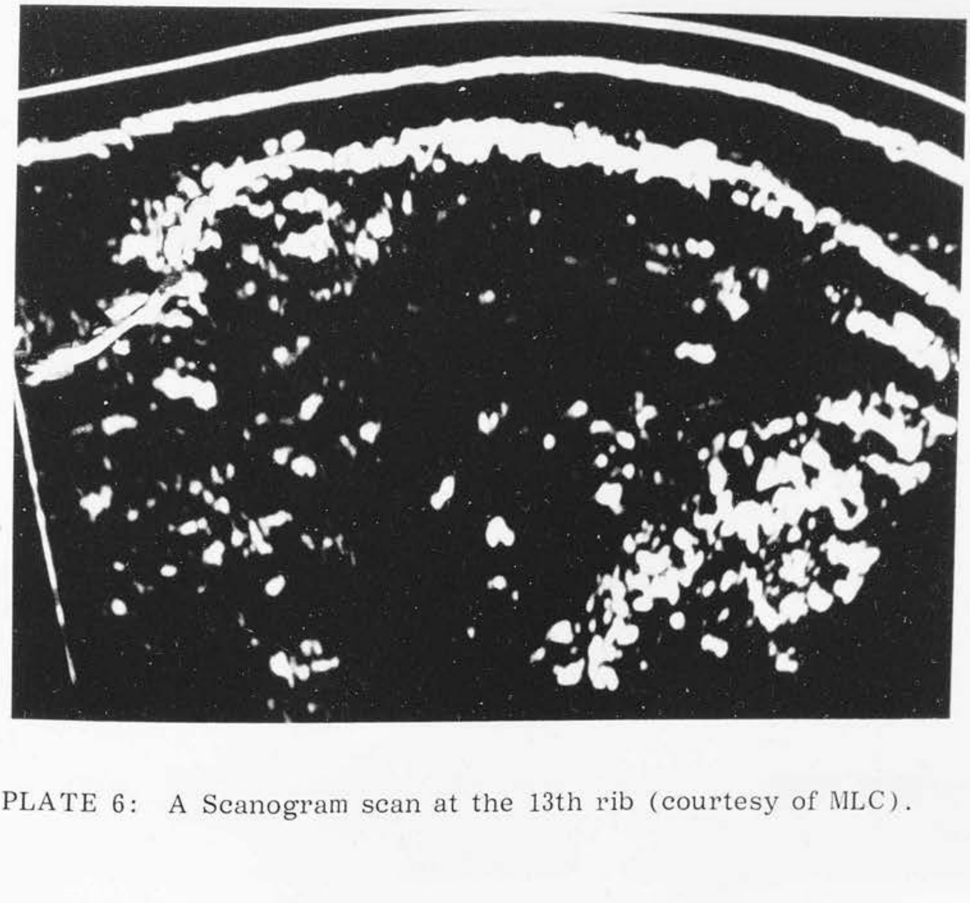


PLATE 6: A Scanogram scan at the 13th rib (courtesy of MLC).

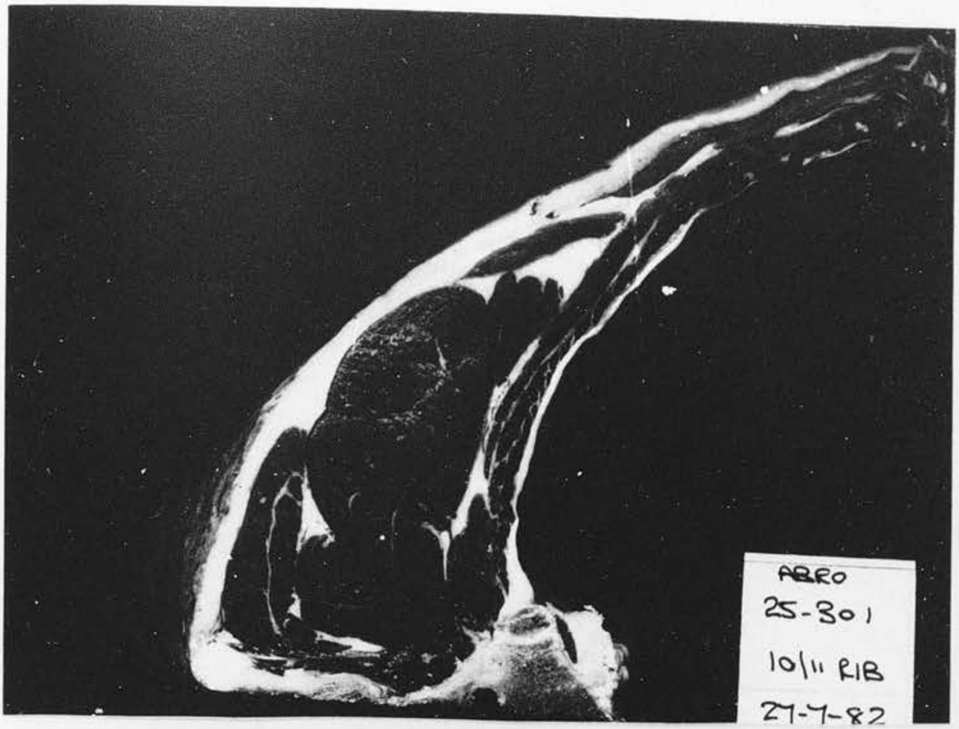


PLATE 7: Cross section of a half carcass at the 10th rib (courtesy of MRI).

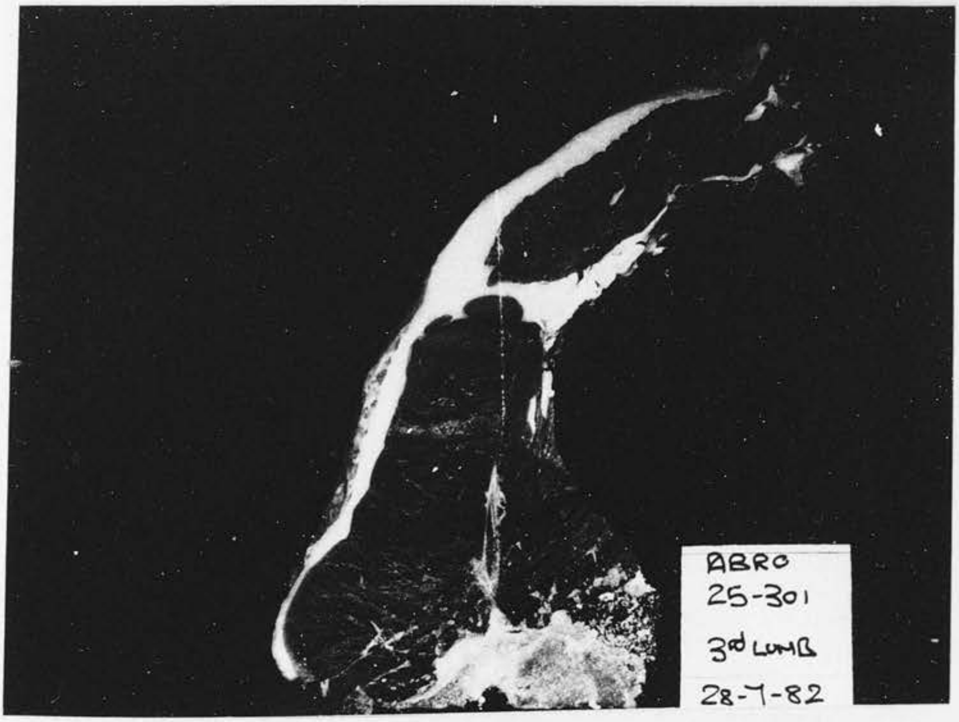


PLATE 8: Cross section of a half carcass at the 3rd lumbar vertebra (courtesy of MRI).

CHAPTER IV

Predicting Carcass Composition

4.1 Introduction

Repeatability measurements and correlations with carcass data can give a useful preliminary indication of the predictive value of live animal measurements. They give little indication, however, of the precision which can be achieved by combining different measurements. Analyses in this chapter were intended to assess the value of ultrasonic measurements, live weight, WB, SFT and AFT when combined in prediction equations for carcass composition.

4.2 Materials and Methods

4.2.1 Animals and measurements

This chapter concerns data on bulls in groups 1 to 8 (Table 4.1). Bulls less than 350 days of age or more than 590 days of age were excluded from the first analysis. The age distribution of remaining bulls was bimodal, with mean ages in the two groups around 400 and 500 days. Analysis was complicated because animals were not scanned at the same position in successive years (Table 4.2). Data were divided into blocks with the same ultrasonic measurements available.

Scanogram scans were interpreted as described in Section 3.2.2. Too few animals had SMA measurements to use these in prediction equations. Danscanner measurements on groups 1 to 5 were made by operator 2 between 1977 and 1980. In groups 1 to 5 DFAs were measured from the vertebra/muscle boundary over the entire width of the *m. longissimus*. Interpretation of Danscanner scans for the other groups has already been described (Section 3.2.2). Mean Danscanner measurements from the two operators on the first measuring occasion were used for bulls in groups 6 to 8. Correlations between DFA measurements and % lean were similar for groups 1 to 5 and groups 6 to 8, so pooling

TABLE 4.1: Data on bulls with live animal measurements.

Group	No. of animals	Dissection agency	Age (days)		Live weight (kg)		Carcass lean (%)		Carcass fat[1] (%)	
			mean	SD	mean	SD	mean	SD	mean	SD
1	5	MLC	561	16	438	69	61.7	3.1	19.3	4.7
2	20	MLC	514	45	471	47	62.5	3.2	19.3	3.3
3	10	MRI	389	18	378	46	64.8	2.7	20.8	4.0
4	10	MRI	517	26	488	39	62.6	2.1	23.7	2.6
5	9	MRI	386	15	403	29	64.6	3.4	21.2	4.4
6	18	ESA	502	19	497	35	59.9	3.6	24.3	4.4
7	10	MRI	507	17	498	40	59.6	4.0	24.6	4.9
8	15	ESA	612	10	507	56	64.5	1.5	17.6	1.8
9	56	-	389	18	392	38	-		-	
10	69	-	378	21	385	43	-		-	

---

[1] Total dissectible fat including perinephric and retroperitoneal fat, scrotal fat and thoracic fat.

TABLE 4.2: Ultrasonic measurements available for different groups of bulls.

Measurement		Group 1	2	3	4	5	6	7	8
DFA	10th rib	✓	✓	✓	✓	✓			
DFA	13th rib	✓	✓	✓	✓	✓	✓	✓	✓
DFA	1st lumbar								✓
DFA	3rd lumbar	✓	✓	✓	✓	✓	✓	✓	✓
DMA[1]		✓	✓	✓	✓	✓			✓
SFA	10th rib	✓				✓	✓	✓	✓
SFA	13th rib	✓		✓		✓	✓	✓	✓
SFA	1st lumbar								✓
SFA	3rd lumbar	✓		✓			✓	✓	✓
SMA[1]		✓							✓

[1] Muscle areas were measured at the same locations as fat areas for each group, except group 8 where muscle areas at the 10th rib were not measured.

data over operators may have reduced the effects of Danscanner machine error discussed in the previous chapter.

A second analysis was conducted to evaluate SFA, live weight, WB, SFT and AFT measurements in prediction equations. This analysis involved bulls in groups 6 and 7 and the older animals excluded from the first analysis (group 8). Mean WB, SFT and AFT from the two measuring occasions were used (see Section 3.3.4).

4.2.2 Statistical methods

Multiple regression equations were constructed by least-squares analysis of variance (Harvey, 1977). Where possible, statistical models included date of slaughter as a fixed effect, thus adjusting implicitly for dissection agency, date of scanning and machine operator/interpreter.

Equations were constructed from the maximum number of measurements in common for each block of data. Age was fitted either as a partial regression or as a main effect with two classes. All other live animal measurements were fitted as partial regressions, with separate regressions calculated for each age class where appropriate. In the first analysis (groups 1 to 7) ages in the two classes ranged from 350 to 450 and from 451 to 590 days of age. Age class was confounded with date of slaughter in models A52 to A65 (Table A4.2) so slaughter date was fitted as a nested effect within age-class. In the second analysis involving SFA, live weight, WB, SFT and AFT measurements, ages in the two classes ranged from 450 to 580 and from 581 to 630 days of age. In this case, data could not be adjusted for date of slaughter and implicit effects, since all bulls in the older age class were slaughtered on the same day. However, all animals were scanned by the same machine operator and Table 4.1 shows little difference in the mean tissue proportions of contemporary bulls dissected by the two different techniques (groups 6 and 7).

Fitting quadratic terms in measurements did not significantly improve the precision of any equations. The least important measurements were eliminated from equations, one at a time. The resulting range of equations is shown in full in Tables A4.1 to A4.3. Choosing the best multiple regression equation is difficult with unbalanced data. Leaving poor predictors in the equation may reduce precision of prediction, but removing a predictor when it is, in fact, important may cause bias in prediction. In this study three methods were used to select prediction equations for carcass lean content. In each case terms were eliminated from equations one at a time and the results re-examined. Where separate regressions for the two age classes did not differ sufficiently for the criterion being used, a single regression was calculated over both age classes. Only then were non-significant single regressions removed.

Method A rejected partial regressions with an F-value less than one. With this method, separate regressions for the two age classes were often retained. Visual examination of graphs with ultrasonic measurements or live weight plotted against carcass lean % showed that slopes for the two age classes were similar. Method B therefore used the same criterion as method A, but was applied to models with regressions pooled over age class. Method C was used on the original full models with separate regressions. In this case, terms which were non-significant at the 0.05 level were eliminated.

4.3 Results

In the first analysis, equations with age fitted as a main effect generally gave more precise prediction of carcass composition than equations with age as a partial regression (Tables A4.1 and A4.2).

Carcass composition was predicted with similar precision by regressions on bull age or live weight, but fitting both age and live weight failed to increase precision much further (Tables 4.3 and A4.1). Including DMA measurements as well as DFAs in equations did not significantly improve the precision of prediction. The best fat area measurements for predicting carcass composition varied, depending on the machine, the group of animals and whether within age-class regressions were fitted. The most precise equations with a pair of fat area measurements did not always include the best single fat area.

The prediction equations for carcass lean selected by the three methods for each block of data are shown in Table 4.3. Equations selected by method A had the highest R^2 values, lowest residual standard deviations and partial regressions with lowest significance. In equations 3, 6, 9 and 12, selected by method A, all of the available measurements were retained. SFA at the 10th rib failed to increase precision of predicting lean % of bulls in groups 1 and 5 to 7. Consequently, equations with only one SFA (at the 13th rib) were chosen by all three selection methods.

Prediction equations selected by method C comprised only one or two partial regressions which were usually highly significant (though the rejection level was $P > 0.05$). Equations selected by method B offered a compromise, using more of the available measurements than equations selected by method C, and having partial regressions of higher significance than equations selected by method A ($P < 0.30$).

Prediction equations 4 and 13, for Danscanner and Scanogram measurements, respectively, are shown in Table 4.4. Both equations were selected by method B. Individually, all fat areas and live weight were negatively correlated with % lean. When the measurements were

TABLE 4.3: Precision of some prediction equations for carcass lean content.

Model	Selection method	Independent variables	Groups	No. of animals	R^2	Residual SD (%)	Original SD (%)	Significance level of least important partial regression term
1	-	Age	1-5	54	0.33	2.92	3.06	*
2	-	LW			0.34	2.91		*
3	A	Age†; LW^a; DFA 10^a, 13, 3^a			0.72	2.08		0.20
4	B	Age†; DFA 10, 13			0.65	2.18		0.06
5	C	Age†; DFA 13			0.61	2.25		***
6	A	Age†; LW^a; DFA 13, 3^a	1-7	78	0.66	2.47	3.52	0.09, 0.35 §
7	B	Age†; LW ; DFA 13, 3			0.63	2.53		0.24
8	C	Age†; DFA 3			0.61	2.58		***
9	A	Age†; LW^a; DFA 13^a, 3	1,3,6,7	39	0.70	2.57	3.78	0.14, 0.62 §
10	B	Age†; LW ; DFA 3			0.66	2.58		0.25
11	C	Age†; DFA 3			0.64	2.59		***
12	A	Age†; LW^a; SFA 13^a, 3			0.77	2.25		0.28, 0.47 §
13	B	Age†; LW ; SFA 13, 3			0.72	2.39		0.29
14	C	Age†; SFA 13			0.68	2.44		***
15	A	Age†; LW ; SFA 13^a	1,5-7	38	0.75	2.34	3.83	0.07
16	B,C	Age†; LW ; SFA 13			0.71	2.45		*
17	-	LW ; WB; SFT; AFT; SFA 10,13	6-8‖	42	0.68	2.32	3.51	0.86
18	B	LW ; SFA 13			0.66	2.24		0.22
19	C	SFA 13			0.65	2.26		***

†Main effect. [a] Partial regression within age-class (bulls 350 to 450 or 451 to 590 days of age). Variables without a superscript are partial regressions over both age classes.

§ Significance level of the within age-class regression and the least important partial regression term.

‖ All animals were over 450 days of age.

TABLE 4.4: Prediction equations for carcass lean content (selected by method B).

Model	Age range (days)	Prediction equation
4	350 - 450	% lean = 72.26 - 0.48 (DFA 10) - 0.82 (DFA 13)
4	451 - 590	% lean = 71.24 - 0.48 (DFA 10) - 0.82 (DFA 13)
13	350 - 450	% lean = 61.54 + 0.02 (LW) - 0.76 (SFA 13) - 0.20 (SFA 3)
13	451 - 590	% lean = 58.07 + 0.02 (LW) - 0.76 (SFA 13) - 0.20 (SFA 3)

combined in prediction equations, several positive partial regression coefficients were observed. The sign of coefficients depends on the matrix of correlations between all variables and is not easy to predict. Prediction equations may therefore be very specific to a given data set, and should be used on other data with caution.

When compared on the same groups of bulls, carcass lean content was predicted more precisely from equations using SFAs than from equations using DFAs (models 9 to 14, Table 4.3). This comparison may not be strictly valid as it involved data on groups 6 and 7, when the Danscanner was producing poor results. However, there was no marked difference between groups of bulls in the correlation between DFAs and % lean. Combining ultrasonic measurements from both machines with live weight in a prediction equation hardly increased precision above that achieved with SFAs and live weight (residual standard deviation [RSD] 2.24% versus 2.25% lean).

Individually, live weight, WB and SFT measurements accounted for a similar amount of the variation in carcass composition (Table A4.3). Residual standard deviations in carcass lean and fat ranged from 2.82 to 2.89% and 3.39 to 3.55%, respectively, with WB being the best predictor in both cases. Including WB, SFT or AFT in prediction equations failed to decrease the residual standard deviation in carcass lean % below that achieved with live weight and SFA at the 13th rib (Table 4.3). However, there was a marginal improvement in precision of predicting % fat when WB measurements were combined with live weight and SFAs (model A98, Table A4.3).

4.4 Predicting Carcass Lean Content of ABRO Bulls

Performance test data were available for 235 ABRO Hereford bulls born between 1978 and 1981. These data included ultrasonic measurements at the end of test (about 400 days of age), but the measurements available varied widely from year to year (Table 4.5). Carcass lean content of these bulls was therefore predicted from May SFA measurements in each year that these were available (bulls born 1979 to 1981). In 1978, only DFA at the 3rd lumbar vertebra was measured, so both April and May measurements were used. Selection of these measurements can be justified because:

1. The correlation between April and May DFA measurements was low, especially in later years (0.40 in 1978, 0.25 in 1979 and 1980 born animals). The correlation between April and May SFA measurements was much higher (0.77 to 0.83).
2. Analysis in Section 4.3 showed that using both DFA and SFA measurements failed to increase precision of predicting % lean above that achieved with SFAs.
3. The best prediction equations in the previous analysis used only one or two fat area measurements from each bull.

In the data used to construct prediction equations in the previous section, only 19 bulls were between 350 and 450 days of age. Not all of these bulls had fat area measurements at the same positions. Consequently, their contribution to evaluation of equations was limited. An additional problem was the range in coefficients of variation (CV) of fat area measurements between years (14 to 45%). The weight given to each component of a product trait depends partly on the coefficients

TABLE 4.5: Ultrasonic measurements available to predict carcass lean content of performance tested bulls.

	Danscanner		Scanogram	
Year	April	May	April	May
1978	DFA 3^1	DFA 3^1	-	-
1979	DFA 10,13,3	DFA 10,13,3	-	SFA 13^1, 3^1
1980	DFA 10,13,3	DFA 10,13,3	SFA 10,13	SFA 10^1,13^1
1981	DFA 10,13,3	DFA 10,13,3	SFA 13, 3	SFA 13^1, 3^1

[1] Measurements actually used in prediction.

of variation of the components (Smith, 1967). Using such variable fat measurements to predict carcass lean % would therefore alter the weighting given to components of LGR and LFCE in different years. To avoid these problems, lean % was predicted as follows.

1. Within each year, each of the two fat areas was expressed as a standardised deviation from the year mean (SFA#), e.g. in data on bulls born in 1979:

$$\text{SFA\# 13} = \frac{\text{SFA 13} - \overline{\text{SFA 13}}}{\text{SD}_{\text{SFA 13}}} \quad \text{and} \quad \text{SFA\# 3} = \frac{\text{SFA 3} - \overline{\text{SFA 3}}}{\text{SD}_{\text{SFA 3}}}$$

2. Within each year, the two standardised fat areas for each animal were summed, and regressed to a constant age of 400 days (to correspond with all other performance traits which were measured to this age). This changes the mean and standard deviation (SD) of fat areas, so the new single value for each animal was expressed as a deviation from the mean and standardised, within years.

3. Within each year the standardised fat area for each animal was multiplied by, i) the standard deviation of dissectible lean at 400 days of age (SD_L, about 2.7% for data in Section 4.3), and ii) the correlation between standardised fat areas and actual carcass lean % at 400 days of age (r, about -0.7 for data in Section 4.3). This accounts for the accuracy of ultrasonic measurements, since,

$$\text{residual } V_L = V_L(1-r^2)\,\frac{n-1}{n-2}$$

if n is large:

$$V_{\hat{L}} \doteq V_L - V_L(1-r^2)$$

$$\doteq V_L r^2$$

$$SD_{\hat{L}} \doteq SD_L r$$

where:

n = number of animals

V_L = variance of carcass lean %

$V_{\hat{L}}$ = variance of predicted carcass lean %

4. The resulting value was then added to the mean dissectible carcass lean % at 400 days of age (about 64% from data in Section 4.3). Predicted carcass lean % at 400 days of age than had a mean of 64% and a standard deviation of 1.89% (0.7 x 2.70%) in each of the four years' data.

Table 4.6 shows correlations between dissectible carcass lean % for the 19 young bulls or 28 older bulls, and lean % predicted from: (1) models 13 or 16 in Table 4.3, or (2) the method described above. The comparison may be biased, as only a proportion of the bulls used to evaluate prediction equations are represented in the comparison in Table 4.6. However, standardised fat areas were reasonably precise predictors of carcass lean %. Standardising pairs of fat area measurements as above gives them equal weighting in prediction. This may be better than using prediction equations where the weightings have been derived from a small data set. As more dissection data on young bulls becomes available to construct prediction equations, it may be possible to improve precision of estimating lean % at the end of test.

4.5 Discussion and Conclusions

Of the measurements examined in this study, live weight and ultrasonic fat areas were the most useful predictors of carcass composition. Since live weight is relatively cheap and easy to obtain it seems sensible to include it in any comparison of predictors. Precision of prediction of carcass lean % in this study was comparable to that in

TABLE 4.6: Comparison of methods of predicting carcass lean content.

		Correlation between dissectible lean % and lean % predicted from:	
No. of animals	Age range (days)	multiple regression	standardised fat areas
10	350 - 450	0.64 (13)[1]	0.83
9	350 - 450	0.70 (16)	0.76
10+9	350 - 450	0.55 (13,16)	0.79
28	451 - 590	0.59 (13)	0.57
10+9+28	350 - 590	0.74 (13,16)	0.76

Correlations >0.60 (n=10), >0.63 (n=9), >0.44 (n=19), >0.37 (n=28) or >0.29 (n=47) are significantly different from zero ($P < 0.05$).

[1] Figures in parentheses are model numbers of prediction equations used (Table 4.3).

a trial reported by Kempster *et al*. (1981). These authors took Scanogram measurements at the 10th rib, 13th rib and 3rd lumbar vertebra on three groups of cattle. Prediction equations were constructed from the best pair of fat depth or fat area measurements for each group. The scanning position giving best results and the precision achieved varied between groups of animals (residual standard deviation 1.84 to 2.63% lean), as in the present study. Including live weight in multiple regression equations did not always improve precision (results in Section 4.3 were similar).

The predictive value of DFA measurements at the 10th rib in equations 3 and 4 is rather surprising, as scans at this position were usually difficult to interpret (see Section 3.3.2 and Miles *et al*., 1972). In contrast, the low predictive value of SFA at the 10th rib in this study is at variance with the results of Tulloh *et al*. (1973) and Kempster *et al*. (1981). Charles (1974) reported highly significant prediction equations for carcass components, based on AFT and live weight measurements. Animals used in his study ranged widely in age, live weight, breed type and carcass composition, which may explain the contradiction with results in Section 4.3.

The best measurements for predicting carcass composition, and the precision achieved, vary considerably according to the breed, age and variation in carcass composition of the animals, operator/interpreter experience and other unknown causes. This indicates that prediction equations must be evaluated on animals which accurately represent the population in which they will be used. When there is insufficient data available to construct prediction equations, or when ultrasonic measurements are heterogeneous, standardised ultrasonic fat areas may give reasonably precise prediction of carcass composition.

One limitation to improving precision is that scans must be fairly easy to interpret. This reduces the number of anatomical sites at which fat and muscle areas can be measured with conventional scanners. The best correlations between ultrasonic fat areas and carcass composition in this trial, and in the literature, are similar to correlations between fat area measurements on the sectioned carcass and total carcass composition. Thus, there may be little scope for further improvements in the *precision* of prediction with results of pulse-echo scanners. However, the *consistency* of results could be improved further. Using frame-freeze oscilloscopes or grey scales, as in human scanners, may help (Chapter II and Andersen *et al.*, 1982). It is possible that future improvements in *in vivo* estimation of carcass composition will come from direct measurement of the velocity of ultrasound, or from more specialised and expensive techniques currently used in human medicine (Miles, 1982; Miles *et al.*, 1982; Section 2.6).

CHAPTER V

A Review on Genetic Aspects of Growth and Efficiency

5.1 Introduction

There is very little published information on the efficiency of lean growth in cattle. This chapter therefore includes results of breed and strain comparisons and results of selection experiments for growth, efficiency and related traits in both laboratory and domestic animals.

In species with a low reproductive rate the efficiency of the breeding population is very important. Beef improvement programmes are therefore discussed with this in mind. The role of performance testing in beef improvement is examined, and alternative schemes are discussed.

5.2 Breed Differences

One of the most striking differences between the many breeds of cattle is the difference in size. It is very difficult to make valid comparisons between species and breeds which differ in size - a problem which was recognised by Brody (1945) in his concept of 'metabolically effective body weight'. Recently, Taylor (1980) proposed two genetic size scaling rules which stem from experimental results showing that most of the variation between species, and to a lesser extent between breeds and individuals, can be accounted for by genetic differences in a single factor, mature body weight (A). This can be defined as 'a mature equilibrium weight containing 15% chemical fat' (Taylor, 1982). According to these rules, age (t) measured from an origin near conception can be genetically scaled by $A^{0.27}$ to give metabolic age, $\theta = t/A^{0.27}$ (Taylor, 1965). On this metabolic age scale, θ, all events in a mammal's life occur at about the same age in 'metabolic days' (Taylor, 1982). Cumulated variables are treated as directly proportional to A, so scaling body weight (W) gives degree of maturity, ($u = W/A$), which is closely related to the animal's physiological stage of development. Genetically standardised mean curves for growth and food efficiency are shown in Figures 5.1 and 5.2.

This theory of growth may be useful in identifying breeds which deviate favourably from their expected performance, but how far can it be applied to within-breed selection? In a breed comparison average mature size can usually be obtained for the different breeds. Within a breed, however, each animal would have to be retained until it reached mature body size, to enable retrospective comparisons at equal degrees of maturity. Clearly this is impractical, but comparing animals at a fixed level of fatness or at equal ratios of live weight/birth weight (after correcting for dam age effects, etc.) may approximate equal degrees of maturity (McClelland, Bonaiti and Taylor, 1976; Kempster *et al.*, 1982c).

Robertson (1982) suggested that although some of the predictions of this generalised theory are correct in practice, others are not, particularly with regard to body composition. He considered the consequences of selecting mice for early growth rate (GR). As expected from the theory, mice selected for high early GR were larger at maturity, and took longer to reach half mature weight than mice selected for low GR. Contrary to expectation, mice with high GR were *fatter* at any given age and at maturity, and females from the high selected line became sexually mature *earlier* than those from the low line. Results of selection experiments in farm animals may help to clarify these issues.

Additive breed differences and heterosis can be exploited to increase the efficiency of beef production by breed substitution, crossbreeding or synthetic breed formation (Baker, 1982; Cundiff, 1982; Gregory, Cundiff and Koch, 1982). In a comparison of 23 British breeds

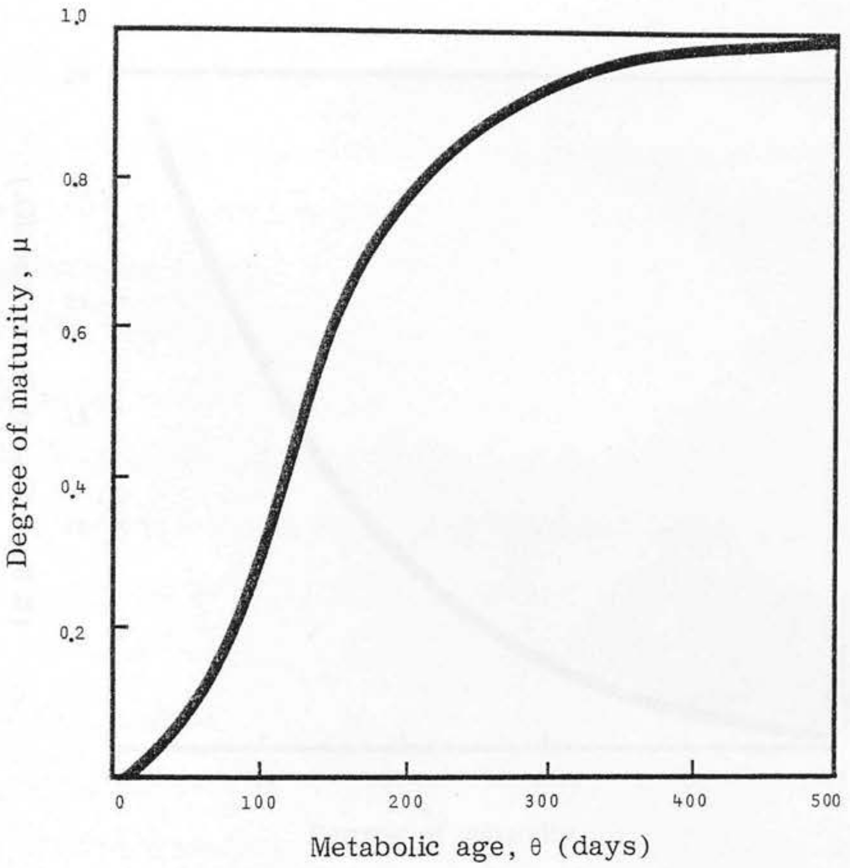


FIGURE 5.1: Mean standardised growth curve for nine species (horse, cow, pig, goat, sheep, rabbit, guinea pig, rat, mouse) in terms of degree of maturity, μ, and metabolic age, θ.

(Taylor, 1982, and earlier)

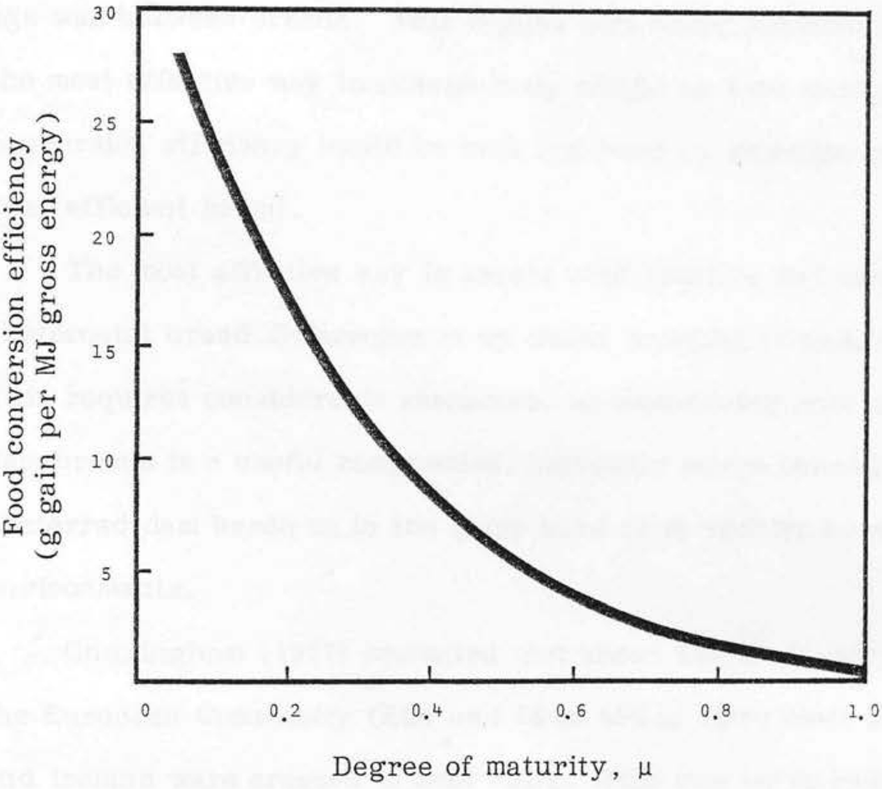


FIGURE 5.2: Genetically standardised mean curve for the food conversion efficiency of an individual in relation to degree of maturity.
(Taylor, 1982)

of cattle, Thiessen (1979) partitioned the genetic variation into components between and within breeds. There was more genetic variation between breeds than within breeds for body weight (67%) and cumulated food intake (57%), but less than 10% of the genetic variation in cumulated food conversion efficiency (FCE) at 72 weeks of age was between breeds. This implies that breed substitution would be the most effective way to change body weight or food intake. Food conversion efficiency would be best improved by selection within the most efficient breed.

The most effective way to assess both additive and non-additive (heterosis) breed differences is by diallel crossing (Cundiff, 1982). This requires considerable resources, so topcrossing onto one or two dam breeds is a useful compromise, especially where there is already a preferred dam breed as in the dairy herd or in suckler herds in harsh environments.

Cunningham (1977) estimated that about 15% of all dairy cows in the European Community (EC) and 35 to 45% of dairy cows in Britain and Ireland were crossed to beef bulls. This may be to reduce the incidence of dystocia in dairy heifers, or to produce a calf with more desirable beef qualities. Liboriussen (1982) suggested that lean tissue growth rate (LGR) was generally of economic importance in such crossbred calves. He combined results of ten crossbreeding experiments involving Friesian or similar dams. These experiments were carried out in six European countries, including the UK, between 1970 and 1980. Liboriussen concluded that a 10 to 15% increase in the genetic capacity for LGR could be achieved by crossing with Blonde d'Aquitaine, Belgian Blue-White, Charolais, Piemontese, Romagnola, Chianina or Simmental bulls rather than purebreeding (Table 5.1). There was, however,

TABLE 5.1: Superiority in beef production traits of beef crosses out of Friesian dams, compared to pure Friesians (Liboriussen, 1982).

Sire breed	% superiority over Friesian GR	killing-out %	lean %	Expected superiority in LGR (%)
Blonde d'Aquitaine	+3	+6	+7	+16
Belgian Blue-White	+3	+7	+5	+15
Charolais	+6	+3	+4	+13
Piemontese	-2	+7	+7	+12
Romagnola	+4	+4	+4	+12
Chianina	+3	+4	+4	+11
Simmental	+5	+2	+3	+10
Limousin	-1	+5	+3	+ 7
German Yellow	+2	+1	+3	+ 6
GRW, DRW[1]	+2	+2	+2	+ 6
South Devon	+1	+2	-1	+ 2
Hereford	-1	+1	-3	- 3
Angus	-7	0	-6	-13

[1] German Red and White, Danish Red and White.

a strong adverse relationship between LGR of the sire breed and calving performance.

Southgate, Cook and Kempster (1982a) and Kempster, Cook and Southgate (1982a) evaluated the live weight gain, FCE, carcass characteristics and rate and efficiency of saleable meat gain in purebred British Friesian steers and crossbred steers from eight sire breeds out of Friesian dams. Southgate, Cook and Kempster (1982b) and Kempster, Cook and Southgate (1982b) evaluated similar traits in Galloway, Luing and Welsh Black steers and in crossbred steers from nine sire breeds out of Blue-Grey and Hereford x Friesian dams. In each of the trials, cattle were slaughtered at a fixed estimated subcutaneous fat level. As well as approximating an equal degree of maturity across breeds, this is the usual criterion for choosing commercial animals for slaughter.

In these trials, larger breeds had faster live weight and saleable meat gain, higher output in a given period, and took longer to reach a fixed level of fatness. Larger breeds ate more food which tended to balance the extra output, so that differences in overall efficiency were relatively small. However, in each trial Hereford and Devon crossbred steers had the highest FCE. Four possible explanations were advanced by the authors:

1. higher digestive and metabolic efficiency, leading to a lower heat production;
2. lower maintenance requirement of earlier maturing breeds because of fewer days to slaughter;
3. higher fat content in the body of earlier maturing breeds at the start of the trial, so that they needed to deposit less fat to reach the fixed end-point;

4. differences in body composition at equal subcutaneous fat concentration, due either to real differences in fat partition or to inaccuracies in the relationship between estimated and actual subcutaneous fat concentrations.

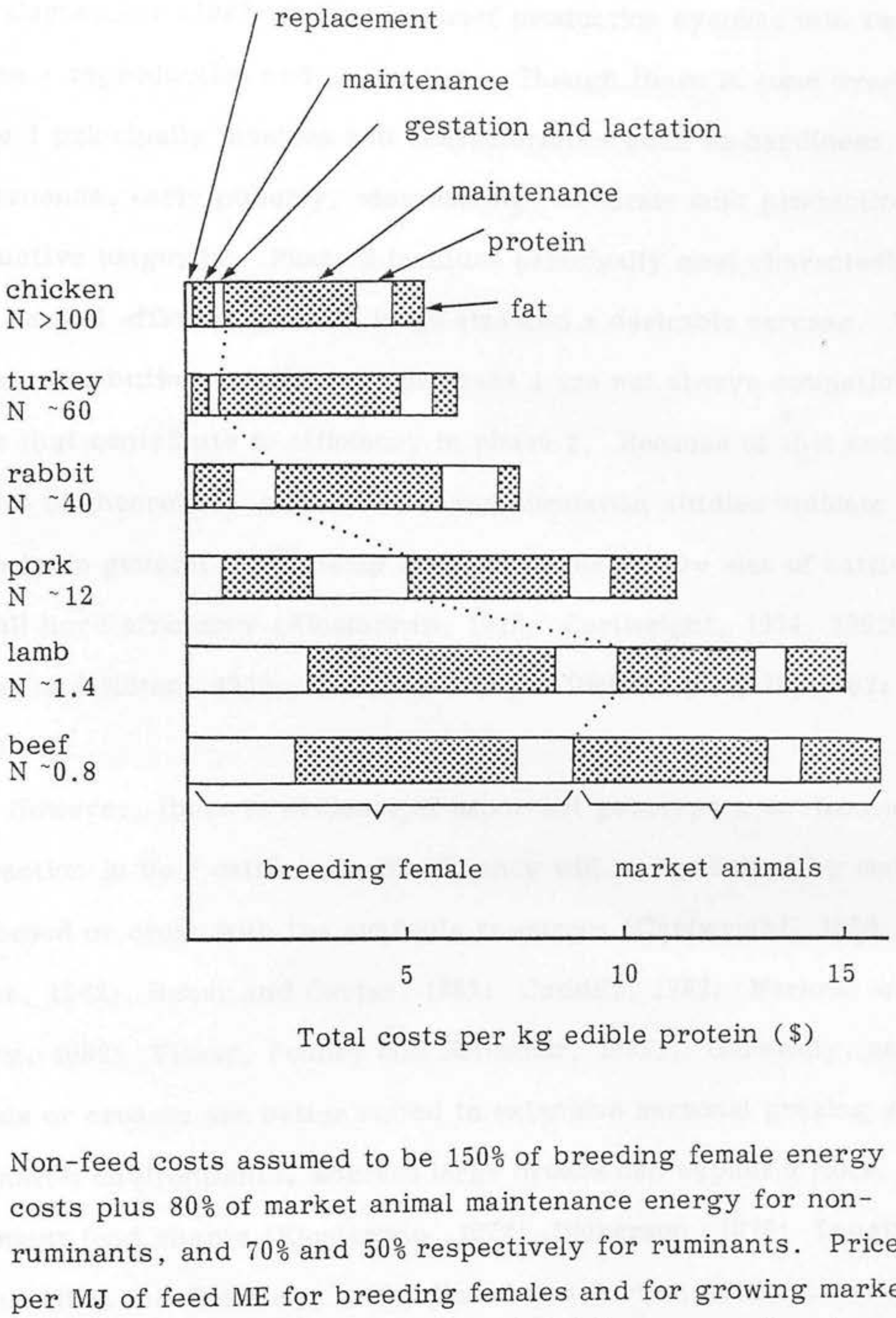
There was no obvious association between the rate of saleable meat gain and its efficiency of production, but Hereford x Friesian steers had consistently high efficiency and purebred Friesian steers had low efficiency of saleable meat production. The poorer efficiency of dairy-type cattle may have been due to greater overall maintenance requirement, since they generally took longer to reach a fixed level of fatness, or to greater daily heat production, or to greater deposition of fat in the non-carcass parts of the body (Kempster *et al.*, 1982a).

A large-scale evaluation of beef breeds differing in milk production, GR, carcass composition and mature size was started at the US Meat Animal Research Center in 1969 (Cundiff, 1982; Gregory *et al.*, 1982). Bulls of 16 breeds were mated to Hereford and Angus dams. Generally, progeny of faster gaining sire breeds had heavier birth weights, more calving difficulty and a higher preweaning mortality rate. Variation in food conversion ratio (FCR) of steers was greatest when measured over a constant weight interval (247 to 470 kg), when steers from faster gaining groups tended to be most efficient. Ranking was similar when measured over a constant time interval of 238 days postweaning. However, when FCR was measured to an estimated 19% fat trim, Hereford and Angus steers were most efficient. This result conforms with results of Southgate *et al.* (1982a,b). As already mentioned, breed comparisons at equal subcutaneous fat levels may be biased. Charles and Johnson (1976) found breed differences in the partition of fat between subcutaneous and other depots.

Steers from faster gaining groups in the US trial had a higher % retail product and lower % fat trim than slower growing breeds at a given age. Females of the faster gaining breeds tended to reach puberty at a later age, though breeds selected for milk production reached puberty at younger ages than unselected breeds of comparable size.

5.3 Herd Efficiency

Many improvement programmes have concentrated on traits of the slaughter animal in isolation, without considering possible effects on the overall productivity of the herd. To illustrate the potential effects of changes in animal growth on herd efficiency, Dickerson (1970, 1976, 1978, 1982) developed a model which partitions inputs and outputs between, 1) the breeding female and preweaning growth of the young, and 2) postweaning growth of the young. The effects of genetic changes in rate, composition or pattern of growth on economic efficiency can differ within a species, depending on the reproductive rate, the relative market values for lean versus fat and young versus adult product, and market weight relative to mature size. Dickerson (1982) concluded that the efficiency advantage of faster GR was greatest in species with a high reproductive rate, because the increased maintenance costs of larger adults can be spread over more progeny marketed (Figure 5.3). This spreading of dam maintenance costs over more progeny underlies the current interest in twinning in beef cattle (Piper, 1982). Similarly, spreading the high maintenance cost of adult cows by combining milk and beef production, or by breeding from heifers prior to slaughter increases the efficiency of beef production (Allen and Kilkenny, 1980). Large (1976) and Holmes (1977) also discussed measures of herd efficiency.



Non-feed costs assumed to be 150% of breeding female energy costs plus 80% of market animal maintenance energy for non-ruminants, and 70% and 50% respectively for ruminants. Prices per MJ of feed ME for breeding females and for growing market animals respectively: 0.956 and 1.076 ¢ for non-ruminants and 0.478 and 0.717 ¢ for ruminants.

N = reproductive rate.

FIGURE 5.3: Total life-cycle costs per unit of edible meat protein output, partioned by components of energy use, for several species.
(Dickerson, 1978, 1982)

Cartwright (1982a,b) divided beef production systems into two phases - reproduction and production. Though there is some overlap, phase 1 principally involves cow characteristics such as hardiness, low maintenance, early puberty, easy calving, moderate milk production and productive longevity. Phase 2 includes principally meat characteristics such as fast efficient growth, large size and a desirable carcass. Thus, traits contributing to efficiency in phase 1 are not always compatible with those that contribute to efficiency in phase 2. Because of this antagonism, results of theoretical, experimental and simulation studies indicate that there is no general relationship between GR or mature size of cattle and overall herd efficiency (Klosterman, 1972; Cartwright, 1974, 1982b; Morris and Wilton, 1975; Andersen, 1978; Dickerson, 1978, 1982; Smith, 1979).

However, there is evidence of important genotype x environment interaction in beef cattle. Herd efficiency will be maximised by matching the breed or cross with the available resources (Cartwright, 1970, 1974; Baker, 1982; Baker and Carter, 1982; Cundiff, 1982; Marlowe and Tolley, 1982; Vissac, Foulley and Ménissier, 1982). Generally, smaller breeds or crosses are better suited to extensive seasonal grazing systems and harsh environments, whereas large breeds can exploit a more abundant food supply (Klosterman, 1972; Dickerson, 1978; Langholz, 1978; Allen and Kilkenny, 1980; Baker and Carter, 1982; Cartwright, 1982b).

Gregory *et al.* (1982) estimated the output of weaned calves from different breeding schemes. Output was largest when crossbred females, which show heterosis for maternal traits, were mated to a larger terminal sire breed to increase the GR of slaughter animals. This may be particularly advantageous in extensive production systems, where 70% of the total food costs may be attributed to the dam (Carter, 1982).

Taylor (1982) calculated the overall efficiency of lean meat production for a dam with four progeny during her breeding life, when either large or small terminal sires were used, and when all calves were either purebred males or purebred females (Figure 5.4). If progeny were slaughtered at the optimum degree of maturity, then overall efficiency was 13% higher for all male offspring versus all female offspring, and 23% higher for large versus small terminal sires.

Systems analysis can be used to optimise breeding programmes for a given set of resources. Using a model which characterised breeds according to size, maturing rate and milk production, Notter, Sanders, Dickerson, Smith and Cartwright (1979a,b,c) simulated a 'Mid-Western [US] cow-calf-feedlot' beef system. They discovered that the optimum milk production level for beef females varied with the price ratio of feedlot : cow herd total digestible nutrient (TDN), and with the emphasis placed on fatness of the slaughter animals. Similarly, a wide range of mature cow sizes (400 to 800 kg) was potentially optimal, depending on the ratios between non-feed costs, feedlot and cow herd TDN costs. The optimal size of breeds for crossing was also a function of feedlot : cow herd TDN prices. However, if calving difficulties in 2-year old cows were avoided, very high relative feedlot TDN prices were required to negate the advantage of a large terminal sire breed.

Eventually, it may be possible to integrate computer models for different species, and for crop and animal enterprises, to predict the best combination of systems for the efficient production of energy and protein for human consumption.

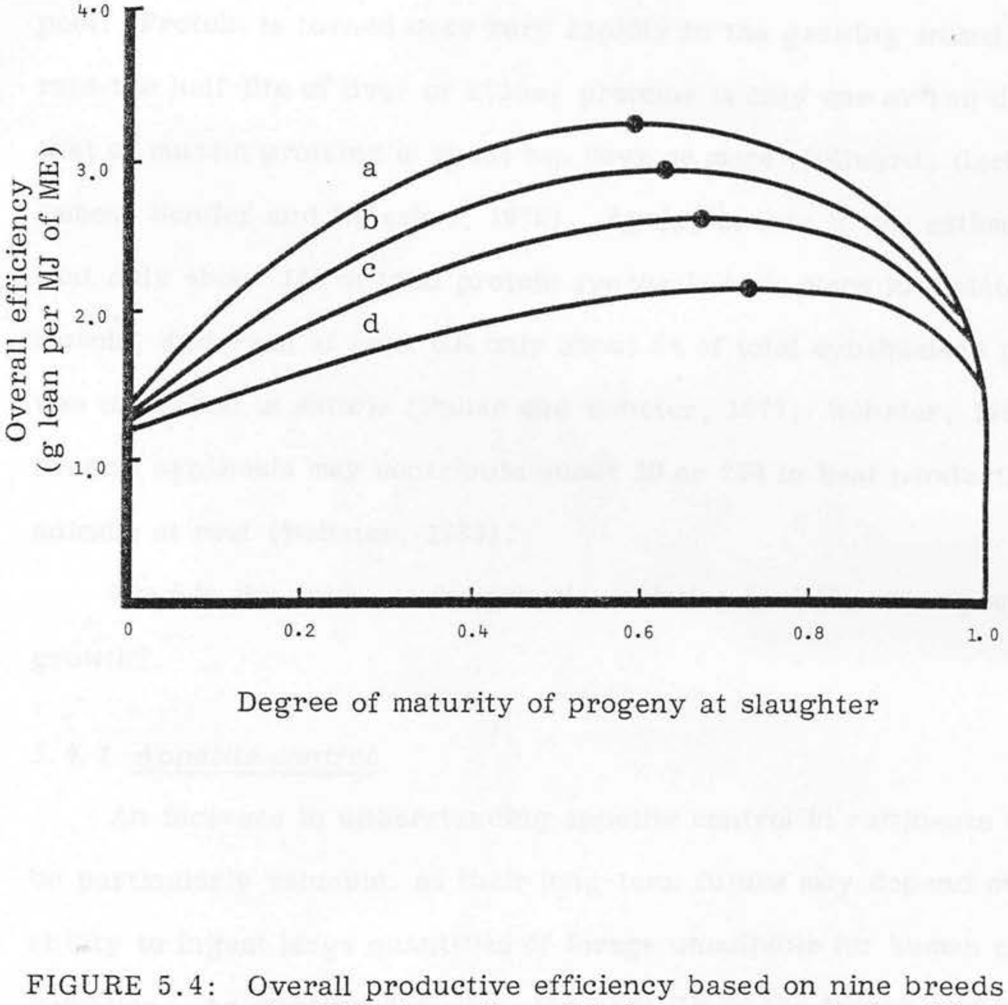


FIGURE 5.4: Overall productive efficiency based on nine breeds of cattle, for a dam with four progeny in her lifetime, all fed the same diet *ad libitum* when (a) a large terminal sire is used, (b) all calves are purebred males, (c) all calves are purebred females, and (d) a small terminal sire is used.

(Taylor, 1982)

5.4 Genetic Aspects of Growth and Efficiency

Robertson (1982) presented a flow diagram as a possible framework for discussing genetic aspects of growth (Figure 5.5). There are two feedback loops in the model: 1) appetite control, and 2) physical feedback of amino acids from the degradation of protein, to the amino acid pool. Protein is turned over very rapidly in the growing animal. In rats the half-life of liver or kidney proteins is only one or two days; that of muscle proteins is about ten days or more (Millward, Garlick, James, Sender and Waterlow, 1976). Again, in rats it was estimated that only about 14% of total protein *synthesis* took place in striated muscle, and even at peak GR only about 8% of total synthesised protein was *deposited* in muscle (Pullar and Webster, 1977; Webster, 1980b). Protein synthesis may contribute about 20 or 25% to heat production in animals at rest (Webster, 1983).

What is the evidence for genetic variation in different aspects of growth?

5.4.1 Appetite control

An increase in understanding appetite control in ruminants would be particularly valuable, as their long-term future may depend on their ability to ingest large quantities of forage unsuitable for human consumption. As mentioned earlier, the high GR of the larger cattle breeds is associated with a high food intake, rather than intrinsically high efficiency.

Selection for increased GR or body weight in mice, quail and poultry under *ad libitum* feeding has generally led to increased food intake and improved gross FCE (Roberts, 1979; McCarthy, 1980, 1982a,b; Pym, 1982; McCarthy and Siegel, 1983). This improvement in FCE may be

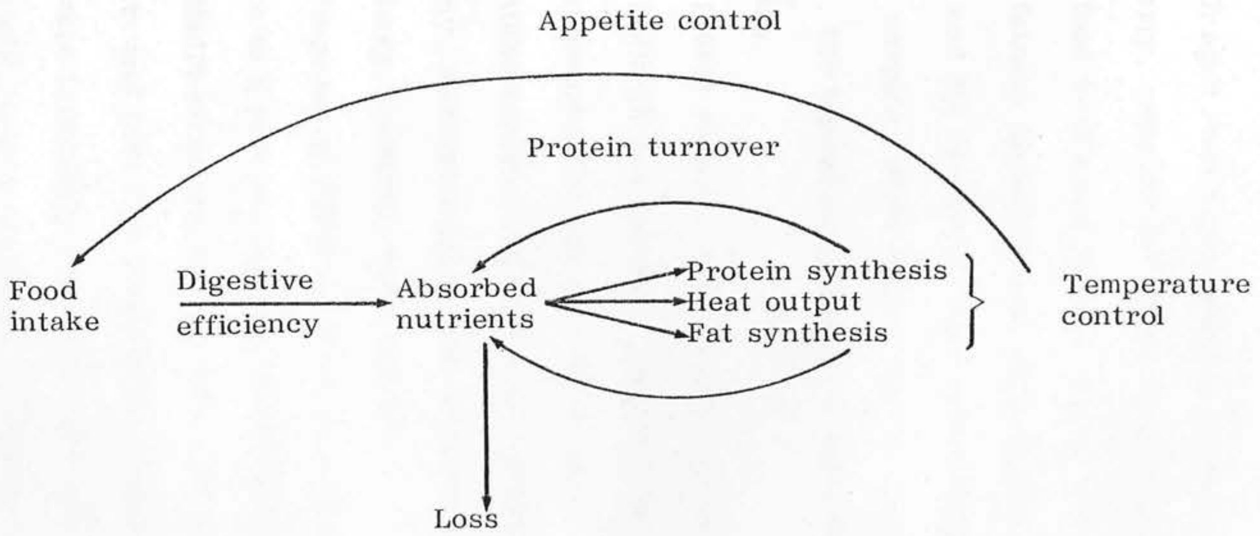


FIGURE 5.5: A possible framework for the discussion of genetic aspects of growth (Robertson, 1982).

due to a reduction in maintenance cost relative to intake (McCarthy, 1982a,b). Selected lines of mice and poultry frequently have increased fat deposition which can impair fertility (Roberts, 1979; McCarthy, 1982a,b; McCarthy and Siegel, 1983). Hayes and McCarthy (1976) found that mice selected for weight at 5 weeks of age tended to be fatter at all ages than those selected at ten weeks of age.

Similarly, selection for improved FCE in mice and rats has led to increased food intake and fatness (Eisen, 1982; Pym, 1982). The increased fatness disagrees with expectations, based on the energy cost of protein and fat synthesis. Pym (1982) suggested that in small laboratory animals, which have a high energetic requirement for thermoregulation, the insulation afforded by extra fat may outweigh the cost of deposition.

Pym (1982) reported that selection for high food intake in poultry increased both GR and fatness. Selection for FCE did not change intake, but reduced fatness at a given age or weight. In mice selection for food intake adjusted for four-week weight increased GR but, surprisingly, selected animals were *leaner* than controls at a constant age (G. Sharp, personal communication).

The leanness of Pietrain compared to Large White x Landrace pigs may be due to a reduced appetite under *ad libitum* feeding (Fuller, Webster, MacPherson and Smith, 1976). In a review of pig selection experiments and breeding programmes Glodek (1982) concluded that GR and FCE were favourably correlated, and originally both were favourably correlated with carcass leanness. However, selection for improved carcass composition under intensive feeding has reduced food intake in some pig populations, with FCE generally unchanged. Important unfavourable changes in meat quality, stress susceptibility and possibly reproductive performance have also been observed. These changes may be associated with an increased frequency of a single recessive gene controlling sensitivity to halothane anaesthesia (Webb, Carden, Smith and Imlah, 1982).

5.4.2 Digestive efficiency

Blaxter (1964) and colleagues found no significant differences between sheep and cattle in the apparent digestibility of energy, when fed the same six diets at maintenance. They concluded that differences between breeds and individuals in digestive efficiency were likely to be small. However, there is evidence of some variation in digestibility or metabolisability of dietary energy in pigs (Siers, 1975), and between *Bos taurus* and *Bos indicus* cattle (Karue, 1975). Pym (1982) also cited reports of differences in metabolisability between breeds and strains of poultry, between lines selected for efficiency (versus control), and between lines selected for divergent eight-week body weight.

5.4.3 Energy partition

During uninterrupted growth body weight, lean mass and body fat content increase from the time of conception, or shortly after, along sigmoid curves to an asymptotic value which is maturity (Webster, 1979). Metabolisable energy (ME) available to the animal is either lost as heat (about 70% of ME; Webster, 1977, 1980a), or is stored, mainly as protein and fat. The energy content of protein is about 24 MJ/kg and that of fat is about 39 MJ/kg (Webster, 1977; Agricultural Research Council [ARC], 1980). Kielanowski (1965) first attempted to estimate the heat loss associated with protein deposition, fat deposition and the residual maintenance component relating heat loss to body weight, in young lambs and piglets. In a later review, Kielanowski (1976) estimated that the increment in heat loss associated with deposition of 1 kg of protein in rats and pigs was about 31 MJ. Thus, the ME required to deposit 1 kg of protein (energy value plus heat increment) was about 55 MJ. The validity of this statistical approach has been questioned (Fowler, 1978; Webster, 1983) but comparison of ME flow in lean and fat Zucker rats produced very similar values of 53 MJ ME/kg protein or fat deposited (Pullar and Webster, 1977). Information on the energy costs of simultaneous protein and fat deposition in ruminants is rather inconsistent (Graham, 1969; Ørskov and MacDonald, 1970, 1976; Kielanowski, 1976; Geay and Robelin, 1979). ARC (1980) assumed that the efficiency of utilisation of ME for growth in ruminants was similar over a range of body composition. In cattle, each gram of tissue protein is associated with about 3 or 4 g of water (van Es, 1976; Geay and Robelin, 1979), so the total energy cost of depositing 1 kg of 'wet' muscle should be much less than that for 1 kg of fat, which has little associated water.

During growth, ME intake exceeds heat loss, but the two values converge as the animal approaches mature size. The overall efficiency of energy retention (retained energy [RE]/ME) reaches a peak at about 25% of mature size and then declines steeply. As an animal matures the ratio of fat to protein in the gain increases, and thus the energy retained per kilogram gain increases. Finally, FCE (expressed as kg gain/MJ ME) which reflects both RE/ME and the energy content of the gain, is relatively constant to about 30% mature size, then declines steeply. Thus, selection for GR, leanness or FCE at a fixed weight, and to a lesser extent at a fixed age, will tend to favour animals which are less mature, and may select for an increase in mature size (Taylor, 1968; Webster, 1977, 1980a,b).

The residual maintenance component of heat loss is traditionally assumed to be the same function of body weight for different animals of the same breed or species, or even for different species (Kleiber, 1961). There is evidence, however, that in growing animals 'maintenance' heat loss is not a constant function of body weight raised to a given power (Webster, 1977). In some cases it appears that the difference in leanness between genotypes is due to the difference in partition of ME between heat loss and fat deposition, with no net gain in the efficiency of lean meat production.

In an experiment with Zucker rats, genetically lean animals converted food to protein gain much more efficiently than fat rats, but dissipated a far higher proportion of ME as heat. In spite of a higher energy content of the gain, fat rats grew more rapidly and efficiently than lean rats at the same food intake (Radcliffe and Webster, 1976; Webster, 1977). However, lines of rats selected for rate or efficiency of protein gain had improved efficiency of protein and live weight gain, slightly *lower* fasting heat loss per unit metabolic weight, and larger adult size (Wang, Dickerson, Hadden and DeShazer, 1980). Correlated changes in some reproductive characteristics were also reported (Allrich, Wang, Dickerson and Zimmerman, 1981).

The leanness of deer compared to sheep, at similar degrees of maturity, appears to be associated with higher heat loss. Again, this confers no energetic advantage to the animal (Webster, 1977).

Webster (1977, 1980a) and colleagues compared ME flow in steers and bulls of several breeds and crosses. Generally, bulls and large lean breeds had the highest heat loss at any stage of growth. When fed low energy forage Hereford x Friesian steers performed best and, because of higher heat loss relative to ME intake, bulls and large lean animals performed worse. As the quality of the diet increased, the greater appetite and lower energy value of the gain of bulls and lean breeds began to overcome the problem of higher heat loss. Similarly, pigs selected for high GR and low backfat had increased maintenance requirements per unit body weight compared to control pigs (Cleveland, Johnson, Mandigo and Peo, 1983; see also Sundstøl, Standal and Vangen, 1979).

Webster (1983) suggested that there was a tendency for fasting heat loss to be related to the potential metabolic performance of the animal. Dairy cows generally having higher heat loss than beef bulls, which had higher heat loss than beef steers and heifers. Also, energy requirements for maintenance were better expressed as a function of lean mass than of body weight; remaining differences between classes of cattle may be due to different rates of turnover of the major body constituents.

Andersen (1978, 1980) demonstrated, by regression analysis, that maintenance requirements of cattle (per unit metabolic weight) differed between feeding levels, breeds and sire progeny groups, even with daily gain, killing-out % and body composition held constant. Within breeds, the estimated heritability of the partial regression coefficient of maintenance energy requirement on metabolic body weight was 0.31. Fowler (1978) estimated that a 10% reduction in maintenance requirements would reduce the energy cost of lean tissue production in a 90 kg pig by about 3%. In extensive beef production systems, such a reduction in maintenance costs could be more beneficial, because of the long growing period. The cost of maintaining suckler cows could also be reduced, and this avenue of improvement is clearly worth investigating.

5.5 Cattle Selection Experiments

Relatively few cattle selection experiments have been undertaken because of the expense and time involved. In a recent review, Dalton and Baker (1980) were critical of beef selection experiments carried out prior to the 1970's because of low numbers, inbreeding and lack of control populations. In a review of genetic parameters, Barlow (1978) concluded that selection for either weaning weight or gain to weaning would increase weight at all ages. He also suggested that selected animals would tend to be fatter when slaughtered at a fixed age but leaner at a fixed weight. Selection for weaning weight should improve FCE to slaughter at a fixed weight, but should have little effect on FCE to a constant fat cover. One standard deviation of selection for weaning weight was expected to increase feed requirements of the breeding cow by 2.5%.

Koch, Gregory and Cundiff (1982c) reviewed beef cattle selection experiments and found that realised heritabilities for birth weight, weaning weight, postweaning GR, final weight and (for one experiment only) FCE were generally in close agreement with estimates from paternal half-sib and offspring-sire regression analyses. There were positive genetic correlations between weights and gains in different periods.

Koch *et al*. (1982c) also reported their own selection experiment for weaning weight, yearling weight or an index of yearling weight and muscling score. Selected bulls showed a correlated improvement in FCE from 227 to 408 kg live weight, which was probably a result of the shorter time required to reach target weight (11 to 15 days less than control bulls). Birth weight and the incidence of calving difficulty and mortality were all higher in selected lines than in the control.

There appear to be no reports of selection for relative growth rate (RGR) in cattle. However, in Hereford cattle, Fitzhugh and Taylor (1971) reported high genetic correlations between RGR and absolute GR in several age periods. Genetic correlations with mature size were lower for RGR than GR. Hence, it may be possible to increase GR with little increase in mature size by selection for RGR. Heritability estimates in different age periods were: 0.35 to 0.48 for GR, 0.22 to 0.46 for absolute maturing rate, 0.24 to 0.47 for RGR (Fitzhugh and Taylor, 1971) and 0.37 for time taken to mature (Taylor and Fitzhugh, 1971). Fitzhugh (1976) predicted that the direction of correlated responses to selection for body weight, degree of maturity, GR, absolute maturing rate and RGR in cattle would differ, depending on the age at selection.

Direct selection for RGR in mice produced a realised heritability of only 0.08 (Bakker, 1974). However, McCarthy and Bakker (1979) were able to alter the relationship between maturing rate and mature size in mice by selecting for different combinations of high and low weights at five and ten weeks of age. Ricard (cited by Robertson, 1982) selected chickens in a similar manner. Birds with rapid early growth and low mature size had the fattest carcasses.

Tables 5.2 to 5.4 show literature estimates of heritability for some traits related to growth and efficiency in cattle and, where available, the phenotypic and genetic correlations among them. There was relatively little information on carcass lean %, so data on edible or saleable meat % are also presented. Most of the correlations show that fast growing animals were fatter than slow growing animals at a given age or weight. This differs from the situation across breeds, where large fast growing breeds tend to be leaner than smaller breeds at any age or

TABLE 5.2: Literature estimates of heritability of performance traits in beef cattle.

Source	Management	End-point	No.	Heritability					Comments
				BW	GR	FCE	US	lean %	
Andersen and Ernst, 1972	Progeny test.	Constant LW 350 kg	213				0.15 0.08		h^2 for US fat area at 5th lumbar, then mean fat area at the 1st and 5th lumbar. 3 breeds, PHS estimate of h^2.
Dinkel and Busch, 1973	Feedlot from 200 days. Hormone implanted.	Time constant at estimated group mean LW of 454 kg	568		0.55(FG) 0.85(FF)			0.38^1	^{1}Wt of edible portion (actual or estimated) in carcass, adjusted to 272 kg carcass wt.
Dickerson *et al.*, 1974	Individual feeding post-weaning.	Constant age.	998- 1036		0.30(W) 0.26(G)			0.50^1	^{1}Wt lean retail product. PHS estimates of h^2.
		Constant LW.						0.35^1	
Baker *et al.*, 1975	Grassland.	Constant age, 15 months	1617, 663	0.27 0.29	0.17(G) 0.24(G) 0.32(Y) 0.60(Y)				Two experimental farms. PHS estimates of h^2. AA and He sires.
Andersen *et al.*, 1977b	*Ad lib.* feeding indoors.	Constant LW 250 kg or 450 kg.	2330, 1011	0.72^1	0.43	[0.36]		0.52	^{1}LW at 15 days. PHS estimate of h^2.
Pabst *et al.*, 1977b	MLC pedigree recorded herds.	Constant age, 400 days.	2650 4439 1760	0.23	 0.38^1 0.27^2				^{1}200 day LW. ^{2}400 day LW. He cattle. PHS estimates of h^2.
Mavrogenis *et al.*, 1978	Individual restricted feeding, complete diet from 205 days.	Constant age, 365 days	695		0.23(G)^1 0.41(G) 0.22	[0.26]^1 [0.38] [0.16]	0.21 -0.05		^{1}Point estimate then regression. He bulls from 2 farms. PHS estimate of h^2. OPR estimates of h^2.
Okantah, 1978	MLC CPT *ad lib.* feeding on complete grass/barley diet from 200 days.	Constant age, 400 days.	522 190	0.89 0.39	0.59 0.61	[0.36] [0.77]			He bulls, PHS estimate. South Devon bulls, PHS estimate.
Nelson and Kress, 1979	Field records in feedlot (bulls) or pasture (heifers).	Constant age, 156 to 178 days on test.	2113	0.40	0.38(W) 0.30(G)				AA bulls and heifers.
			1379	0.51	0.41(W) 0.26(G)				He bulls.
Collins-Lusweti, 1981	MLC CPT from 200 days.	Constant age, 400 days.	203	0.49	0.16(W) 0.63^1 0.12^1	[0.43]			^{1}Daily gain in early and late test. He bulls, PHS estimate.
			582	0.14	0.45(W) 0.38(G)	[0.48]			Pooled over 4 breeds.

TABLE 5.2 (continued): Literature estimates of heritability of performance traits in beef cattle.

Source	Management	End-point	No.	Heritability					Comments
				BW	GR	FCE	US	lean %	
Jensen and Andersen, 1982	Restricted feeding by age.	Constant age, 42 to 336 days.	2217		0.53	[0.45]	0.56^1		^{1}Adjusted to constant LW.
Koch *et al.*, 1982a	*Ad lib.* feeding conc. and corn silage.	Constant age, 224 days on test from about 200 days.	2410		0.55^1 0.55				^{1}Point estimate of gain, then regression. Wide range crossbred steers. PHS.
	Fed grain or silage/grain.		3088		0.24^1 0.25				He bulls, PHS estimates.
Koch *et al.*, 1982b	*Ad lib.* feeding conc. and corn silage.	Constant age (about 450 days?).	2453	0.43	0.07(W) 0.57(G)			0.63^1	^{1}% retail product. PHS estimates wide range crossbred steers.
Renand and Gaillard, 1982	Progeny testing station.	Constant age?	647-699	0.32	0.40(G) 0.32(Y)				Charolais cross young bulls, PHS estimates.
Preston and Willis, 1974*	Various	Various		0.38 n=54	0.27(W) n=35	[0.36] n=15		0.34^1 n=4	^{1}% first quality meat. ^{2}% edible meat.
					0.52(FG) n=56			0.40^2 n=2	
					0.70(FW) n=30			0.23 n=1	
Andersen *et al.*, 1977b*	Various	Various			0.50 n=11				Dual purpose breeds.
Woldehawariat *et al.*, 1977*	Various	Various		0.45 n=75	0.30(W) n=62	0.45^1 n=20			Weighted PHS or OPR estimates of h^2. ^{1}FCR, FCE or adjusted consumption.
					0.34(FG) n=43				
					0.30(PG) n=14				
					0.46(FF) n=36				
					0.44(FP) n=19				
Koch *et al.*, 1982b*	Various	Various						0.41^1 n=4	^{1}% retail product (actual or estimated from 4 joints)
Koch *et al.*, 1982c*	Various	Various		0.43 n=9	0.47(W) n=11	[0.58] n=3			
					0.39(G) n=10				

Heritabilities in square brackets refer to FCR not FCE; * Results from a literature survey.

TABLE 5.3: Literature estimates of phenotypic correlations amongst performance traits in cattle.

Source	Management	End-point	No. or df	Phenotypic correlations between:										Comments
				BW GR	BW FCE	BW US	BW lean%	GR FCE	GR US	GR lean%	FCE US	FCE lean%	US lean%	
Dinkel and Busch, 1973	Feedlot from 200 days. Hormone implanted.	Time constant at estimated group mean LW of 454 kg.	568							0.11(FG)[1] 0.15(FF)				[1] Wt of edible portion.
Dickerson *et al.*, 1974	Individual feeding postweaning.	Constant age	998-1036							0.71(G)[1]				[1] G with wt of lean retail product.
		Constant LW								-0.17(G)[1]				
Andersen *et al.*, 1977b	*Ad lib.* feeding indoors.	Constant LW 250 kg or 450 kg.	2330, 1011	0.24[1]	[0.27][1]			[0.89]		0.20		[0.28]		[1] LW at 15 days not BW.
Pabst *et al.*, 1977b	MLC pedigree recorded herds.	Constant age, 400 days.		0.25[1]										[1] 400 day LW, He cattle.
Mavrogenis *et al.*, 1978	Individual restricted feeding complete diet from 205 days.	Constant age, 365 days.	695					[0.34][1] [0.47]	0.10		[0.10]			[1] Point estimate, then regression.
Lewis and Jones, 1978	MLC CPT, *ad lib.* feeding on complete grass/barley diet from 181 kg.	Constant LW 408 kg.						[0.84]						Several dual-purpose breeds.
Moran and Holmes, 1978	MLC CPT *ad lib.* feeding on complete grass/barley diet.	Constant LW	116						0.08		[-0.18]			Mean of 3 breeds.
Steane *et al.*, 1978	MLC CPT, *ad lib.* feeding on complete grass/barley diet from 200 days.	Constant age, 400 days.	247						0.32[1]					[1] LW on day of scanning - different ages and LWs.
Okantah, 1978	MLC CPT from 200 days.	Constant age, 400 days.	522 190	0.06 0.04	[0.01] [0.21]			[0.36] [0.27]						Hereford bulls. South Devon bulls.
Nelson and Kress, 1979	Field records in feedlot (bulls) or pasture (heifers).	Constant age, 156-178 days on test.	2113	0.19										AA bulls and heifers.
			1379	0.22										He bulls.
Collins-Lusweti, 1981	MLC CPT from 200 days.	Constant age, 400 days	203	0.08[1] 0.12[1]	[0.03]			[0.74]						[1] Daily gain early and late test. He bulls.
			582	0.06[1] 0.04[1]	[0.05]			[0.71]						Pooled over 4 breeds.

TABLE 5.3 (continued): Literature estimates of phenotypic correlations amonst performance traits in cattle.

Source	Management	End-point	No. of df	Phenotypic correlations between: BW GR	BW FCE	BW US	BW lean%	GR FCE	GR US	GR lean%	FCE US	FCE lean%	US lean%	Comments
Jensen and Andersen, 1982	Restricted feeding by age.	Constant age, 42-336 days	2217					[0.94]	-0.14^1		$[-0.13]^1$			^{1}Ultrasonic measurements adjusted for LW.
Koch *et al.*, 1982b	*Ad lib*. feeding on conc. and corn silage.	Constant age (about 450 days?)	2453	0.12(W) 0.32(G)			0.05^1			$-0.29(W)^1$ -0.15(G)				^{1}% retail product wide range crossbred steers.
Renand and Gaillard, 1982	Progeny testing station.	Constant age?	647	0.19(G) 0.18(Y)										Charolais-cross young bulls.
Preston and Willis, 1974*	Various	Various		0.21(G) n=3				[0.44](G) n=8		$-0.16(G)^1$ $-0.21(FW)^1$				^{1}% first quality cuts.
Woldehawariat *et al.*, 1977*	Various	Various		0.43(FF) $n=13^1$				[-0.55] [0.50] [0.26]						^{1}Weighted average.

Correlations in square brackets refer to FCR not FCE, so signs have been reversed.

* Results from a literature survey.

TABLE 5.4: Literature estimates of genetic correlations amongst performance traits in cattle.

Source	Management	End-point	No. or df	Genetic correlations between:										Comments
				BW GR	BW FCE	BW US	BW lean%	GR FCE	GR US	GR lean%	FCE US	FCE lean%	US lean%	
Dinkel and Busch, 1973	Feedlot from 200 days. Hormone implanted.	Time constant at estimated group mean LW of 454 kg.	568							0.48(FG)^1 0.80(FF)				^{1}Wt of edible portion.
Dickerson *et al.*, 1974	Individual feeding post weaning.	Constant age	998-1036							0.85(G)^1				^{1}Wt of lean retail product.
		Constant LW								0.11(G)^1				
Baker *et al.*, 1975	Grassland; bull progeny test.	Constant age 15 months	1617, 663	-0.09(G)^1 0.11(G)^1 0.40(Y) 0.50(Y)										^{1}Not significant. 2 experimental farms. AA and He sires.
Andersen *et al.*, 1977b	*Ad lib.* feeding indoors.	Constant LW 250 kg or 450 kg.	2330, 1011	0.56^1	[0.72]^1			[0.95]		0.24		[0.34]		^{1}LW at 15 days not BW.
Pabst *et al.*, 1977b	MLC pedigree recorded herds.	Constant age, 400 days.	?	0.26^1										^{1}400 day LW. He cattle.
Mavrogenis *et al.*, 1978	Individual restricted feeding, complete diet from 205 days.	Constant age, 365 days.	695					[-0.23]^1 [0.06]	-0.11		[-0.14]			^{1}Point estimate, then regression.
Okantah, 1978	MLC CPT from 200 days.	Constant age, 400 days.	522 190	0.24 -0.37	[0.13] [0.26]			[0.35] [-0.15]						He bulls. South Devon bulls.
Nelson and Kress, 1979	Field records in feedlot (bulls) or pasture (heifers).	Constant age, 156-178 days on test.	2113	0.43										AA bulls and heifers.
			1379	0.74										He bulls.
Collins-Lusweti, 1981	MLC CPT from 200 days.	Constant age, 400 days	203	0.09^1 0.33^1	[-0.23]			[0.85]						^{1}Daily gain early and late test. He bulls.
			582	-0.72	[0.29]			[0.00]						Pooled over 4 breeds.
Jensen and Andersen, 1982	Restricted feeding by age.	Constant age, 42-336 days.	2217					[0.94]	-0.33^1		[-0.26]^1			^{1}Ultrasonic measurements adjusted for LW.
Koch *et al.*, 1982b	*Ad lib.* feeding conc. and corn silage.	Constant age, (about 450 days?).	2453	0.28(W) 0.61(G)			0.05^1			-0.03(W)^1 -0.13(G)				^{1}% retail product. Wide range crossbred steers.
Renand and Gaillard, 1982	Progeny testing station.	Constant age?	647	0.18(G) 0.27(Y)										Charolais-cross young bulls.

TABLE 5.4 (continued): Literature estimates of genetic correlations amongst performance traits in cattle.

Source	Management	End-point	No. or df	Genetic correlations between: BW GR	BW FCE	BW US	BW lean%	GR FCE	GR US	GR lean%	FCE US	FCE lean%	US lean%	Comments
Preston and Willis, 1974 *	Various	Various		0.36(G) n=3				[0.51](G) n=5		-0.45(G)[1] -0.25(FW)[1]				[1]% first quality cuts.
Woldehawariat *et al.*, 1977 *	Various	Various		0.60(FF) n=13[1]				[-0.31] [0.32] [0.41] [0.34]						[1]Weighted average.

Correlations in square brackets refer to FCR not FCE, so signs have been reversed.

* Results from a literature survey.

TABLE 5.5: Summary of literature estimates of heritability of performance traits.

	BW	GR	FCE	US	Lean %	KO %
Heritability	0.42	0.41	0.42	0.19	0.39	0.39
(No. estimates)	(149)	(354)	(45)	(5)	(14)	(11)[1]

[1] From Dinkel and Busch (1973), Preston and Willis (1974), Andersen *et al.* (1977b), Benyshek (1981).

TABLE 5.6: Summary of literature estimates of correlations amongst performance traits at a constant age.

	Correlations between:							
	BW GR	BW FCE	BW lean %	GR FCE	GR US	GR lean %	FCE US	US lean %
Genetic (No. estimates)	0.39 (30)	0.11 (4)	0.05 (1)	0.28 (15)	-0.11 (1)	-0.22 (4)	-0.14 (1)	
Phenotypic (No. estimates)	0.29 (27)	0.08 (4)	0.05 (1)	0.39 (17)	0.21 (2)	-0.20 (4)	0.10 (1)	-0.56 (12)[1]

[1] From Table 2.3 - some estimates adjusted for LW

weight. Genetic information on ultrasonic measurements was also scarce. The size and the sign of most correlations was variable, presumably because of differences in breed, sex, environment, diet, feeding regime and end-point. This indicates that correlated responses to selection will depend on the conditions of testing. Mean values of heritabilities are shown in Table 5.5. Mean values of correlations between traits from experiments ending at a constant age are shown in Table 5.6. Several authors presented results from literature surveys (marked *). Where possible, overlap of results was avoided, and mean estimates of parameters were weighted by the number of trials reviewed. The mean heritability of GR was calculated from heritabilities of preweaning and postweaning GR and live weight at constant ages. Heritabilities of FCE and correlations between FCE and GR relate to the postweaning period.

5.6 Predicted Results of Index Selection

Several authors have predicted responses to different selection indices. Dickerson, Künzi, Cundiff, Koch, Arthaud and Gregory (1974) combined live weight, postweaning food consumption and backfat measurements to predict efficiency. This was defined as the value of retail cuts, adjusted for marbling score, less feed and time variable costs from 200 days to either 410 kg slaughter weight (E1), or a constant age at slaughter (E3). Accuracy of index selection for E1 was maximum (R = 0.45) when the index included 200 day weight, postweaning GR and backfat. For E3 the best measurements were yearling weight and backfat (R = 0.59). The authors expected potential improvement in efficiency to be about twice as great on an age-constant as on a weight-constant basis. A third measure of efficiency (EH) was defined to include effects of calf mortality, reproduction and cow size (Table 5.7). Restricting genetic increases in birth weight was detrimental to individual animal performance, but overall herd efficiency was improved. Foulley (1976) also considered the effects of restricting increases in birth weight on overall genetic progress. In France specialised sire lines have been selected for ease of calving (Vissac *et al.*, 1982).

Andersen (1978) presented results based on genetic parameters for growth and carcass traits in Danish dual-purpose cattle. Restricting increases in birth weight in the index generally reduced cow mature weight, and depressed the genetic response in GR. This depression was minimised by restricting both birth weight and mature weight, and including gestation length of the bull in the index.

Koch, Cundiff and Gregory (1982b) predicted responses in carcass traits, at constant age or weight, following one standard deviation of selection on various growth and carcass traits. Generally, they expected selection for gain to increase fatness at a constant age, but decrease fatness at a constant weight. Selection for retail product weight was expected to produce a greater reduction in fatness at a constant weight than at a constant age (Table 5.8).

5.7 Performance Testing

The objective of any improvement programme is to identify and breed from animals with the highest breeding value for specified traits. When traits can be measured on the live animal, and are reasonably heritable, genetic progress may be more rapid using individual selection rather than progeny testing. The loss in accuracy from individual selection is frequently offset by a reduced generation interval and increased selection intensity (Dickerson and Hazel, 1944; Allen and

TABLE 5.7: Expected genetic changes from selection (ΔG) for weight constant (E1) or for age constant efficiency (E3 and EH)[1]. (Adapted from Dickerson *et al*., 1974.)

Trait	Initial mean	ΔG from index selection for: E1	E3	EH
Birth weight (kg)	34.9	0.5	-	0.4
Yearling weight (kg)	401.0	14.9	16.3	14.7
Mature cow weight (kg)	507.0	8.5	13.9	10.7
Trimmed retail product (kg)	152.6	0.8	6.3	-
E1 ($)	186.1	4.6	-	-
E3 ($)	214.0	-	8.9	8.1
EH ($)	112.8	4.6	5.8	6.2

[1] Per generation with mean selection differential for parents of one standard deviation in each index.

TABLE 5.8: Expected responses to one standard deviation of selection for (1) GR to weaning, (2) GR in feedlot, (3) side weight, (4) retail product weight, (5) retail product percentage, or (6) reduced fat thickness. (After Koch *et al.*, 1982b).

Trait	Regime[1]	Selection criteria and (standard deviations) 1 (96 g)	 2 (117 g)	 3 (12 kg)	 4 (8.3 kg)	 5 (3.3%)	 6 (-3.4 mm)
Side weight (kg)	A	1.52	5.30	5.17	4.87	-0.69	-0.40
Retail product							
weight (kg)	A	1.03	3.48	3.35	4.80	2.30	1.37
	W	0.33	1.03	0.96	2.56	2.62	1.56
percentage	A	-0.02	-0.25	-0.19	0.91	2.05	1.23
	W	0.24	0.66	0.70	1.74	1.94	1.16
Fat trim							
weight (kg)	A	0.37	1.33	1.29	-0.40	-3.17	-2.08
	W	-0.40	-1.26	-1.23	-2.78	-2.83	-1.88
percentage	A	0.06	0.26	0.24	-0.94	-2.19	-1.41
	W	-0.28	-0.89	-0.87	-1.99	-2.04	-1.32
Fat thickness (mm)	A	0.02	0.08	0.11	-0.56	-1.26	-1.37
	W	-0.23	-0.79	-0.74	-1.36	-1.15	-1.31

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[1] Data adjusted to a constant age (A) or a constant side weight (W).

Kilkenny, 1980; Falconer, 1981). Accuracy can be improved further by adding information from other relatives (Willham, 1982a). Alternatively, performance test results can be used to screen bulls for subsequent progeny testing (MLC, 1971; Kräusslich, 1974; Baker, Carter and Beatson, 1975; Foulley, 1976). Morris, Jones and Hopkins (1980) compared the theoretical rates of progress from individual selection versus a co-operative progeny testing scheme after screening on individual performance. In this special case, the most rapid genetic progress was expected from progeny testing. However, the efficiency of individual selection programmes could be greatly increased by using superovulation and embryo transfer. Land and Hill (1975) suggested that it should be possible to achieve about twice the response of a conventional performance testing programme for GR, by using such techniques.

Research on central performance testing began in the US in the 1930's. The technique was first used in beef improvement programmes in the late 1940's in the US (Baker, 1967) and in 1957 in the UK (Baker, 1965). Since that time, central testing has become important in many countries (MLC, 1971; Lewis and Allen, 1974; Lindhé, 1974; Dalton and Morris, 1978; Andersen, de Baerdemaeker, Bittante, Bonaiti, Colleau, Fimland, Jansen, Lewis, Politiek, Seeland, Teehan and Werkmeister, 1981; Tong, 1982).

In principle, central testing permits accurate comparison of animals from different herds, under uniform conditions. This is especially useful in countries where the small size and the wide calving spread of breeding herds limits independent genetic improvement (Özkütük and Bichard, 1977; Dalton and Morris, 1978; Kilkenny, Guy and Cook, 1980).

Dalton and Morris (1978) drew attention to the lack of data comparing the rank order of bulls in a central test with rank order from a progeny test, and questioned the value of central testing in New Zealand (NZ). The NZ Dairy Board therefore progeny tested 66 Hereford bulls, representatively sampled from a total of 100 performance tested bulls (Wickham, 1977; Baker, Wickham and Morris, 1982). Semen was used on Jersey or Jersey x Friesian cows in 60 to 70 herds, to produce about 20 progeny per sire. These were reared either artificially or on foster dams, and then tested in one location from about four months to 18 months of age. The correlation between performance test and progeny test results for final weight was 0.15, which was not significantly different from zero, and significantly different from the expected value of 0.48. The effective heritability from offspring-sire regression was 0.06, which was significantly different from the expected value of 0.35 to 0.45. Sires were quite old at the start of their performance test (average 297 days) and both sires and progeny were tested at pasture, but the result still may have implications for central testing in Europe and elsewhere. De Roo and Fimland (1983) analysed performance and progeny test results from sons of selected AI sires used in Norway. The sons were performance tested from 90 to 360 days of age, and their progeny were slaughtered at 15, 16 or 17 months of age. Genetic correlations between bulls' own GR or final test weight, and progeny slaughter weight were 0.38 and 0.34. This indicates that performance testing will be effective for improving growth traits, if bulls are tested from an early age.

British data on the accuracy of performance testing are limited. Lessels and Francis (1968) tested an average of 12 crossbred progeny from each of 39 performance tested Hereford bulls. The overall regression of progeny daily gain on sire daily gain was 0.21 ± 0.04, giving an effective heritability of 0.42 (Smith, Steane and Jordan, 1979). However, bulls were reared uniformly from a younger age than in current UK central tests (Baker, 1965; MLC, 1983) which may explain the fairly high effective heritability.

Smith *et al*. (1979) calculated regressions of progeny GR and age at 464 kg on 400 day weight of 63 Hereford sires. Thirteen of the sires had been performance tested in MLC central stations. Offspring-sire regressions for these bulls were very low, but had high standard errors. Adding information from the remaining bulls, which had only farm weight records, produced low estimates of effective heritability of 400 day weight (0.16 to 0.35 ± 0.09 to 0.17).

The low accuracy of central testing reported by the NZ workers, and the low estimates of heritability from field data may be attributed to environmental variation. There are several reports of negative environmental correlations between pre-test GR and GR on test, whereas genetic correlations are positive. The combination of these two effects often leads to low or negative phenotypic correlations, indicating some degree of compensatory growth on test (Willis and Preston, 1970; Kennedy and Henderson, 1975; Collins-Lusweti, 1981; Tong, 1982).

5.8 Environmental Effects on Test Results

Animals which have had their growth restricted by inadequate nutrition generally grow faster than unrestricted animals when they are subsequently given a high plane of nutrition (Wilson and Osbourn, 1960; Allden, 1970; Morgan, 1972; Lopez Saubidet and Verde, 1976; Horton and Holmes, 1978). The degree of compensation depends on the animal's age, the severity and duration of the restriction and duration of realimentation. Everitt and Jury (1977) suggested that differences in nutrition induced soon after birth and applied for around 3 months, would have a lasting effect on growth. Dalton and Morris (1978) summarised much of the NZ literature on compensatory growth and found that in many cases animals failed to compensate fully by the end of a trial. They suggested that variable degrees of compensation would affect the correlation between test performance and the breeding objective.

Compensatory growth is associated with increased food intake and when compared at a fixed age or a fixed immature weight, compensating animals may show increased FCE. This advantage usually disappears when the period of restriction as well as the period of compensation is taken into account (Wilkinson and Tayler, 1973). This is an added complication in central tests where FCE is recorded.

There are several environmental effects which may give rise to compensatory growth when animals are brought to a central location and fed a high energy diet.

5.8.1 Season of birth

Season of birth was a significant source of variation in most performance traits for most breeds in MLC central test data analysed by Okantah (1978). The effect accounted for up to about 10% of the variation in growth and efficiency traits (Okantah, 1978; Collins-Lusweti, 1981). In Britain, spring-born calves generally have higher weaning weights than autumn-born calves. This may be due to the poorer nutrition of dams and lower health status of calves, housed during winter. There is, however, quite large variation in performance from one month of birth to another, within a season. This variation is partly due to differences in the quality and quantity of herbage available, which can affect the calf's GR either directly or via the dam's milk supply. Generally, calves which have suffered seasonal restriction of GR will compensate, so season of birth has a much lower effect on 400 than 200 day weight (Pabst, Kilkenny and Langholz, 1977a; Kilkenny *et al.*, 1980). Creep feeding may reduce seasonal effects on calf GR (Marlowe and Gaines, 1958).

5.8.2 Herd effects

Herd of origin can have a very important effect on station and farm performance data, though in some cases it is confounded with the effects of sire and rearing method. Okantah (1978) found that herd effects were highly significant, commonly accounting for up to 55% of the total variation in growth and efficiency traits on test. Similar results were obtained by Collins-Lusweti (1981), though herd effects were generally less important in centrally tested bulls than in farm recorded bulls.

The Milk Marketing Board (1966) recorded weights of over 3900 crossbred cattle from five sire breeds, in 283 herds. About 53% of the variation in 360 day weight was accounted for by farm effects, whereas sire and sex together accounted for only about 4% of the variation. Similar results were reported in NZ by Everitt, Evans and Franks (1969). Estimates of between herd variance were lower in the report by Kilkenny *et al.* (1980). (See also Okantah and Curran, 1982).

5.8.3 Rearing method

Okantah (1978) reported that the method of suckling (dam, nurse cow or both) had a significant effect on test growth and live weight of Charolais bulls, accounting for up to 5.3% of the variation. In other breeds, the effect was usually non-significant. The effects of creep feeding also varied from breed to breed, in most cases accounting for less than 6% of the variation in performance (see also Okantah and Curran, 1982). Pabst *et al.* (1977a) found that preweaning management had a significant effect on 400 day weight of several beef breeds. Generally, differences in weight at weaning still remained at 400 days of age. Kilkenny *et al.* (1980) reported a marked change in bull management systems in Britain in recent years, with very few bulls now having access to a nurse cow.

5.8.4 *Maternal effects*

As well as affecting calf performance through the genes transmitted, the dam has an influence through the intra-uterine and preweaning environment provided (Koch and Clark, 1955c). Thus dam age, live weight and milk yield, which are inter-related and have both genetic and environmental components, can all influence calf performance (Koch and Clark, 1955a,b; Drewry, Brown and Honea, 1959; Brumby, Walker and Gallagher, 1963; Marlowe, Mast and Schalles, 1965; Singh, Schalles, Smith and Kessler, 1970). Dam age can have highly significant effects on performance, but the persistence of the effect is very variable (Brown, 1960; Brinks, Clark, Kieffer and Quesenberry, 1962b; Schalles and Marlowe, 1967; Pabst *et al.*, 1977a; Kilkenny *et al.*, 1980). Nicoll and Rae (1978) found that dam age still had a highly significant effect on 550 day weight of Hereford and Angus cattle in NZ. In Australia, Raymond, Chambers and Hammond (1982) reported that dam age was an important influence on weight of Angus heifers at 420 days of age, accounting for 7.8% of the variation. However, by 550 days of age the effect was not important.

Generally, performance increases with dam age, up to an optimum of 4 to 8 years of age, after which it declines. Woldehawariat, Talamantes, Petty and Cartwright (1977) summarised the many estimates of correction factors for age of dam. Estimates of constants for older dams may be biased if they have remained in the herd because of genetic superiority (Koch and Clark, 1955a; Swiger, 1961; Pabst *et al.*, 1977a).

5.9 Maximising the Accuracy of Central Testing

In addition to the sources of environmental variation discussed, there may be differences in average performance between years and between testing stations (Batra and Wilton, 1972; Wilton and Batra, 1972; Pabst *et al.*, 1977a; Okantah, 1978; Kilkenny *et al.*, 1980). Results should only be compared within station-year-seasons, or compared to a rolling station average.

The influence of pre-test environment on test results has long been recognised as a potential problem (Baker, 1965). There is often a wide range in the ages and weights of bulls at the start of test (e.g. Dalton, 1976), and this can significantly affect results (Tong, 1982). Ideally, animals should enter test in large batches, soon after birth. In dual-purpose breeds, where calves are reared artificially, this presents no problem. However, in pure beef breeds calves are rarely weaned at less than six months of age (Lewis and Allen, 1974; Dalton and Morris, 1978; Andersen *et al.*, 1981). Artificial rearing is generally not acceptable to breeders because of the high cost, concern that the dam's maternal ability is not expressed (though this is not important in terminal sire breeds) and because of poorer GR of bucket reared calves, compared to suckled calves (Everitt, Phillips and Whiteman, 1968; Dalton and Morris, 1978).

Many recommendations for reducing pre-test effects have been made. These include: 1) starting test at a younger age; 2) provision of a high energy diet during a 'settling-in' period, to allow compensatory growth; 3) selecting animals on final weight rather than GR on test; and 4) measuring FCE over a constant weight interval (Rollins, Carroll, Pollock and Kudoda, 1962; Carter, 1971; MLC, 1971; Kräusslich, 1974; Lewis and Allen, 1974; Dalton and Morris, 1978; Andersen *et al.*, 1981).

In practice, final weight may be highly correlated with earlier weights, which seems to obviate the need for testing. However, final weight may be less affected by pre-test management (MLC, 1971). Pre-selection of bulls for testing on their early GR may be an effective compromise (Willis and Preston, 1970; MLC, 1983).

5.10 Testing Systems

The test regime and end-point chosen for the comparison of animals is likely to have an effect on the ranking of animals and the response to selection (Wood and Hodges, 1976; Falconer, 1977; Smith and Fowler, 1978). In Europe most beef performance tests last for at least five months, but there is a wide variety of feeding regimes (Andersen *et al*., 1981).

In Britain, beef bulls start performance test at 150 to 190 days of age and finish test at about 400 days of age (Allen and Kilkenny, 1980; Kempster *et al*., 1982c; MLC, 1983). This system has several adminiistrative advantages and is relatively free from measurement error. Also, it probably equates well with extensive beef systems linked to the seasonal pattern of grass growth, which have a target age for slaughter. The bias from comparing animals at equal ages or weights, rather than at equal degrees of maturity, is less serious within than between breeds. However, it may be advisable to alter the age at the end of test so that different breeds finish test at about the same degree of maturity (preferably at optimum fatness for a given market).

There is ample evidence of genotype x environment interactions in cattle, involving a change in the ranking of breeds on different feeding levels (Andersen, 1978; Béranger, 1978; Langholz, 1978; Geay and Robelin, 1979). Additionally, Andersen and Andersen (1974) and

Liboriussen, Neimann-Sorensen and Andersen (1977) detected sire x final age, sire x final weight and sire x feeding level interactions in growth traits when there were large differences in final age, final weight or feeding level. Wood and Hodges (1976) tested the crossbred progeny of 32 Hereford bulls, on both grass-based and barley-based feeding regimes. They reported differences in the rank order of sires for GR and some carcass traits, on the two testing systems. Other authors have failed to detect sire x feeding level interactions (Ahlschwede, Dillard, Legates and Robison, 1969; others cited by Langholz, 1978). Performance tests could perhaps be improved if the diet and test end-point were tailored to suit the breed, according to the system in which bulls' progeny will be reared.

Fowler (1982) reported that lean tissue food conversion in pigs was relatively insensitive to the level of feeding, but economic efficiency always improved at higher levels of feeding. Whittemore (1978) suggested that the rate of fat deposition was controlled extrinsically by the ration scale, and intrinsically by factors like the minimum ratio of fat : lean and appetite in relation to lean growth potential (see also Geay and Robelin, 1979). He also suggested that UK domestic animals may have been prevented from reaching their 'ceiling' rates of protein gain on test because of the ration used or because of restricted appetite. Animals may have been selected for increased appetite rather than the intrinsic ability to grow lean. According to Whittemore, selection for LGR would be best achieved under high level feeding.

Andersen *et al*. (1981) also concluded that where lean tissue growth capacity, appetite and FCE were part of the selection objective in beef production, tests should be on *ad libitum* feeding.

5.11 Alternatives to Central Testing

In 1971 an MLC Scientific Study Group considered that progeny testing *per se* had a strictly limited role in beef improvement programmes (MLC, 1971). They suggested that central testing should be more closely linked to specific breeding programmes, and proposed MLC support for co-operative schemes using young tested bulls. This has been achieved to some extent through the MLC Young Bull Proving Schemes (Allen, 1974). However, there are several problems with the schemes: 1) use of AI has not been satisfactory; 2) low numbers of progeny and contemporaries; and 3) breeders have often used the young bulls on their poorest cows (Kilkenny *et al.*, 1980).

Another recommendation of the Study Group (which has not been adopted) was that MLC should establish its own breeding herd to provide selected bulls for AI. The report also suggested that performance testing dairy sires for beef characteristics would be useful if costs could be reduced.

One method of overcoming the problem of small herd size is the formation of Group Breeding Schemes. Group Breeding Schemes were developed in NZ in the late 1960's. Basic principles of these schemes (summarised by Smith [1976] and Parker and Rae [1982]) are: 1) co-operation among breeders in running a jointly owned nucleus to produce breeding males; 2) a two-way flow of tested stock - males going from the nucleus to the breeders, and females going from breeders to the nucleus; and 3) selection on records for commercially important traits. The most important genetic advantages of Group Breeding Schemes are large numbers of animals, reduced inbreeding, intense selection, short generations and testing under commercial conditions. Currently there are four sheep Group Breeding Schemes and a Welsh Black cattle Group Breeding Scheme in the UK (Williams, 1982).

Reference sires can also form the basis of co-operative breeding schemes. In a theoretical study, Morris *et al.* (1980) compared the relative efficiency of individual selection for yearling weight with reference sire progeny test schemes. They assumed that 25 co-operating breeders would each use semen from two selected progeny-tested reference sires, on half of their herd. Home-bred bulls can then be compared with progeny of the reference sires, the best bulls being selected for progeny testing in co-operating herds. Reference sires are then replaced by the best progeny tested bulls. The authors concluded that annual genetic progress would be 26 to 38% higher using this scheme rather than individual selection. Morris and Baker (1982) reported results from the NZ Angus Sire Reference Scheme which follows the theory of Morris *et al.* (1980). Reference sire breeding values for weaning and yearling weights were 1.8 kg and 5.7 kg above the mean breeding value of all AI bulls. Similar schemes are also operating in the USA (Allen, 1979; Willham, 1979, 1982b) and in France (Ménissier, Foulley and Sapa, 1982).

5.12 Conclusions

1. The most effective way of improving GR or LGR is by breed substitution with large European breeds.
2. Breed substitution may not increase *herd* productivity or efficiency.
3. Crossbreeding and the use of large terminal sires can increase herd output and efficiency, but again there is a trade-off: sire breeds with the highest LGR also increase the incidence of calving difficulty and perinatal mortality.

4. When compared at estimated equal degrees of maturity, breed differences in FCE or lean tissue food conversion efficiency (LFCE) are small. There is some evidence that early maturing breeds are most efficient, but comparison at equal subcutaneous fat levels may be biased.
5. FCE and LFCE could be improved most effectively by selection within the most efficient breeds.
6. The generalised theory of growth which explains many of the differences between species and breeds may not explain changes brought about by within-breed selection.
7. More information is needed on selecting livestock for improved FCE, selection for rapid early growth without increasing mature size, and direct selection for reduced maintenance requirements.
8. Correlated responses to selection must be monitored, especially those in calving difficulty, mature size, maintenance costs, fertility and meat quality.
9. Unless bulls are performance tested from a young age, and under controlled conditions, results may be of little value.
10. Group Breeding Schemes or Sire Reference Schemes may provide useful alternatives to central testing.

CHAPTER VI

Environmental Effects on Bull Performance

6.1 Introduction

In the previous chapter it was shown that environmental factors, such as season or date of birth, and age of dam, often have significant effects on bull performance in central tests. One of the objectives of the ABRO Hereford project was to assess the value of artificial rearing or early weaning in reducing this environmental variation in performance. This chapter is concerned with the effects of rearing treatment, date of birth and dam age on the performance of bulls tested in the first four years of the experiment. The description of animals, data and methods of analysis applies both to this chapter and the following chapter.

6.2 Materials and Methods

6.2.1 Animals

A total of 235 bulls, born in the Hereford experiment between 1978 and 1981, had data available for analysis (Table 6.1). The herd comprised two selection lines and a smaller genetic control line. Selection criteria were lean growth rate (LGR) from birth to 400 days of age and lean food conversion efficiency (LFCE) from 200 to 400 days of age. Five bulls were selected for mating from each selection line, in each of the first two years of the experiment (bulls born in 1978 and 1979 and tested in 1979 and 1980). Bulls which ranked in the top group for both LGR and LFCE were assigned to the line in which their rank was highest. Each selected bull was then assigned at random to a group of cows for mating, with a check that no close matings occurred.

In 1981, each of the selection lines and the control line were divided into three replicates. At the end of performance tests in 1981 and 1982 two bulls were selected within each replicate, in each of the two lines (i.e. six bulls per year in the LGR line and six bulls per year

TABLE 6.1: Number of bulls in analysis.

Year of birth	Test completed	Age at weaning (days) 0	84	168	Total number
1978	1979	16	15	18	49
1979	1980	14	23	19	56
1980	1981	21	26	28	75
1981	1982	18	16	21	55
Total number		69	80	86	235

in the LFCE line). These bulls were then assigned to groups of cows for mating, within replicates. Control line cows were inseminated with semen collected from bulls born in the herd in 1978 and 1979.

Bulls born in 1980 and 1981 were the progeny of bulls tested in 1979 and 1980. However, at this early stage in the selection experiment there was no marked difference between lines in the means or variances of performance traits. Data were therefore pooled over lines for analysis.

6.2.2 Rearing treatments

All bull calves born in the herd were randomly allocated to one of three rearing treatments. The first rearing treatment involved weaning soon after birth, followed by tube- or bucket-feeding of pooled colostrum for two days. Calves were penned indoors in small groups and fed generously (1978-1980) or *ad libitum* (1981 onwards) on milk replacer, until 84 days of age. Acidified milk replacer was used from 1981. Calf-rearing concentrates and hay were provided from two weeks of age. The second and third rearing treatments involved single suckling on the calf's own dam, with access to creep feed. Weaning ages in these rearing treatments were 84 and 168 days of age. After weaning, all bull calves were introduced to the test diet and trained to use Calan-Broadbent electronic feed gates. The performance test started when bulls were about 200 days of age and ended when bulls were about 400 days of age.

6.2.3 Data

The following data were available for 235 bulls:

1. Live weight (LW) at four-weekly intervals from birth to about 400 days of age.

2. Food intakes during four-weekly intervals from about 200 to 400 days of age.
3. Estimated carcass lean % at 400 days of age (ECL %, see Section 4.4).

A total of 21 animals had missing data. Missing values for live weight were interpolated or extrapolated from the bull's own growth curve. Missing values of food intake were predicted from within-animal multiple regression on the three previous monthly food intakes. Similarly, missing ultrasonic fat areas were replaced by regression of standardised fat area (Section 4.4) on the standardised deviation of live weight from the mean live weight (within year). To examine the effects of replacing missing data the main analysis was run including or excluding the 21 animals with replaced values. On average, correlations between performance traits differed only in the third decimal place, so further discussion applies to data including replaced values.

In these data, single 'point' estimates of live weight were almost perfectly correlated with estimates from within-animal regressions of weight on age. For simplicity point estimates were used in all calculations. To reduce auto-correlation, independent estimates of live weight and food intake were used to calculate GR, RGR or FCE in successive age intervals. For example, pre-test GR was calculated from birth to 170 days of age, and GR on test was calculated from live weight at 198 and 393 days of age. In the following discussion, however, ages are rounded to the nearest 100 days for convenience.

RGR was calculated as:

$$\frac{\ln LW_2 - \ln LW_1}{t_2 - t_1}$$

where:

ln = natural logarithm;
t = age at weighing.

FCE was calculated as live weight gain in a given age interval divided by cumulated food intake in that interval. LGR was estimated as:

ECL % x KO % x GR from birth to 400 days

In the absence of a good *in vivo* predictor, the mean killing-out (KO) % of bulls at 400 days was used for each animal (57% in data in Chapter IV). Estimating LGR in this way assumes that:

1. killing-out % is constant for all bulls at 400 days of age;
2. killing-out % is the same at birth and 400 days of age;
3. carcass lean % is the same at birth and 400 days of age (in fact, it probably decreases slightly, but there are no satisfactory *in vivo* estimation techniques for young calves).

Because birth weight is a relatively small proportion of weight at 400 days of age, errors due to assumptions 2 and 3 are probably small. Effects of assumption 1 are discussed in Chapter VIII.

LFCE was calculated as:

ECL % x KO % x FCE from 200 to 400 days of age.

In addition to assumption 1 above, this assumes:

1. killing-out % is the same at 200 and 400 days of age;
2. carcass lean % is the same at 200 and 400 days of age.

6.2.4 Statistical methods

Distributions of GR and FCE in different age intervals were plotted for bulls from each rearing treatment in each year. All distributions appeared normal. Additionally, variance-covariance matrices of these traits were tested for heterogeneity using a multivariate generalisation of the Bartlett test (Morrison, 1976). There was no consistent heterogeneity between rearing treatments or between years, though a few tests approached significance. Data were therefore analysed by least-squares analysis of variance (Harvey, 1977).

In each of the four years most calves were born during a two-month spring calving period. Three statistical models were compared to account for date of birth. In the first model the calving period was divided into 'early' and 'late' in each year, giving eight year-seasons which were fitted as fixed effects. In the second model date of birth was fitted as a linear or quadratic regression over all years. In the third model date of birth was fitted as a linear or quadratic regression within-years.

The proportion of variation accounted for by the three models (R^2 values), adjusted for degrees of freedom, were compared for 27 performance traits. Generally, fitting year-season of birth as a fixed effect accounted for as much or more of the variation in performance than fitting linear or quadratic regressions. This may be explained by the inconsistent effects of early or late calving in different years.

Dam age was fitted as a fixed effect with five classes (dams of two, three, four and five years of age or six and more years of age). Live weight and food intake were usually recorded ± 2 days from 'target' ages, and fitting deviation from target age as a regression failed to reduce variation in performance. For the 27 traits examined, there were fewer significant first-order interactions than expected by chance, so the model used was:

$$Y_{ij} = u + S_i + D_j + e_{ij}$$

where:

Y_{ij} = the individual animal's performance
u = the overall mean
S_i = fixed effect of year-season of birth
D_j = fixed effect of dam age
e_{ij} = error term, assumed random.

To estimate the effects of year-season or dam age separately, either D or S was dropped from the model. Differences between least-squares means of traits in the three rearing treatments were tested by the t-test at the 0.01 level of significance (Snedecor and Cochran, 1980), using the appropriate standard error of the difference. Differences between residual variances were tested using the F-test (Snedecor and Cochran, 1980), at the 0.01 level of significance. Conservative significance levels were chosen to account for the number of comparisons between rearing treatments.

6.3 Results

6.3.1 Live weight, food intake and efficiency

Figures 6.1 and 6.2 show the mean live weight and cumulated food intake at different ages for bulls from the three rearing treatments. Artificially reared bulls had very low early GR, and had lower live weight at all ages than bulls weaned at 84 or 168 days of age. Bulls weaned at 84 days of age had similar or slightly higher live weight at all ages than bulls weaned at 168 days.

Cumulated food intake from 200 to 400 days of age was similar for bulls weaned at 84 and 168 days of age; both groups had higher total food intake than bulls weaned at birth. Cumulated food intake was also examined at monthly intervals between 200 and 400 days of age. Data were first adjusted for year-season and dam age, then analysed by least-squares analysis of variance with animals nested within rearing treatment. Variation between animals was removed by absorption and quadratic partial regressions of food intake on age or live weight, or age together with weight were then fitted separately, within animals, for each rearing treatment. Regressions for the different rearing treatments were tested for significance against the within-animal error mean square (Harvey, 1977, model 3; see Table 6.2).

Quadratic regressions of food intake on age and live weight were highly significant. There were also significant differences between regressions for the different rearing treatments ($P < 0.05$). Quadratic regressions of food intake on age and live weight together were significant ($P < 0.01$), but did not differ between rearing treatments. This indicates that differences in food intake between rearing treatments were due to differences in weight at the same age.

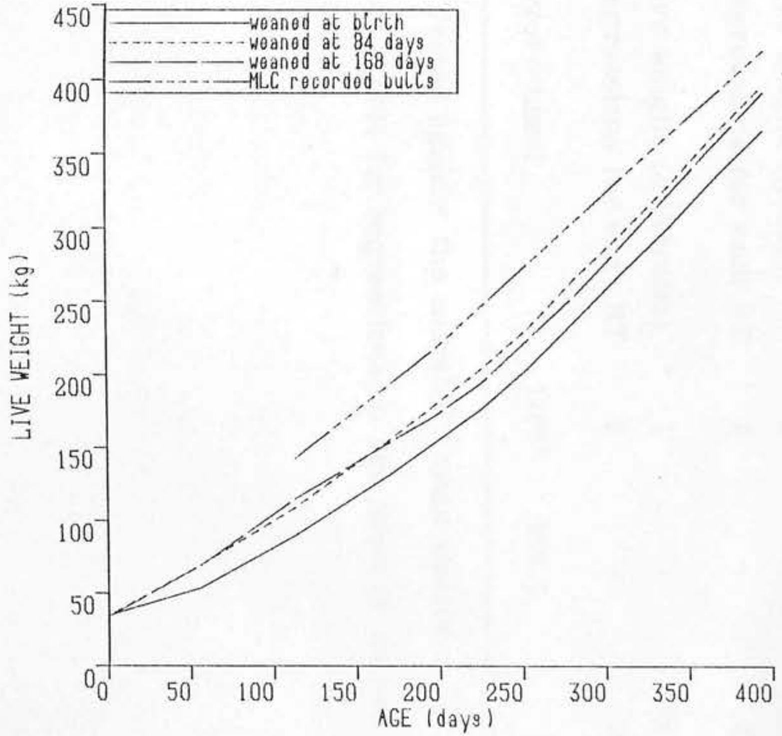

FIGURE 6.1: Live weight gain of bulls from three rearing treatments, compared to MLC on-farm recorded Hereford bulls.

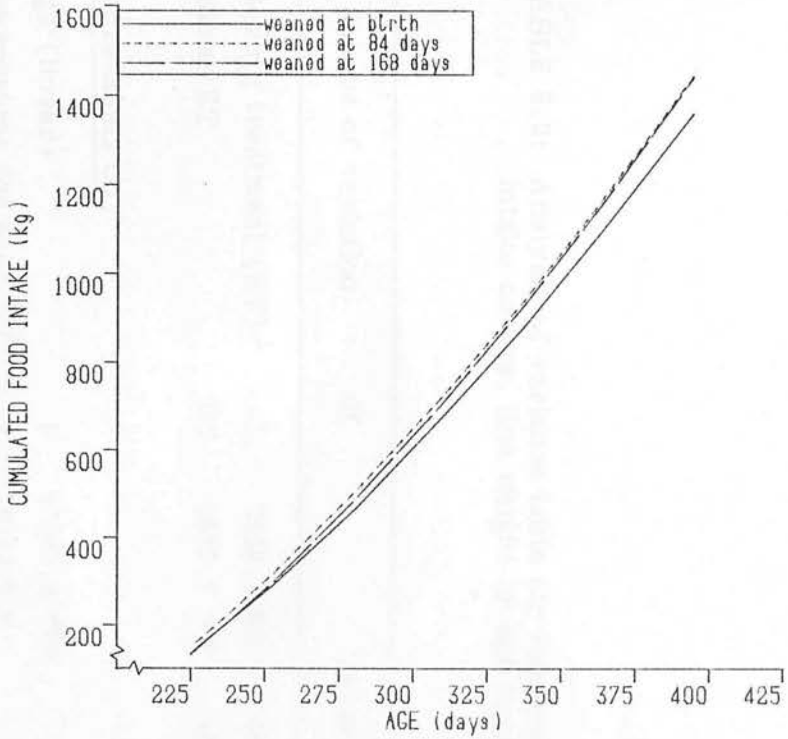

FIGURE 6.2: Cumulated food intake from 200 days of age, for bulls from three rearing treatments.

TABLE 6.2: Analysis of variance table for regressions of monthly food intake on age, live weight or age together with live weight.

Source of variation	df	Mean square		
Rearing treatment (RT)[1]	2	2558.4 NS	4563.7 NS	2531.7 NS
Animal/RT	232	3699.7 ***	1931.6 ***	1826.0 ***
Regressions on:				
Age (linear)	1	87682.6 ***	-	22071.9 ***
Regressions for each RT	2	2134.9 *	-	561.5 NS
Age (quadratic)	1	29436.4 ***	-	16050.2 ***
Regressions for each RT	2	1744.6 *	-	1212.7 NS
Live weight (linear)	1	-	204408.3 ***	13416.3 ***
Regressions for each RT	2	-	2814.3 **	1523.7 NS
Live weight (quadratic)	1	-	46885.2 ***	3811.8 **
Regressions for each RT	2	-	2093.2 *	762.8 NS
Error/animal	1398[2]	562.1	565.1	547.7

[1] Tested against the animal/RT mean square.

[2] df = 1404 for regressions on age alone or on live weight alone.

Residual standard deviations (RSD) were similar for regressions on age, on live weight or on age together with weight (Table 6.3). Residual standard deviations were also very similar in the different rearing treatments. Artificially reared bulls, which had the lowest pre-test GR, had lower food intake than other bulls at all ages. However, food intake was similar for bulls from each rearing treatment at equal live weights over 250 kg. At equal lighter weights, artificially reared bulls had slightly higher food intake than bulls weaned at 84 or 168 days of age (Figures 6.3 and 6.4). As a consequence of this and the lower live weight but similar GR on test, artificially reared bulls had higher cumulated FCE than other bulls, especially between 200 and 300 days of age (Figure 6.5).

6.3.2 Variation due to year-season and dam age

1) Duration of effects on live weight, food intake and FCE

There was no clear difference between rearing treatments in the effect of year-season of birth on live weight. However, the effect seemed most important at early ages, accounting for up to 31% of the variation in live weight (Table A6.1, Figure 6.6). The effect probably operates via the dam, causing environmental variation in calf birth weight and (for calves reared on their dam) in milk supply. Year-season had a significant effect on cumulated food intake of artificially reared bulls, accounting for up to 29% of the variation. The effect was much less important in bulls weaned at 84 and 168 days of age (Table A6.1, Figure 6.7).

Dam age had a highly significant effect on birth weight, but no other weights, in bulls weaned at birth (Table A6.2, Figure 6.8). In bulls weaned at 84 days of age, dam age had a highly significant effect on live weights up to 113 days of age, but no later weights. In contrast,

TABLE 6.3: Variation in monthly food intake (from 200 to 400 days of age) accounted for by quadratic regressions on age, live weight or both age and live weight.

Quadratic regression	Age at weaning (days)	Food intake (kg) mean	Food intake (kg) SD	Residual SD (kg)	R^2
Age	0	194.4	46.0	21.9	0.52
	84	206.5	45.7	23.9	0.48
	168	202.6	50.8	24.9	0.51
Live weight	0			21.8	0.53
	84			24.2	0.47
	168			24.8	0.51
Age, live weight	0			21.6	0.53
	84			23.8	0.48
	168			24.4	0.52

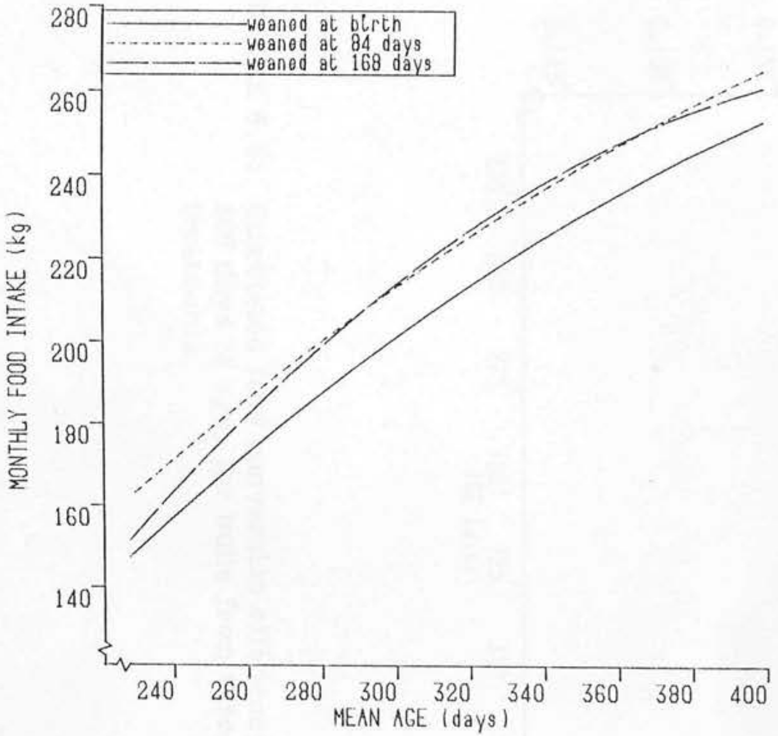

FIGURE 6.3: Fitted quadratic regressions of monthly food intake on age, for bulls from three rearing treatments.

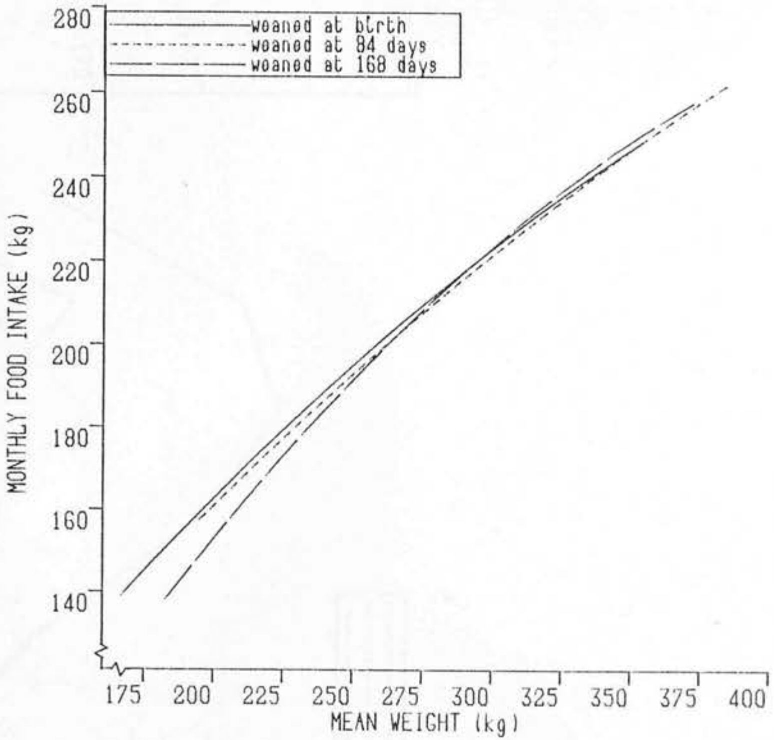

FIGURE 6.4: Fitted quadratic regressions of monthly food intake on live weight, for bulls from three rearing treatments.

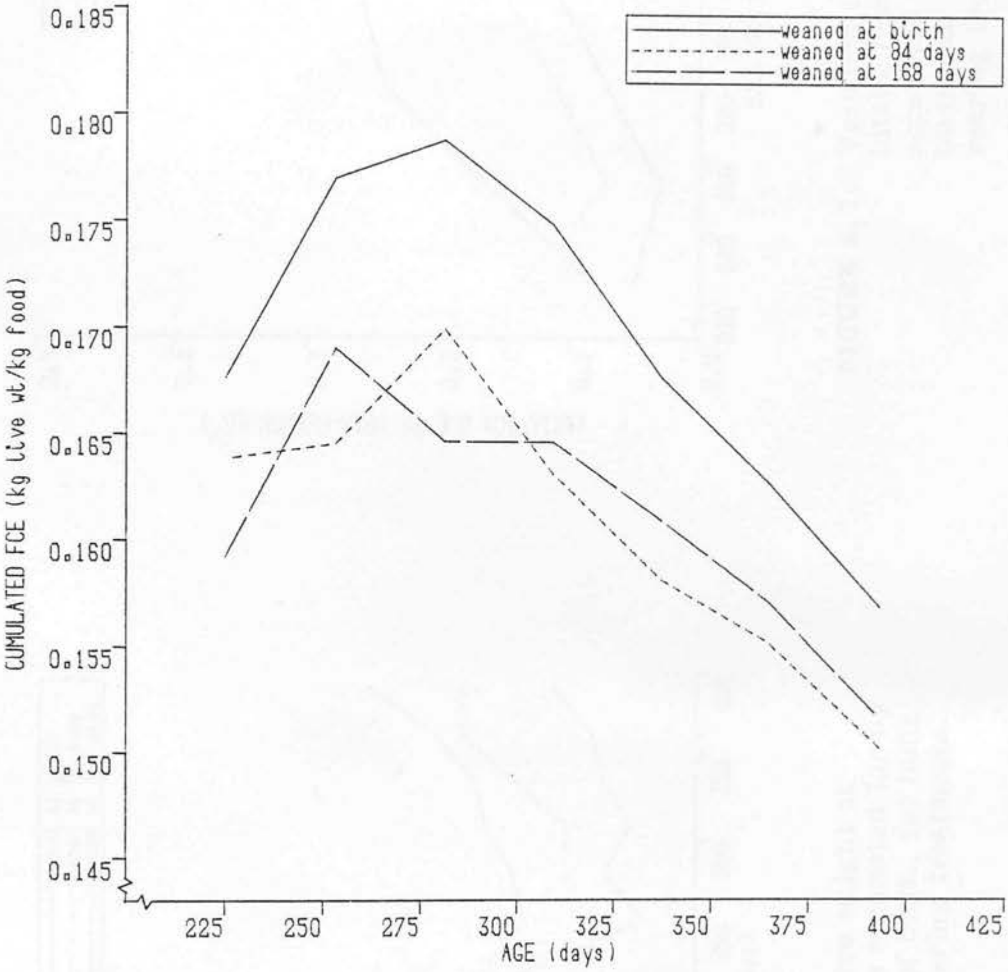

FIGURE 6.5: Cumulated food conversion efficiency (FCE) from 200 days of age, for bulls from three rearing treatments.

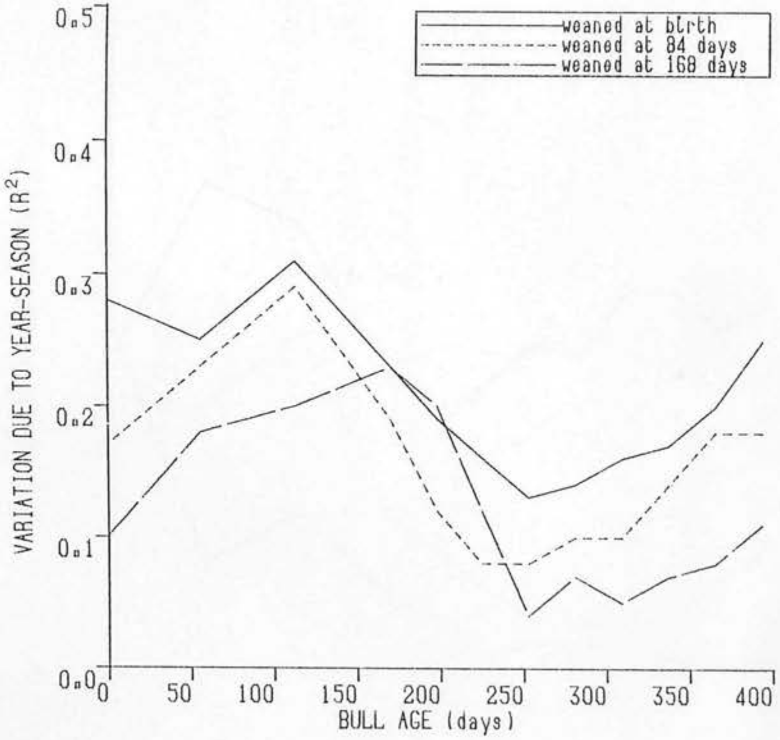

FIGURE 6.6: Variation in live weight at different ages accounted for by year-season of birth, for bulls from three rearing treatments.

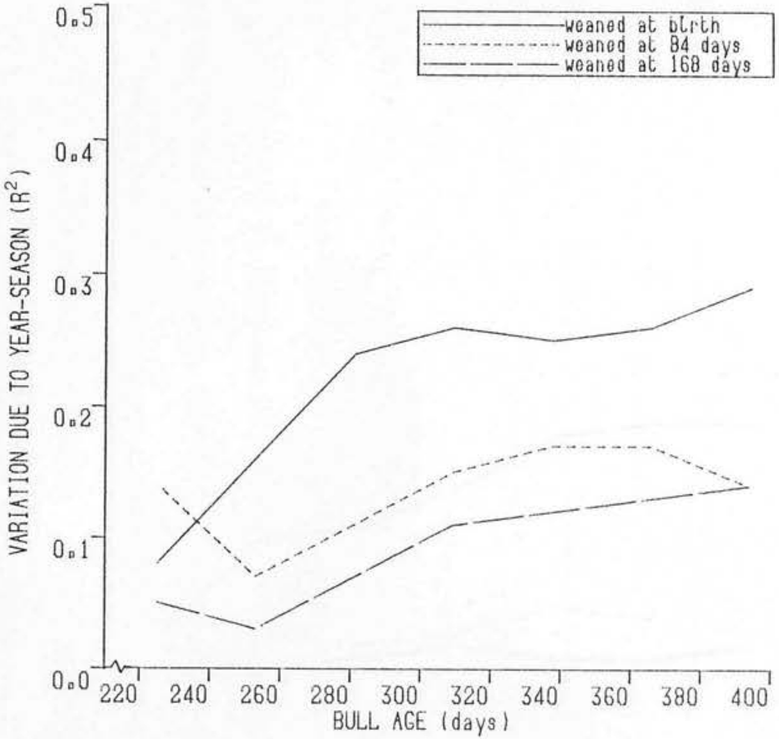

FIGURE 6.7: Variation in cumulated food intake from 200 days of age accounted for by year-season of birth, for bulls from three rearing treatments.

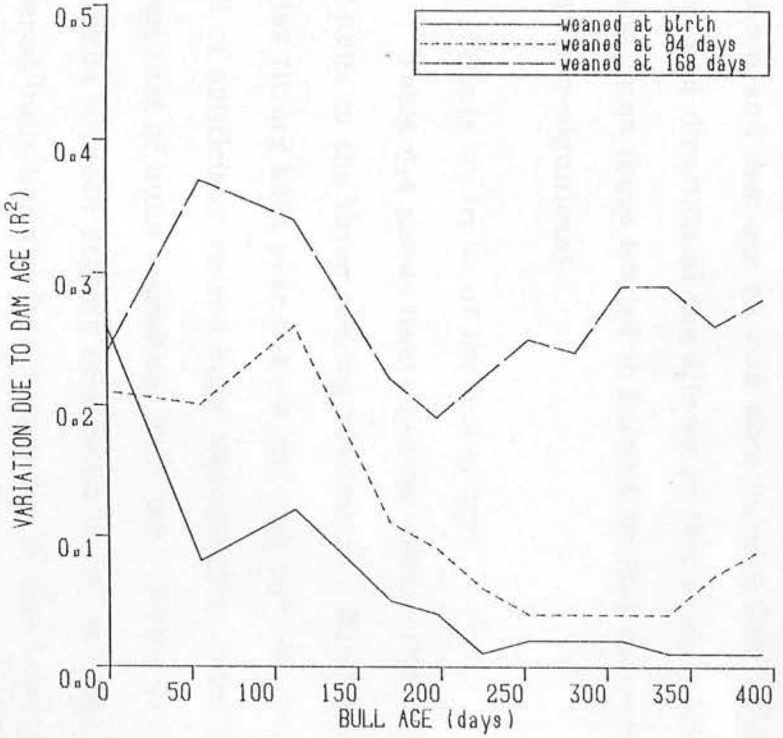

FIGURE 6.8: Variation in live weight at different ages accounted for by age of dam, for bulls from three rearing treatments.

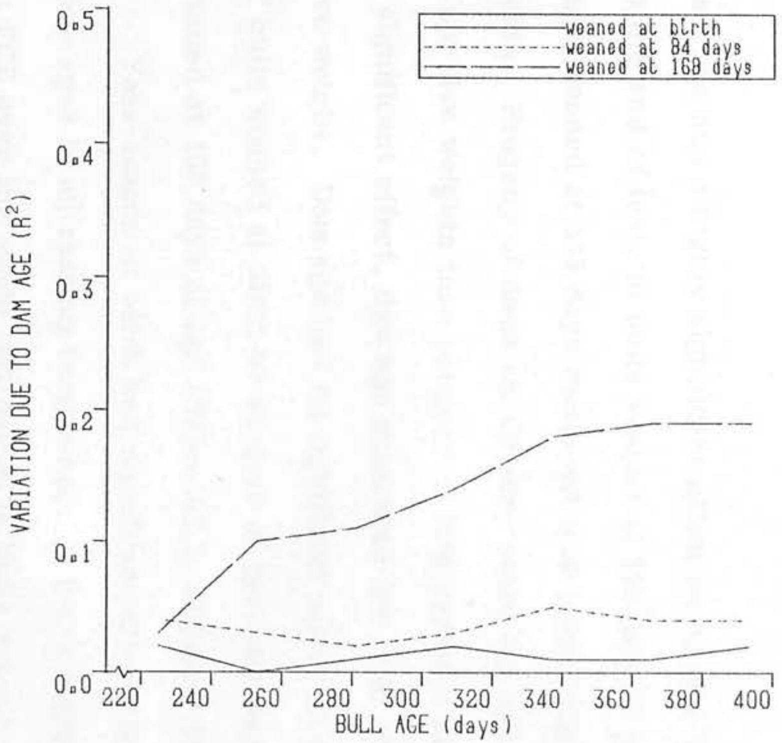

FIGURE 6.9: Variation in cumulated food intake from 200 days of age accounted for by age of dam, for bulls from three rearing treatments.

dam age had a highly significant effect on all live weights from birth to the end of test, in bulls weaned at 168 days of age. Weights of bulls weaned at 168 days increased with increasing dam age up to five years. Progeny of dams six or more years old had similar or slightly lower live weights than progeny of five year-old dams. When it was a significant effect, dam age accounted for 19 to 37% of the variation in live weight. Dam age had no significant effect on cumulated food intake of bulls weaned at birth or 84 days of age, but was important in bulls weaned at 168 days of age (Table A6.2, Figure 6.9).

Year-season of birth had significant effects on cumulated FCE at some ages in all rearing treatments. It had a highly significant effect on FCE over the whole test period in bulls weaned at 168 days, but was less important for other bulls (Table A6.1). Dam age had no significant effect on FCE at any ages, except for FCE over the whole test in bulls weaned at 168 days (Table A6.2). The effects of year-season and dam age on FCE were inconsistent, as they depend on the size and direction of the effects on live weight and food intake. In some cases these tended to balance so that the overall effect on FCE was non-significant.

2) Effects on traits at the end of test

Table 6.4 shows least-squares means (LSM) for performance traits of bulls in the three rearing treatments. Residual standard deviations after fitting both year-season and dam age are also shown. Pre-test GR of artificially reared bulls was markedly lower and more variable than that of bulls reared on their dam. There was no significant difference between rearing treatments in GR on test, but artificially reared bulls had the lowest variation in this trait. GR or LGR from birth to the end of test was lowest for bulls weaned at birth, but variation was similar for bulls from each rearing treatment.

TABLE 6.4: Effects of year-season of birth and dam age on bull performance in three rearing treatments.

Trait	Effects of fitting season and dam age	Age at weaning (days) 0	84	168
Estimated lean %	LSM ± SE	64.6 ± 0.2	63.9 ± 0.2	64.0 ± 0.2
	RSD	1.9	1.9	1.8
	R^2	0.17	0.18	0.31
	P of effects†	NS,NS	NS,NS	NS,***
Pre-test GR	LSM ± SE	570 ± 21a	712 ± 17b	708 ± 14b
(g/day)	RSD	166a	138ab	121b
	R^2	0.22	0.22	0.36
	P	NS,NS	NS,NS	**,*
GR 200-400 days	LSM ± SE	1085 ± 13	1105 ± 17	1113 ± 14
(g/day)	RSD	101a	140b	114ab
	R^2	0.40	0.26	0.46
	P	***,NS	*,NS	***,**
GR 0-400 days	LSM ± SE	843 ± 11a	919 ± 13b	909 ± 10b
(g/day)	RSD	91	102	87
	R^2	0.27	0.20	0.32
	P	*,NS	NS,NS	NS,***
LGR 0-400 days	LSM ± SE	310 ± 4a	334 ± 4b	331 ± 4b
(g lean/day)	RSD	30	33	30
	R^2	0.27	0.22	0.27
	P	*,NS	NS,NS	NS,*
FCE 200-400 days	LSM ± SE	157 ± 3	150 ± 2	152 ± 2
(g gain/kg food)	RSD	22a	18ab	15b
	R^2	0.14	0.25	0.42
	P	NS,NS	*,NS	***,NS
LFCE 200-400 days	LSM ± SE	58 ± 1	55 ± 1	55 ± 1
(g lean/kg food)	RSD	9a	7ab	6b
	R^2	0.14	0.26	0.41
	P	NS,NS	*,NS	***,NS
FCE 200-400 days	LSM ± SE	156 ± 2	150 ± 2	152 ± 2
Initial LW fitted as third effect	RSD	17	16	14
	R^2	0.47	0.42	0.53
	P†	NS,NS,***	*,NS,***	**,*,***
LFCE 200-400 days	LSM ± SE	57 ± 1a	55 ± 1b	55 ± 1ab
Initial LW fitted as third effect	RSD	7	6	5
	R^2	0.51	0.47	0.53
	P	NS,NS,***	*,NS,***	*,NS,***

Least squares means (LSM) or residual standard deviations (RSD) with different subscripts differ significantly from each other ($P < 0.01$).

† Probability refers to year-season, dam age and, where appropriate, the regression on initial live weight (in that order).

FCE or LFCE on test was highest and most variable for artificially reared bulls, probably because of their lower weights at the start of test. Including initial test weight as a partial regression in the analysis accounted for most of the between-rearing treatment difference in residual variation.

Year-season of birth had significant effects on several traits, but tended to be most important in bulls weaned at 168 days of age. Similarly, there were significant effects of dam age on all traits except LFCE adjusted for initial weight, in bulls weaned at 168 days. Dam age had no significant effect on any performance trait of bulls weaned at birth or at 84 days of age. For most traits bulls weaned at 84 days had the lowest proportion of variation due to year-season and dam age. Artificially reared bulls had the lowest proportion of variation in unadjusted FCE and LFCE due to year-season and dam age, giving the false impression that environmental variation had been reduced. When initial weight was included as a covariate in the model, about 50% of the variation in FCE and LFCE was explained in each of the rearing treatments. Thus, artificial rearing reduced the influence of year-season and dam age on FCE, but introduced additional environmental variation by restricting pre-test GR.

6.3.3 Correlations between traits

Correlations between traits, adjusted for year-season and dam age, are shown in Table 6.5. There was a low negative correlation between pre-test GR and GR on test in bulls weaned at birth. The correlation between these traits was low and positive for naturally reared bulls. A higher positive correlation was expected from the genetic relationship between these traits (Section 5.4). Correlations between pre-test GR and FCE on test were negative for all rearing treatments, but the

TABLE 6.5: Correlations between performance traits in three rearing treatments.

Age at weaning (days)	0	84	168
No. of animals	69	80	86
Correlation between:			
Pre-test GR, GR on test	-0.06	0.07	0.15
Pre-test GR, GR from birth	0.81	0.68	0.69
Pre-test GR, food intake[1]	0.69	0.48	0.40
Pre-test GR, FCE	-0.60	-0.51	-0.31
GR on test, food intake	0.17	0.63	0.59
GR on test, FCE	0.55	0.40	0.44
GR from birth, food intake	0.73	0.75	0.74
GR from birth, FCE	-0.24	-0.05	-0.02
FCE, food intake	-0.71	-0.45	-0.44

Correlations >0.25 or <-0.25 are significantly different from zero ($P < 0.05$).

[1] Cumulated food intake on test.

TABLE 6.6: Correlations between performance traits for the top and bottom 70 bulls ranked on 200 day weight.

		Top	Bottom
No. of animals:	RT0[1]	10	34
	RT84[1]	33	15
	RT168[1]	27	21
	Total	70	70
200 day weight (kg):	Mean	204.0	132.3
	SD	12.5	16.7
Correlation between:			
Pre-test GR, GR on test		0.19	0.03
Pre-test GR, food intake[2]		0.14	0.38
Pre-test GR, FCE		0.09	-0.32
FCE, food intake		-0.30	-0.55

Correlations >0.23 or <-0.23 are significantly different from zero (P <0.05).

[1] Three rearing treatments (RT); bulls weaned at 0, 84 or 168 days of age.

[2] Cumulated food intake on test.

correlation was strongest for artificially reared bulls. The negative relationship between FCE and food intake on test was most marked in artificially reared bulls. Together with evidence in the previous section, these results indicate that some bulls from each rearing treatment were undergoing compensatory growth on test, but this was greatest in artificially reared bulls. Further evidence for compensatory growth across all rearing treatments was provided by correlations between traits in the top 70 versus the bottom 70 bulls, ranked on unadjusted 200-day weight (Table 6.6). Bulls with the lowest early GR, from all rearing treatments, showed a low correlation between pre-test GR and GR on test (0.03) and a negative correlation between pre-test GR and FCE on test (-0.32). Corresponding correlations for bulls with higher pre-test GR were both positive (0.19 and 0.09).

6.4 Discussion and Conclusions

Live weights of all bulls in this study were lower at all ages than live weights of MLC farm-recorded Hereford bulls (Kilkenny *et al.*, 1980). Bulls involved in the MLC scheme may well be above the breed average live weight, because of pre-selection by the breeders, or extra feeding. However, it would still be desirable to improve the GR of ABRO bulls.

Lopez Saubidet and Verde (1976) studied food intake of steers following four months of restricted feeding from eight months of age. At equal live weights steers which had been restricted had higher food intake than control animals. Food intakes of all animals were similar at equal ages. The authors also found that age was better than live weight for predicting food intake following restricted feeding. In the present study, age and live weight were of similar value in predicting food intake. Food intake was similar for bulls from different rearing treatments at equal weights greater than 250 kg, but differed at equal ages in the present study. Artificially reared bulls failed to compensate fully for early restriction of GR. This supports the hypothesis of Everitt and Jury (1977), that a low plane of nutrition early in life may have a lasting effect on growth. The contradiction of Lopez Saubidet and Verde's result may be due to differences in the age of animals when restricted, and differences in the degree of compensation achieved in the two experiments. Comparison of trials may well be infuenced by whether food restriction is physical or energetic, the timing and duration of both restriction and realimentation, and the choice of the age or live weight for comparison of animals (see also Chapter V).

In MLC central test data effects of year and season each accounted for up to 10% of the variation in growth and efficiency traits (Okantah, 1978; Collins-Lusweti, 1981). Year-season was equally important for some traits in the present study. Compared to published work, dam age accounted for a very high proportion of the variation in performance of bulls weaned at 168 days in this study. Heifers first calved at two years of age in the present study, which may have increased the variation in performance compared to herds where heifers calved at later ages. Also, differences in the age structure of herds may have caused confounding of dam age and herd effects in the published trials.

In this study, artificial rearing failed to reduce environmental variation in bull performance. The low GR achieved would not be acceptable to breeders submitting bull calves for testing. Low GR also caused compensatory growth on test which could bias selection of bulls. Additionally, the mortality rate of artificially reared bulls was twice that of bulls reared on their dams (Table A6.3).

But mostly too high

Bulls weaned at 84 days of age were least affected by environmental factors, and performed as well as bulls weaned at 168 days of age. It appears that early weaned bulls are only temporarily affected by dam age. It is possible that dams of all ages can satisfy the calf's milk requirement to 84 days of age. Growth of older calves may be restricted by dams with a low milk yield or a short lactation. Data on machine-milked Hereford cows gives tenuous support to this hypothesis (Table 6.7).

There was some compensatory growth on test, even among bulls reared on their dam. The low or negative correlations between pre-test GR and GR on test agree with published results (Okantah, 1978; Collins-Lusweti, 1981; Tong, 1982). Probably the only way to avoid bias from such effects is to measure GR and FCE from birth to the end of test. Clearly, it would be expensive to measure food intake over this period, but recording several 'sample' periods from an early age may be a useful compromise.

TABLE 6.7: Mean daily milk yields for machine-milked Hereford cows.

	First lactation	Second lactation
No. of animals	7	4
Week of lactation	*Daily milk yield (kg)*	
1	3.62	5.46
6	6.42	8.00
12	5.54	5.70
18	4.32	5.40 [1]
24	2.52	4.00 [2]

[1] 3 animals only
[2] 2 animals only

Data kindly supplied by Dr. R.B. Thiessen, ABRO.

CHAPTER VII

Phenotypic Relationships Among Growth and Efficiency Traits

7.1 Introduction

Considerable evidence has already been presented that the test regime may affect the relationship among traits (Chapter V). In the ABRO Hereford experiment, bulls were performance tested from about 200 days to about 400 days of age. However, live weights were recorded at about 28-day intervals from birth to the end of test, and food intake was recorded over successive 28-day periods on test. It was therefore possible to measure growth and efficiency traits for each animal over a constant age interval and, with less accuracy, over a constant weight interval. Additionally, a small number of animals were retained on test until 500 days of age.

There were too few data for a useful genetic analysis, so this chapter is concerned with the phenotypic relationships among growth and efficiency traits, measured on different test regimes.

7.2 Materials and Methods

Data were available for a total of 235 bulls, from the three rearing treatments. Analysis was similar to that described in Chapter VI. Dam age, year-season of birth and rearing treatment were fitted as fixed effects in the statistical model. There was a significant dam age x rearing treatment interaction for several of the traits examined, so this term was also included in the model. This interaction arose because dam age had an important effect on many traits for bulls weaned at 168 days of age, but was seldom important for bulls weaned at birth or at 84 days of age. Fitting the interaction term in analysis of traits where it was not significant had only a trivial effect on correlations obtained, so the full model was used for all traits.

For comparison with the constant age test regime, GR and FCE for each animal were calculated over a constant live weight interval. Initially, a target range of 225 to 325 kg live weight was chosen for comparison with the age regime, since virtually all bulls had records of live weight and food intake over this weight range. However, final weights of 325 kg do not relate to commercial slaughter weights. In a second analysis bulls which failed to reach a final weight of 400 kg ± 25 kg were excluded, leaving 187 animals. As live weight (and food intake) was recorded at specific ages there was considerable variation between animals in the deviation from target initial and final test weights on both weight regimes. To account for this variation, traits measured over a constant weight interval were adjusted to a constant mean live weight on test, as well as adjusting for the other fixed effects.

Fifty-five bulls, born between 1978 and 1981, were retained on test until about 500 days of age. It was not feasible to fit the dam age x rearing treatment interaction term in analysis of data on these bulls, because of small numbers in each sub-class. Deviations from target final age were larger at 500 days than at 400 days of age. However, fitting this deviation as a partial regression in the statistical model had no effect on GR or FCE, so it was excluded.

7.3 Results

7.3.1 Performance testing to 400 days of age

Table 7.1 shows correlations between performance traits at 400 days of age, adjusted for fixed effects. As in the previous analysis, there was a low correlation between pre-test GR and GR on test and a negative correlation between pre-test GR and FCE on test (see also Figure 7.1). This was probably caused by differential environmental restriction of

TABLE 7.1: Correlations between traits from 200 to 400 days of age (235 animals).

		A	B	C	D	E	F	G	H	I	J
Pre-test GR	A	1.00	0.04	0.72	-0.34	-0.05	0.70	-0.50	-0.01	-0.54	-0.01
GR on test	B		1.00	0.68	-0.35	0.96	0.64	0.45	0.59	0.34	0.48
GR from birth	C			1.00	-0.49	0.59	0.96	-0.10	0.36	-0.21	0.29
Estimated lean %	D				1.00	-0.09	-0.22	0.17	-0.02	0.38	0.22
LGR on test	E					1.00	0.62	0.53	0.62	0.48	0.58
LGR from birth	F						1.00	-0.07	0.39	-0.12	0.39
FCE on test	G							1.00	0.85	0.97	0.82
Adjusted FCE [1]	H								1.00	0.79	0.97
LFCE on test	I									1.00	0.82
Adjusted LFCE [1]	J										1.00

Correlations >0.14 or <-0.14 are significantly different from zero (P <0.05).

[1] Adjusted for initial weight on test.

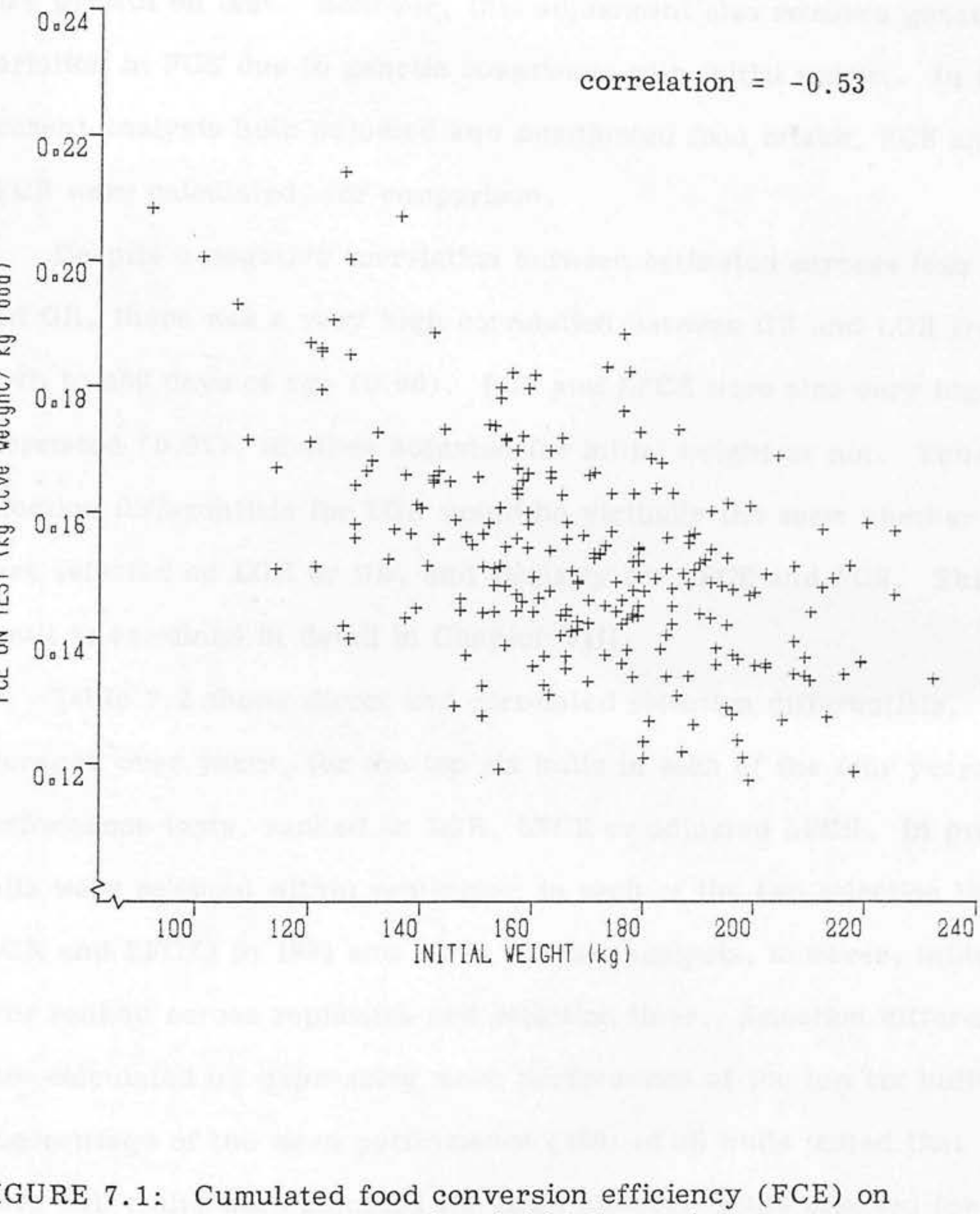

FIGURE 7.1: Cumulated food conversion efficiency (FCE) on test plotted against initial live weight on test. (Both traits adjusted for year-season of birth, dam age and rearing treatment.)

early growth. Prior to selection in each year of the Hereford experiment, FCE and LFCE were adjusted, by linear regression, to a constant initial live weight on test. This was to avoid selection of bulls which were highly efficient because of a low initial test weight and compensatory growth on test. However, this adjustment also removes genetic variation in FCE due to genetic covariance with initial weight. In the present analysis both adjusted and unadjusted food intake, FCE and LFCE were calculated, for comparison.

Despite a negative correlation between estimated carcass lean % and GR, there was a very high correlation between GR and LGR from birth to 400 days of age (0.96). FCE and LFCE were also very highly correlated (0.97), whether adjusted for initial weight or not. Thus, selection differentials for LGR would be virtually the same whether bulls were selected on LGR or GR, and similarly for LFCE and FCE. This result is examined in detail in Chapter VIII.

Table 7.2 shows direct and correlated selection differentials, averaged over years, for the top six bulls in each of the four years performance tests, ranked on LGR, LFCE or adjusted LFCE. In practice, bulls were selected within replicates, in each of the two selection lines (LGR and LFCE) in 1981 and 1982. In this analysis, however, bulls were ranked across replicates and selection lines. Selection differentials were calculated by expressing mean performance of the top six bulls as a percentage of the mean performance (100) of all bulls tested that year. All traits were adjusted for fixed effects. Bulls selected for high LGR would have relatively high birth weight, high GR, high total food intake, high adjusted FCE and slightly lower than average estimated lean %. Bulls selected for high adjusted LFCE would have above average birth weight, relatively high unadjusted and adjusted FCE, low unadjusted

TABLE 7.2: Performance of selected bulls compared to the mean performance of all bulls tested.

	LGR 0-400 days	LFCE on test	Adjusted LFCE[1]	Birth weight	GR 0-400 days	Food intake on test	Adjusted food intake[1]	FCE on test	Adjusted FCE[1]	Estimated lean %
Coefficient of variation (%)	9	12	10	12	10	11	9	11	10	3
	Performance of selected bulls relative to mean of all bulls tested (100)									
<u>Selection criterion</u>:[2]										
LGR 0-400 days	115	99	108	104	116	112	104	101	108	99
LFCE on test	96	124	115	99	95	87	95	122	115	102
Adjusted LFCE[1]	103	121	118	102	101	89	91	119	117	101

All traits adjusted for fixed effects.

[1] Adjusted for initial weight on test.

[2] Averages for top six bulls for each selection trait in each of four years (total number of animals = 235).

and adjusted total food intake, about average GR and slightly higher than average estimated lean %. Bulls selected for high LFCE would have even lower total food intake and higher FCE than bulls selected for adjusted LFCE. Animals with high unadjusted FCE or LFCE had lower live weight during test, but similar GR *on test* to bulls with high adjusted FCE or LFCE. Consequently, they would have lower maintenance requirements during test, which may explain the lower total food intake and higher efficiency. These effects are probably due to bulls attempting to compensate for environmental restriction of early growth.

Table 7.3 shows correlations between GR, RGR and FCE in different age intervals. RGR was more highly correlated than GR with FCE during the same age interval. GR or LGR in all age intervals were positively correlated with birth weight (Table 7.4). There was a strong negative correlation between birth weight and RGR measured from birth to 200 or 400 days of age. Correlations between birth weight and RGR after 200 days of age were not significantly different from zero. Animals which are undergoing compensatory growth will have high RGR, so these phenotypic correlations may not give a good idea of the genetic relationship between RGR and other traits. FCE and LFCE were uncorrelated with birth weight, but adjusted FCE and adjusted LFCE were positively correlated with birth weight.

7.3.2 Comparison of age and live weight intervals for testing

The proportion of variation in GR and FCE accounted for by year-season of birth and dam age, in each of the rearing treatments, was similar on a constant live weight regime to that described for the age regime (Chapter VI).

Figure 7.2 shows the relationship between bull live weight and age, in the three rearing treatments. Artificially reared bulls had

TABLE 7.3: Correlations between GR, RGR and FCE in corresponding age intervals (235 animals).

Traits	Age interval (days)	Correlation
GR, RGR	0 - 200	0.85
	200 - 300	0.70
	300 - 400	0.78
	200 - 400	0.47
	0 - 400	0.53
GR, FCE	200 - 300	0.66
	300 - 400	0.74
	200 - 400	0.45
RGR, FCE	200 - 300	0.80
	300 - 400	0.84
	200 - 400	0.74

Correlations >0.14 or <-0.14 are significantly different from zero (P <0.05).

TABLE 7.4: Correlations of some performance traits with birth weight (235 animals).

Trait	Age interval (days)	Correlation[1]
GR	0 - 200	0.12
	200 - 300	0.16
	300 - 400	0.18
	200 - 400	0.25
	0 - 400	0.27
LGR	200 - 400	0.23
	0 - 400	0.25
RGR	0 - 200	-0.37
	200 - 300	-0.05
	300 - 400	-0.03
	200 - 400	-0.08
	0 - 400	-0.64
FCE	200 - 400	0.00
LFCE	200 - 400	-0.02
Adjusted FCE[2]	200 - 400	0.17
Adjusted LFCE[2]	200 - 400	0.17
Estimated lean %	400	-0.13

[1] Birth weight adjusted for year-season and dam age only.

[2] Adjusted for initial weight on test.

Correlations >0.14 or <-0.14 are significantly different from zero ($P < 0.05$).

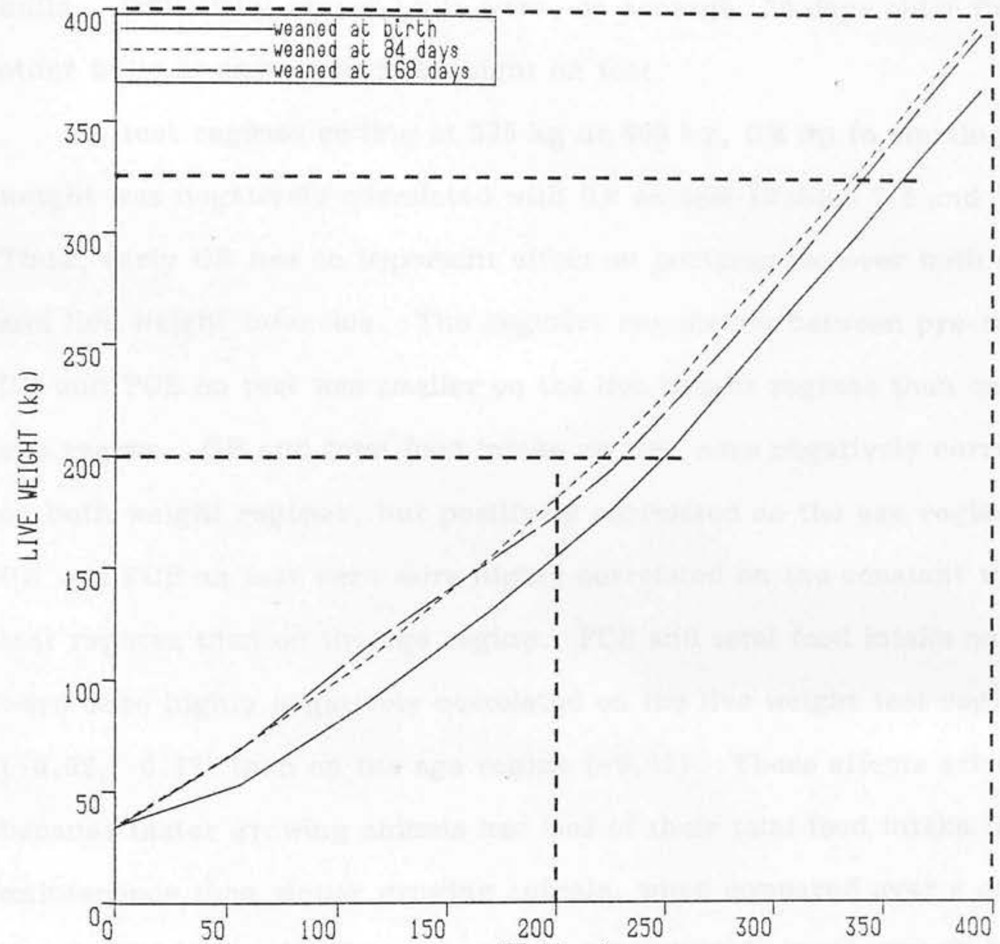

FIGURE 7.2: Comparison of live weight gain over constant age or constant live weight intervals, for bulls from three rearing treatments.

lower mean weight than other bulls at all ages, and relatively few of them reached final weights of 400 kg. However, mean GR from 200 to 400 days of age was similar for bulls from each rearing treatment, and hence RGR over the same interval was higher for artificially reared bulls. Artificially reared bulls were, on average, 30 days older than other bulls at any given live weight on test.

In test regimes ending at 325 kg or 400 kg, GR up to starting weight was negatively correlated with GR on test (Tables 7.5 and 7.6). Thus, early GR has an important effect on performance over both age and live weight intervals. The negative correlation between pre-test GR and FCE on test was smaller on the live weight regimes than on the age regime. GR and total food intake on test were negatively correlated on both weight regimes, but positively correlated on the age regime. GR and FCE on test were more highly correlated on the constant weight test regimes than on the age regime. FCE and total food intake on test were more highly negatively correlated on the live weight test regimes (-0.62, -0.77) than on the age regime (-0.47). These effects arise because faster growing animals use less of their total food intake for maintenance than slower growing animals, when compared over a constant live weight interval. Over a constant age interval, rapid growth is still most efficient, but large animals have higher daily maintenance requirements than smaller animals.

Correlations between individual bull performance measured from 200 to 400 days of age and from 200 to 400 kg live weight are shown in Table 7.7. There was a high correlation between GR from birth to the end of test on the two regimes (0.93). The correlation between FCE measured in age or live weight intervals was lower (0.77). This may reflect the different emphasis on high GR when FCE is measured over a live weight or an age interval.

TABLE 7.5: Correlations between traits measured over age or live weight intervals (235 animals).

	Target test age 200 - 400 days	Target test LW 225 - 325 kg
Actual mean age (days)	295	300
Mean age range (days)	-	256 - 344
Actual mean LW (kg)	278	275
Mean LW range (kg)	168 - 382	-
Traits	Correlation	
Pre-test GR, GR on test	0.04	-0.21
Pre-test GR, GR from birth	0.72	0.83
Pre-test GR, FI on test [1]	0.52	0.21
Pre-test GR, FCE on test	-0.50	-0.06
GR on test, FI on test	0.51	-0.49
GR on test, FCE on test	0.45	0.78
GR from birth, FI on test	0.74	-0.23
GR from birth, FCE on test	-0.10	0.28
FCE on test, FI on test	-0.52	-0.65

Correlations >0.14 or <-0.14 are significantly different from zero (P <0.05).

[1] FI = cumulated food intake on test.

TABLE 7.6: Correlations between traits measured over age or live weight intervals (187 animals).

	Target test age 200 - 400 days	Target test LW 225 - 325 kg	Target test LW 200 - 400 kg
Actual mean age (days)	296	289	307
Mean age range (days)	-	245 - 335	221 - 393
Actual mean LW (kg)	289	275	299
Mean LW range (kg)	180 - 398	-	-
Traits		Correlation	
Pre-test GR, GR on test	-0.06	-0.19	-0.33
Pre-test GR, GR from birth	0.60	0.76	0.56
Pre-test GR, FI[1] on test	0.31	0.20	0.26
Pre-test GR, FCE on test	-0.37	-0.03	-0.20
GR on test, FI on test	0.51	-0.44	-0.49
GR on test, FCE on test	0.50	0.76	0.70
GR from birth, FI on test	0.64	-0.28	-0.43
GR from birth, FCE on test	0.08	0.37	0.31
FCE on test, FI on test	-0.47	-0.62	-0.77

Correlations >0.16 or <-0.16 are significantly different from zero (P <0.05).

[1] FI = cumulated food intake on test.

TABLE 7.7: Correlation between bull performance measured from 200 to 400 days of age and from 200 to 400 kg live weight (187 animals).

Trait	Correlation
Pre-test GR	0.77
GR on test	0.72
GR from birth	0.93
FI on test [1]	0.22
FI on test [2]	0.23
FCE on test	0.75
FCE on test [2]	0.77

[1] FI = cumulated food intake on test.

[2] Adjusted for initial weight on age test regime.

Correlations >0.16 or <-0.16 are significantly different from zero ($P < 0.05$).

7.3.3 Comparison of tests ending at 400 and 500 days of age

There was virtually no correlation between GR from birth to 400 or from 200 to 400 days of age and GR from 400 to 500 days of age (Table 7.8). Similarly, the correlation between FCE from 200 to 400 days and FCE from 400 to 500 days of age was not significantly different from zero. Positive genetic correlations are expected between GR in different periods, and between FCE in different periods. The low phenotypic correlations in this study show that restriction of early growth disrupts the relationship between growth and efficiency in different periods.

Pre-test GR was negatively correlated with GR in successive 100-day periods up to 400 days of age. Pre-test GR and GR from 400 to 500 days of age were slightly positively correlated. Correlations between pre-test GR and FCE in successive 100-day periods were all negative, but smallest for FCE from 400 to 500 days of age. This shows that the influence of pre-test growth on performance diminishes after 400 days of age. However, the correlation of pre-test GR with GR from birth to either 400 or 500 days of age was very similar (0.49 and 0.47). Correlations of pre-test GR and FCE from 200 to 400 or 200 to 500 days of age were also similar (-0.61 and -0.56). To some extent similar correlations are expected, because of the part-whole relationship. They indicate, however, that extending the test to 500 days of age has only slightly reduced the influence of pre-test performance on GR or FCE *over the whole test period*.

The correlation between GR from birth to 400 days and GR from birth to 500 days of age was 0.83. The correlation between FCE from 200 to 400 and from 200 to 500 days of age was 0.84. Thus, it appears that there would be some difference in the choice of bulls, depending

TABLE 7.8: Correlations between GR and FCE in different age intervals (55 animals).

Trait	Age interval (days)		A	B	C	D	E	F	G	H	I	J	K	L	M
GR	0 - 200	A	1.00	-0.06	-0.33	0.07	-0.25	-0.22	0.49	0.47	-0.38	-0.49	-0.08	-0.61	-0.56
	200 - 300	B		1.00	-0.04	0.01	0.73	0.63	0.60	0.56	0.73	-0.26	-0.12	0.12	0.02
	300 - 400	C			1.00	0.09	0.55	0.36	0.25	0.12	0.00	0.83	0.05	0.53	0.32
	400 - 500	D				1.00	0.04	0.37	0.06	0.37	-0.06	0.06	0.89	0.02	0.22
	200 - 400	E					1.00	0.78	0.67	0.53	0.57	0.29	-0.07	0.53	0.29
	200 - 500	F						1.00	0.46	0.71	0.55	0.19	0.23	0.46	0.54
	0 - 400	G							1.00	0.83	0.14	-0.17	-0.18	-0.11	-0.31
	0 - 500	H								1.00	0.18	-0.21	0.10	-0.12	-0.05
FCE	200 - 300	I									1.00	-0.01	-0.05	0.53	0.43
	300 - 400	J										1.00	0.16	0.74	0.61
	400 - 500	K											1.00	0.15	0.42
	200 - 400	L												1.00	0.84
	200 - 500	M													1.00

Correlations >0.27 or <-0.27 are significantly different from zero (P <0.05).

on the age at the end of performance test. In this analysis it is impossible to tell whether this is due to a genotype x final age interaction, or due to the slight reduction in pre-test environmental effects on the longer test period.

7.4 Discussion and Conclusions

The phenotypic correlations between traits measured on the age regime in this study are very similar to mean correlations from the literature, on similar regimes (Table 5.6). Literature estimates of phenotypic and genetic correlations between a given pair of traits tended to be similar, except for correlations involving carcass composition, where information was scarce. If this generalisation holds in the present study, then selection for GR, LGR, adjusted FCE or adjusted LFCE would probably lead to a genetic increase in birth weight and mature size. Selection for unadjusted FCE or LFCE, rather than FCE or LFCE adjusted for initial weight, would perhaps reduce direct response in FCE and LFCE and alter correlated responses in other traits. Adjusting FCE or LFCE for initial weight on test will reduce the effects of environmental restriction prior to test, but may complicate interpretation of response to selection. Obviously, the aim should be to minimise pre-test effects rather than attempt to correct for them statistically.

Selection for GR is expected to lead to genetic increase in mature size (Chapter V). Thus, breed substitution with large European cattle breeds may give similar results to within-breed selection for GR. This is an acceptable conclusion from the national viewpoint, but might be less acceptable to breeders who are already committed to a smaller terminal sire breed. The major problems with the large terminal sire breeds are the high incidence of calving difficulty and the high perinatal mortality rate of their progeny. Clearly it would be useful to increase GR to slaughter weight, without increasing birth weight (and mature size). Selection for RGR or maturing rate at different ages may achieve this (Fitzhugh and Taylor, 1971), but more genetic information is required. In the present study, there were favourable phenotypic correlations between RGR and GR or FCE, and RGR from birth was highly negatively correlated with birth weight. Phenotypic correlations between RGR and other traits are probably very sensitive to pre-test effects, so it is unwise to predict the genetic relationships from the data presented. Index selection for GR with a restriction on genetic change in birth weight, or selection for high early GR and low later GR also need investigating further in cattle.

The correlations between GR and LGR and between adjusted FCE and adjusted LFCE in the present study were very high. This indicates that virtually the same bulls would be selected, whether ranked on GR or LGR (and the same for rankings on adjusted FCE or adjusted LFCE). Thus, *in vivo* estimation of carcass composition may not be worthwhile in improving LGR and LFCE of beef cattle. If genetic change in carcass lean % is economically desirable, then index selection on components of LGR or LFCE may be more effective than direct selection for LGR or LFCE. The correlation between LGR and LFCE in the present study was much lower than that reported by Fowler *et al.* (1976) for pigs fed semi *ad libitum* (0.39 versus 0.90).

Comparison of FCE on a constant live weight regime removes bias due to the different maintenance requirements of bulls which are genetically similar but differ in live weight at the same age, for non-genetic reasons. However, bulls which are growing rapidly to compensate for earlier restricted growth will appear more efficient over both age and live weight intervals. Differences between results from the two regimes will depend on the actual age and live weight intervals chosen. Thus, neither regime reduces the bias in selection due to environmental effects. Bias in measuring FCE may be reduced, on both age and live weight regimes, by recording food intake and live weight from an early age. Similarly, environmental effects on GR will be minimised by selection for GR from birth to the end of test, rather than GR on test.

No definite conclusions can be drawn from this study, on the effects of ending test at 500 days of age. However, it appears that pre-test effects are not readily reduced by manipulating either the age or the live weight at the end of test. The test regime should therefore reflect the production system in which bulls' progeny will be used, to avoid any genotype x environment interaction (Chapter V). For terminal sires used in extensive production systems, a test to 18 or 20 months of age, on a high fibre diet may be appropriate. If progeny are to be fed intensively to a target slaughter weight, as in cereal beef systems, then it may be more appropriate to test bulls on a high energy diet, to a constant live weight.

In national performance tests there are likely to be environmental effects due to herd of origin, in addition to the environmental effects found in this study (Okantah, 1978; Collins-Lusweti, 1981). Together these may bias bull selection, especially on measurements made over a relatively short time interval (e.g. FCE in most central tests). If genetic analyses confirm the importance of pre-test effects found in this preliminary study, then the role of central testing in UK and European beef improvement programmes should be re-evaluated.

CHAPTER VIII

Efficacy of Selection on a Product Trait

8.1 Relationship Between a Product Trait and One Component

8.1.1 Introduction

In analyses in the previous chapter, it was shown that there was a very high correlation between GR and LGR, when LGR was estimated as the product of GR and estimated lean %. Similarly, there was a very high correlation between FCE and LFCE. Product traits are frequently used as selection criteria in animal breeding. For example, yield of milk protein or milk fat is a product of milk yield and % protein or fat. Similarly, litter size is a product of ovulation rate and embryo survival. Before starting a selection programme for a product trait it would be useful to examine the phenotypic and genetic relationships between the product trait and individual components. Formulae were therefore derived for estimating phenotypic and genetic correlations between a component trait and the product trait, and for estimating the heritability of the product trait. Results are discussed in general terms, and then for the specific case of selection for LGR or LFCE in livestock.

8.1.2 Materials and methods

Formulae were derived for estimating the phenotypic and genetic correlations between a component trait (x) and a product trait of either two or three components (xy or xyz). Similarly, formulae were derived for estimating the heritability of a product trait of either two or three components. The following notation was used:

V = phenotypic variance
V_G = genetic variance
SD = phenotypic standard deviation
SD_G = genetic standard deviation
COV = phenotypic covariance
COV_G = genetic covariance

r = phenotypic correlation
r_G = genetic correlation
h^2 = heritability
x, y, z = component traits
$\bar{x}, \bar{y}, \bar{z}$ = means of component traits
CV = coefficient of variation = [(100 SD)/mean] %

Then:

$$V_{xy} \doteq \bar{y}^2 V_x + \bar{x}^2 V_y + 2\bar{x}\bar{y}\,COV_{x,y} \tag*{[a]}$$

$$COV_{x,xy} \doteq \bar{y} V_x + \bar{x}\,COV_{x,y} \tag*{[b]}$$

$$V_{Gx,y} \doteq \bar{y}^2 V_{Gx} + \bar{x}^2 V_{Gy} + 2\bar{x}\bar{y}\,COV_{Gx,y} \tag*{[c]}$$

$$COV_{Gx,xy} \doteq \bar{y} V_{Gx} + \bar{x}\,COV_{Gx,y} \tag*{[d]}$$

$$\begin{aligned} V_{xyz} \doteq\ & \bar{y}^2\bar{z}^2 V_x + \bar{x}^2\bar{z}^2 V_y + \bar{x}^2\bar{y}^2 V_z + 2\bar{x}\bar{y}\bar{z}^2 COV_{x,y} \\ & + 2\bar{x}\bar{y}^2\bar{z}\,COV_{x,z} + 2\bar{x}^2\bar{y}\bar{z}\,COV_{y,z} \end{aligned} \tag*{[e]}$$

$$COV_{x,xyz} \doteq \bar{y}\bar{z} V_x + \bar{x}\bar{z}\,COV_{x,y} + \bar{x}\bar{y}\,COV_{x,z} \tag*{[f]}$$

etc.

(See Kendall and Stuart [1963] and Colquhoun [1971] for general proofs.)

Higher order terms were ignored, as they have only a trivial effect on results if coefficients of variation of component traits are less than 15 or 20%. If coefficients of variation are higher than this, higher order terms should be added to the expansion of phenotypic or genetic variances of products. For example, the term $V_x V_y (1+r^2_{x,y})$ should be added to the expansion of the variance V_{xy} in equation [a] and to the expansion of equivalent variances in other equations (R. Thompson, personal communication).

(a) Phenotypic correlations

For a product trait of two components (xy):

$$r_{x,xy} = \frac{COV_{x,xy}}{\sqrt{(V_x\ V_{xy})}}$$

Substituting equations [a] and [b]:

$$r_{x,xy} \doteq \frac{\bar{y}V_x + \bar{x}SD_x SD_y r_{x,y}}{\sqrt{[V_x(\bar{y}^2 V_x + \bar{x}^2 V_y + 2\bar{x}\bar{y}SD_x SD_y r_{x,y})]}}$$

Transforming each trait to a mean of 1 and a standard deviation equal to the coefficient of variation (N[1,CV]), by dividing by the mean, then collecting terms:

$$r_{x,xy} \doteq \frac{1 + (\frac{CV_y}{CV_x}) r_{x,y}}{\sqrt{[1 + (\frac{CV_y}{CV_x})^2 + 2(\frac{CV_y}{CV_x}) r_{x,y}]}} \qquad \textit{... [Formula 1]}$$

For a product trait of three components (xyz):

$$r_{x,xyz} = \frac{COV_{x,xyz}}{\sqrt{(V_x\ V_{xyz})}}$$

Substituting equations [e] and [f], then transforming as before, and collecting terms:

$$r_{x,xyz} \doteq \frac{1 + (\frac{CV_y}{CV_x})r_{x,y} + (\frac{CV_z}{CV_x})r_{x,z}}{\surd[1 + (\frac{CV_y}{CV_x})^2 + (\frac{CV_z}{CV_x})^2 + 2(\frac{CV_y}{CV_x})r_{x,y} + 2(\frac{CV_z}{CV_x})r_{x,z} + 2(\frac{CV_y}{CV_x})(\frac{CV_z}{CV_x})r_{y,}}$$

... *[Formula 2]*

(b) <u>Genetic correlations</u>

For a product trait of two components:

$$r_{Gx,xy} = \frac{COV_{Gx,xy}}{\surd(V_{Gx}\ V_{Gxy})}$$

Substituting equations [c] and [d] then dividing throughout by V_x, and simplifying:

$$r_{Gx,xy} \doteq \frac{\bar{y}h^2{}_x + \bar{x}h_x h_y(\frac{SD_y}{SD_x})r_{Gx,y}}{\surd[h^2{}_x(\bar{y}^2h^2{}_x + \bar{x}^2h^2{}_y(\frac{V_y}{V_x}) + 2h_x h_y(\frac{SD_y}{SD_x})r_{Gx,y})]}$$

Transforming to N(1,CV) as before, and collecting terms:

$$r_{Gx,xy} \doteq \frac{1 + (\frac{h_y}{h_x})(\frac{CV_y}{CV_x})r_{Gx,y}}{\surd[1 + (\frac{h_y}{h_x})^2(\frac{CV_y}{CV_x})^2 + 2(\frac{h_y}{h_x})(\frac{CV_y}{CV_x})r_{Gx,y}]}$$

... *[Formula 3]*

For a product trait of three components:

$$r_{Gx,xyz} = \frac{COV_{Gx,xyz}}{\surd(V_{Gx}\ V_{Gxyz})}$$

Substituting and tranforming as before:

$$r_{Gx,xyz} \doteq \frac{1 + (\frac{h_y}{h_x})(\frac{CV_y}{CV_x})r_{Gx,y} + (\frac{h_z}{h_x})(\frac{CV_z}{CV_x})r_{Gx,z}}{\surd[1 + (\frac{h_y}{h_x})^2(\frac{CV_y}{CV_x})^2 + (\frac{h_z}{h_x})^2(\frac{CV_z}{CV_x})^2 + 2(\frac{h_y}{h_x})(\frac{CV_y}{CV_x})r_{Gx,y} + 2(\frac{h_z}{h_x})(\frac{CV_z}{CV_x})r_{Gx,z} + 2(\frac{h_y}{h_x})(\frac{h_z}{h_x})(\frac{CV_y}{CV_x})(\frac{CV_z}{CV_x})r_{Gy,z})]} \quad \ldots \textit{[Formula 4]}$$

(c) Heritabilities

For a product trait of two components:

$$h^2{}_{xy} = \frac{V_{Gxy}}{V_{xy}}$$

Substituting equations [a] and [c], then dividing throughout by V_x, and simplifying:

$$h^2{}_{xy} \doteq \frac{\bar{y}^2h^2{}_x + \bar{x}^2h^2{}_y(\frac{V_y}{V_x}) + 2\bar{x}\bar{y}h_xh_y(\frac{SD_y}{SD_x})r_{Gx,y}}{\bar{y}^2 + \bar{x}^2(\frac{V_y}{V_x}) + 2\bar{x}\bar{y}(\frac{SD_y}{SD_x})r_{x,y}}$$

Transforming to N(1,CV) as before, and collecting terms:

$$h^2_{xy} \doteq \frac{h^2_x\left[1 + \left(\frac{h_y}{h_x}\right)^2\left(\frac{CV_y}{CV_x}\right)^2 + 2\left(\frac{h_y}{h_x}\right)\left(\frac{CV_y}{CV_x}\right)r_{Gx,y}\right]}{1 + \left(\frac{CV_y}{CV_x}\right)^2 + 2\left(\frac{CV_y}{CV_x}\right)r_{x,y}}$$

... [Formula 5]

For a product trait of three components:

$$h^2_{xyz} = \frac{V_{Gxyz}}{V_{xyz}}$$

Substituting and transforming as before:

$$h^2_{xyz} \doteq$$

$$\frac{h^2_x\left[1 + \left(\frac{h_y}{h_x}\right)^2\left(\frac{CV_y}{CV_x}\right)^2 + \left(\frac{h_z}{h_x}\right)^2\left(\frac{CV_z}{CV_x}\right)^2 + 2\left(\frac{h_y}{h_x}\right)\left(\frac{CV_y}{CV_x}\right)r_{Gx,y} + 2\left(\frac{h_z}{h_x}\right)\left(\frac{CV_z}{CV_x}\right)r_{Gx,z} + 2\left(\frac{h_y}{h_x}\right)\left(\frac{h_z}{h_x}\right)\left(\frac{CV_y}{CV_x}\right)\left(\frac{CV_z}{CV_x}\right)r_{Gy,z}\right]}{1 + \left(\frac{CV_y}{CV_x}\right)^2 + \left(\frac{CV_z}{CV_x}\right)^2 + 2\left(\frac{CV_y}{CV_x}\right)r_{x,y} + 2\left(\frac{CV_z}{CV_x}\right)r_{x,z} + 2\left(\frac{CV_y}{CV_x}\right)\left(\frac{CV_z}{CV_x}\right)r_{y,z}}$$

... [Formula 6]

Pearson (1897) first examined the correlation between two ratios with a common denominator. More recently, Turner (1959) and Sutherland (1965) examined the phenotypic and genetic relationships between a ratio (such as food conversion ratio) and its numerator (see also Turner and Young, 1969). Turner (1959) derived formulae by expressing:

$$\log (y/x) = \log (y) - \log (x)$$

assuming that heritabilities and correlations were similar for actual measurements and for the logarithm of measurements. Sutherland (1965) used a more direct approach, following Pearson's original formulae. The formulae derived by these authors are identical to those presented above for a product trait of two components, except that all terms involving genetic or phenotypic correlations between the components of a ratio trait are preceded by a negative sign.

8.1.3 General results

(a) Phenotypic correlations

The expected phenotypic correlations between a product trait and one component were calculated from formula 1, for a range of CVs of component traits from 2 to 10%, and for correlations between them from -0.8 to 0.8. Results were verified by Monte Carlo simulation (with assistance of E. Avalos). Figure 8.1 shows that when the ratio [CV of trait y : CV of trait x] is less than 1 the phenotypic correlation between trait x and the product trait xy will always be greater than 0.75, for the range of correlations examined. As the ratio [CV of trait y : CV of trait x] increases, the correlation between x and xy depends increasingly on the correlation between x and y.

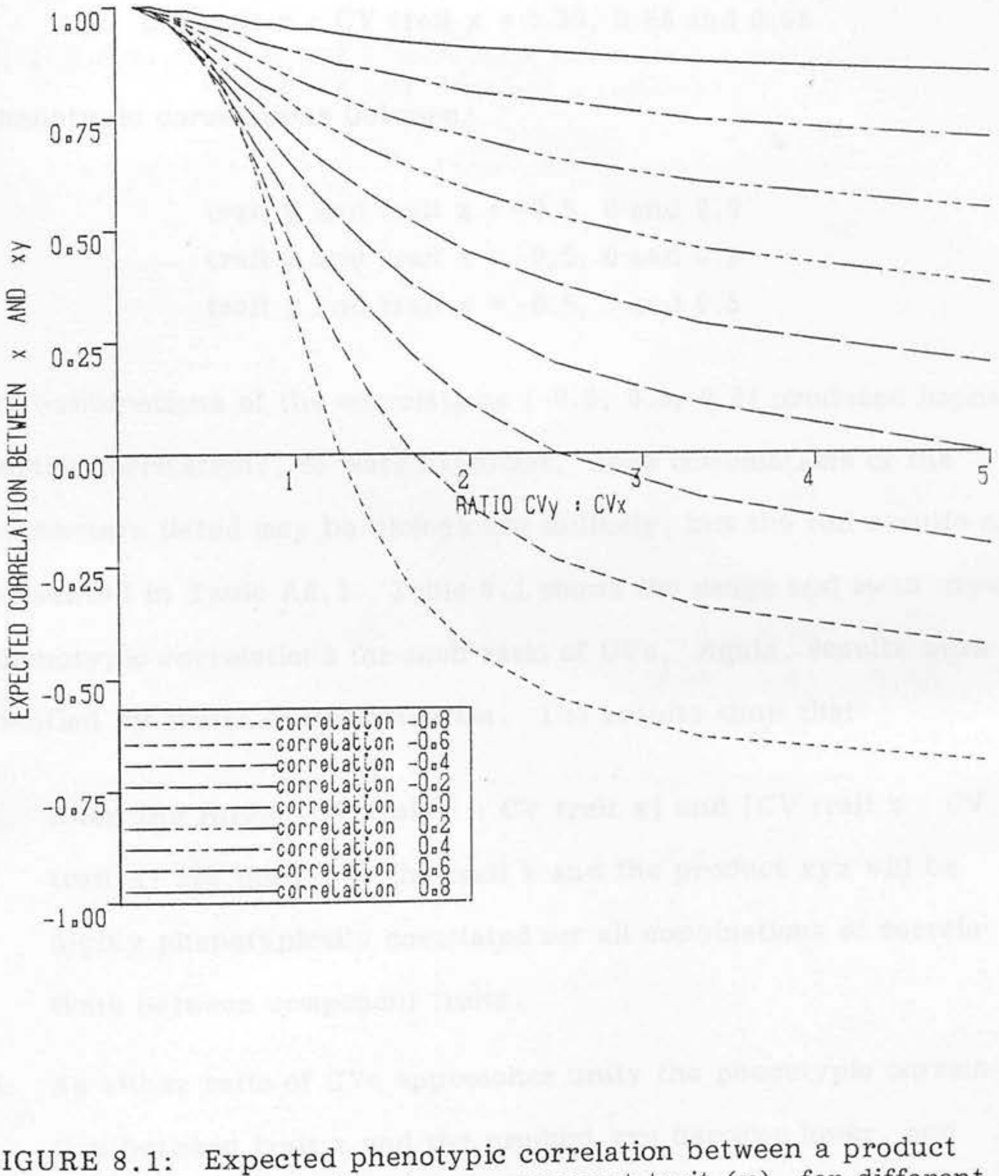

FIGURE 8.1: Expected phenotypic correlation between a product trait (xy) and one component trait (x), for different ratios of coefficients of variation of component traits, and different phenotypic correlations between components.

Expected phenotypic correlations were then calculated from formula 2, for a product trait of three components. Correlations were derived for combinations of:

CV trait y : CV trait x = 0.30, 0.65 and 1.00
CV trait z : CV trait x = 0.30, 0.65 and 0.95

phenotypic correlations between:

trait y and trait x = -0.5, 0 and 0.5
trait z and trait x = -0.5, 0 and 0.5
trait y and trait z = -0.5, 0 and 0.5

All combinations of the correlations [-0.5, 0.5, 0.5] produced impossible partial correlations, so were excluded. Some combinations of the parameters listed may be biologically unlikely, but the full results are presented in Table A8.1. Table 8.1 shows the range and mean expected phenotypic correlations for each ratio of CVs. Again, results were verified by Monte Carlo simulation. The results show that:

1. When the ratios [CV trait y : CV trait x] and [CV trait z : CV trait x] are both low, the trait x and the product xyz will be highly phenotypically correlated for all combinations of correlations between component traits.
2. As either ratio of CVs approaches unity the phenotypic correlation between trait x and the product xyz becomes lower, and more dependent on the combination of correlations between component traits.
3. For each value of the ratio of CVs there are specific combinations of correlations between component traits which result in high phenotypic correlations between x and xyz.

TABLE 8.1: Ranges and mean expected correlations between a product trait and one component.

Ratio of coefficients of variation		Expected correlation between x and xyz	
CV_y/CV_x	CV_z/CV_x	Range	Mean
0.30	0.30	0.86 - 1.00	0.93
0.30	0.65	0.60 - 0.94	0.82
0.30	0.95	0.37 - 0.90	0.69
0.65	0.30	0.60 - 0.94	0.82
0.65	0.65	0.36 - 1.00	0.75
0.65	0.95	0.17 - 0.91	0.64
1.00	0.30	0.34 - 0.90	0.67
1.00	0.65	0.15 - 0.90	0.63
1.00	0.95	0.02 - 0.90	0.57

Correlations between the three component traits range from -0.5 to 0.5.

(b) Genetic correlations

If heritabilities of the components of a product trait are equal, and genetic correlations between component traits are equal to the phenotypic correlations, then the expected genetic correlation between trait x and the product xy (or xyz) will equal the expected phenotypic correlation between x and xy (or xyz). In this case, Figure 8.1 applies to both phenotypic and genetic correlations between a product trait and one component. If the heritability of trait x is greater than the heritability of trait y (and trait z), then the genetic correlation between x and xy (or xyz) will be greater than the phenotypic correlation (and *vice versa*). Similarly, if genetic correlations between component traits are more positive than phenotypic correlations, the genetic correlation between x and xy or xyz will be higher than the phenotypic correlation between x and xy or xyz.

(c) Heritabilities

When heritabilities of components of a product trait are equal, and genetic correlations between component traits are equal to the phenotypic correlations, the expected heritability of the product trait is equal to that of the component traits. Figures 8.2 and 8.3 show the expected heritability of a product trait of two components, for a range of correlations between components ($r_G = r$), and a range of ratios [CV trait y : CV trait x]. The heritability of the product trait tends to be closest to the heritability of the most variable component trait. If trait y is most variable, and has the highest heritability, then the heritability of the product trait is highest when the component traits are negatively correlated. However, when the ratio of CVs falls below a critical value (0.7 to 0.8 for values used in Figure 8.2) the reverse is true, the heritability of the product trait being highest when

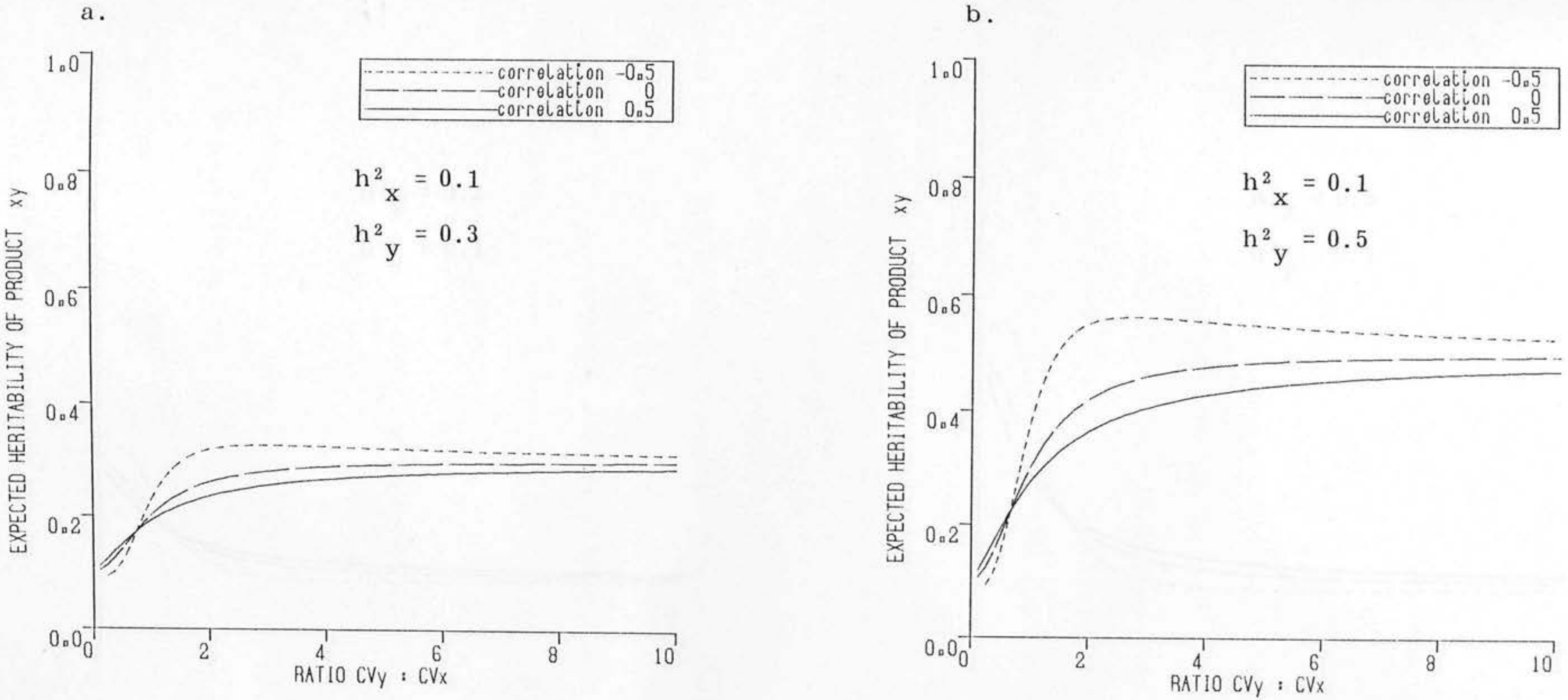

FIGURE 8.2: Expected heritability of a product trait (xy) for different heritabilities, different ratios of coefficients of variation, and different correlations between component traits (x and y).

$(r_G = r \quad , \quad h^2_x < h^2_y)$

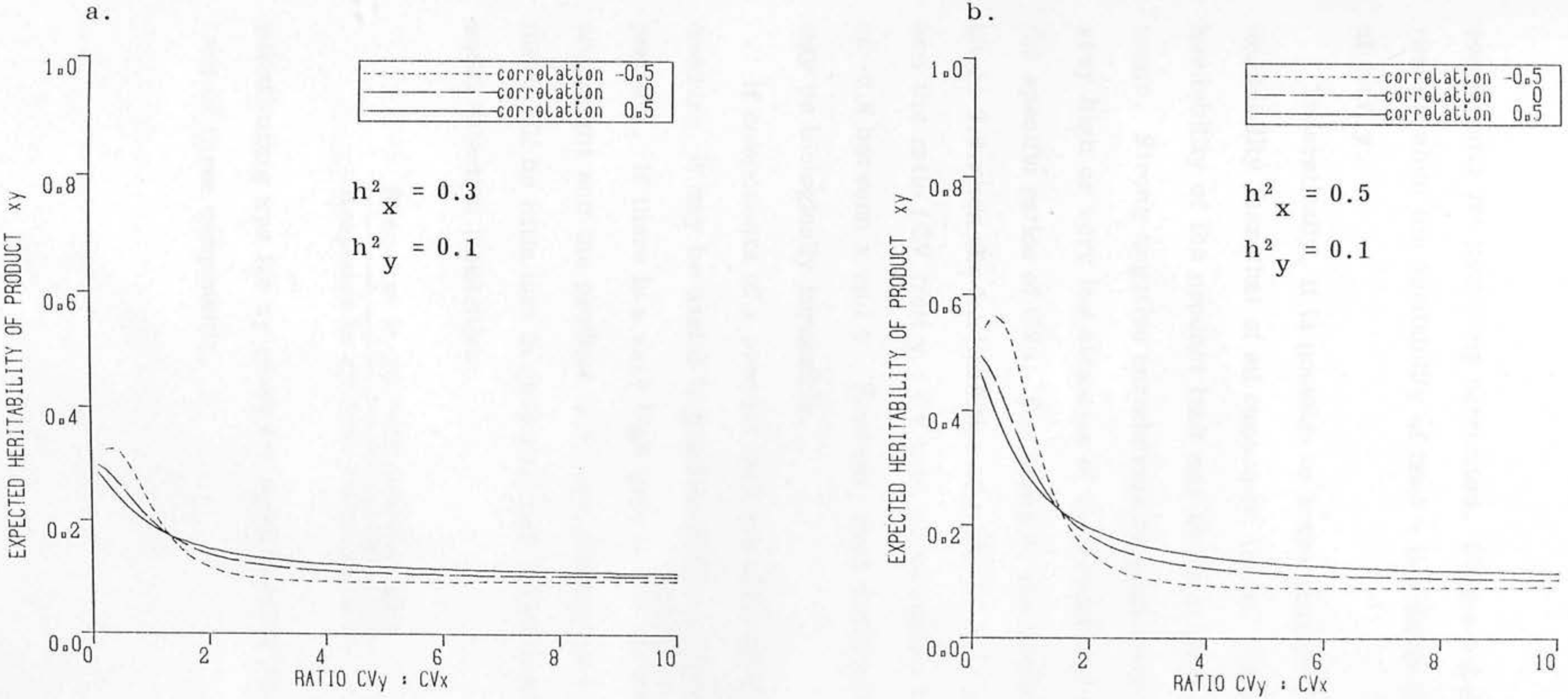

FIGURE 8.3: Expected heritability of a product trait (xy) for different heritabilities, different ratios of coefficients of variation, and different correlations between component traits (x and y).

$(r_G = r \quad , \quad h^2_x > h^2_y)$

components are positively correlated. Figure 8.3 shows corresponding results when the heritability of trait x is greater than the heritability of trait y.

Theoretically, it is possible to have a product trait with a higher heritability than that of all component traits. Conversely, the heritability of the product trait may be lower than that of all component traits. Strong negative correlations between component traits led to very high or very low estimates of the heritability of the product trait, for specific ratios of CVs. For example, the heritability of xy was about 0.8 when the heritabilities of traits x and y were 0.5 and 0.1, and the ratio [CV trait y : CV trait x] was about 0.7, with a correlation of -0.8 between x and y. However, such combinations of parameters may be biologically impossible.

If components of a product trait are difficult or expensive to measure, it may be useful to practise indirect selection on other components. If there is a very high genetic correlation between one component and the product trait, and the two have similar heritabilities, there will be little loss in response from indirect selection. Assuming equal selection intensities:

$$\frac{\text{Response in xy from selection on x}}{\text{Response in xy from selection on xy}} = \left(\frac{h_x}{h_{xy}}\right) r_{Gx,xy}$$

Substituting xyz for xy gives the equivalent formula for a product trait of three components.

8.1.4 Selection for LGR or LFCE

Lean growth rate is estimated as the product of three traits: growth rate, killing-out % and carcass lean %. Similarly, LFCE is estimated as the product of FCE, killing-out % and lean %. In the absence of *in vivo* estimates of killing-out %, LGR or LFCE may be estimated as the product of lean % and GR or FCE (as in the ABRO Hereford experiment). The phenotypic correlation between a component trait x and a product trait xyz, where z is constant, is equal to the correlation between x and xy. Results in Figure 8.1 therefore apply when killing-out % is assumed constant. The coefficients of variation of GR and FCE in livestock are usually higher than the coefficient of variation of carcass lean % (around 7 to 15% versus 3 to 7%). Figure 8.4 therefore shows expected phenotypic correlations when the ratio [CV of trait y : CV of trait x] is less than 1.25. The graph shows that GR and FCE will be highly correlated with estimated LGR and LFCE (assuming that killing-out % is not estimated *in vivo*), if:

1. the coefficient of variation of lean % is less than half the coefficient of variation of GR or FCE; or
2. if lean % and GR or lean % and FCE are highly positively correlated.

If both killing-out % and lean % are estimated *in vivo*, then results in Tables 8.1 and A8.1 apply. Again, GR or FCE will be very highly phenotypically correlated with LGR or LFCE when the CVs of killing-out % and lean % are much lower than the CV of GR or FCE.

Table 8.2 shows some literature estimates of CVs for component traits of LGR and LFCE, and phenotypic correlations between them, in

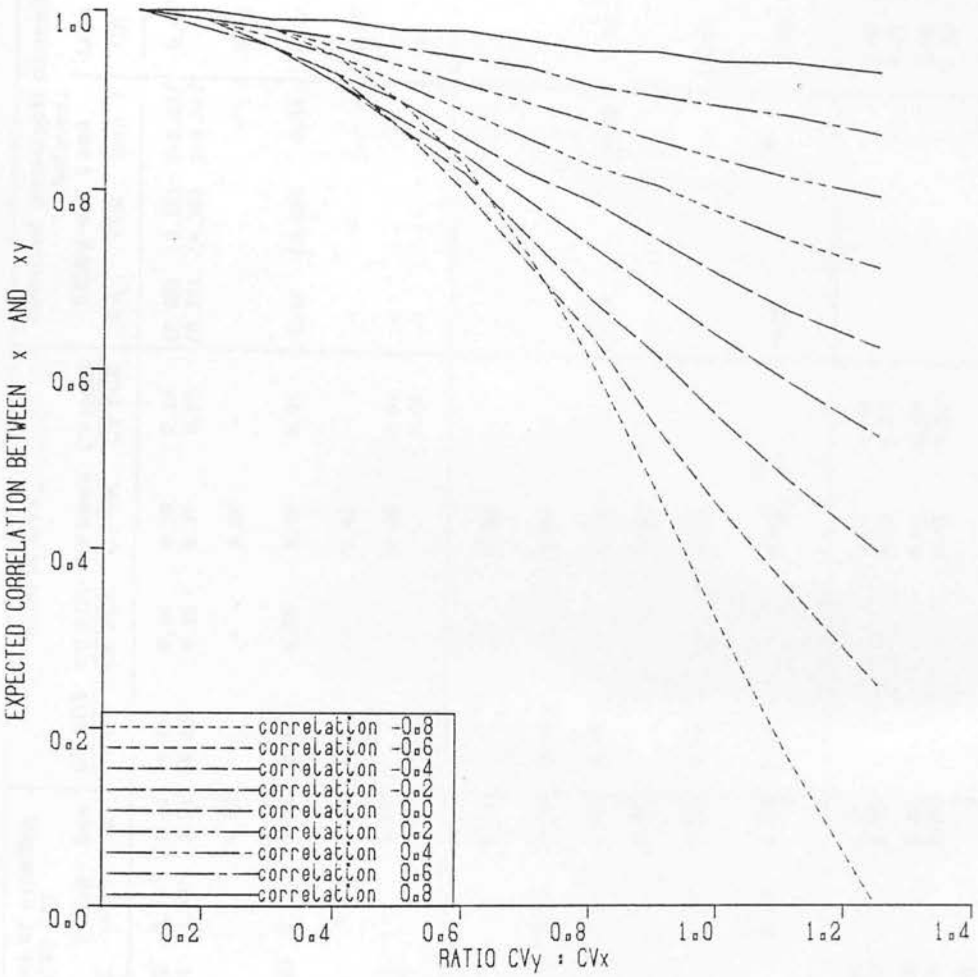

FIGURE 8.4: Expected phenotypic correlation between a product trait (xy) and one component trait (x), for different ratios of coefficients of variation of component traits, and different phenotypic correlations between components.

TABLE 8.2: Literature estimates of coefficients of variation of component traits of LGR and LFCE in cattle, sheep and pigs.

Source	Species	Feeding regime	End-point	Coefficient of variation (CV) (%)				Ratio of CVs				Observed phenotypic correlations between:					Comments
												Killing-out % and			Lean % and		
				GR	FCE	killing-out %	lean %	CV KO% / CV GR	CV KO% / CV FCE	CV lean% / CV GR	CV lean% / CV FCE	GR	FCE	lean %	GR	FCE	
Hereford experiment	cattle	*ad lib.*	age	10.00	10.00	3.88^1	3.00^2	0.39	0.39	0.30	0.30	(0.69)	(0.16)	(-0.63)^1	-0.49^2	-0.02^2	^{1}Dissection; ^{2} estimated (low numbers ~ 20)
		ad lib.	LW	5.58	11.04	2.90^1	3.91^1	0.52	0.26	0.70	0.35	(0.27)	(0.20)	(-0.50)^1	-	-	
Swiger *et al.*, 1965	cattle	*ad lib?*	age	12.49^1	-	-	4.44^2	-	-	0.36	-	-	-	-	-0.16	-	^{1}Postweaning; ^{2}% retail produc
Andersen *et al.*, 1977b	cattle	*ad lib.*	LW ^{1}	5.60	(7.10)	2.70	2.50	0.48	0.38	0.45	0.35	-0.17	(0.20)	0.35	0.20	(-0.28)	^{1}250 and 450 kg, (FCR)
Koch *et al.*, 1982b	cattle	*ad lib.*	age	11.20^1	-	-	4.74^2	-	-	0.42	-	-	-	-	-0.22^1	-	^{1}Avg. pre- and postweaning; ^{2}% retail product
Renand *et al.*, 1982	cattle	*ad lib.*	age	17.17	11.52	-	6.92^1	-	-	0.40	0.60	-	-	-	-	-	^{1}% protein in empty body; D$_2$O estimation
					10.78	-		-	-	-	0.64	-	-	-	-	-	
Latham *et al.*, 1966	sheep	grazing	LW	23.01^1	-	-	6.71	-	-	0.29	-	-	-	-	-	-	^{1}Carcass daily gain
Kirton *et al.*, 1974	sheep	grazing	age	11.42^1	-	5.16	5.09	0.45	-	0.45	-	-	-	-	-	-	^{1}LW; mean CVs at 3 ages
Olson *et al.*, 1976	sheep	*ad lib.*	age	16.88^1	-	5.35	1.96^2	0.32	-	0.12	-	-0.05	-	-0.23	-0.20	-	^{1}10 weeks - slaughter ^{2}predicted % trimmed cuts
Owen, 1976	sheep	*ad lib*	LW	6.85^1	-	-	3.99	-	-	0.58	-	-	-	-	-	-	^{1}Age at 40 kg
More O'Ferrall and Timon, 1977 a,b	sheep	grazing	LW	28.00	-	7.80	8.80^1	0.28	-	0.31	-	-	-	-	-0.03	-	^{1}Estimated from sample joint
Wolf *et al.*, 1980, 1981 Wolf, 1981	sheep	grazing	LW	19.92	-	6.77	5.92	0.34	-	0.30	-	0.29	-	-	0.08	-	
Fowler *et al.*, 1976	pigs	semi *ad lib.*	LW	7.14	(6.80)	-	6.50	-	-	0.91	0.96	-	-	-	0.29	(0.54)	(FCR); 2 trials
				7.21	(6.35)	-	6.42	-	-	0.89	1.01	-	-	-	0.17	(0.42)	
Pedersen, 1979	pigs	semi *ad lib.*	LW	4.67	(5.08)	-	2.40^1	-	-	0.51	0.47	-	-	-	0.08	(-0.19)	(FCR); ^{1}% meat
		ad lib.	LW	8.05	(5.23)	-	2.72^1	-	-	0.34	0.52	-	-	-	-0.25	(-0.04)	
Evans and Kempster, 1982	pigs	restricted	LW	4.50	(5.00)	-	-	-	-	-	-	-	-	-	-	-	(FCR)
		ad lib.	LW	7.60	(5.50)	-	-	-	-	-	-	-	-	-	-	-	
Webb and King, 1983	pigs	*ad lib.* and restricted	LW	17.82	(10.04)	4.02	10.97^1	0.23	0.40	0.62	1.09	-	-	-	-	-	(Pen FCR); ^{1}in rump back

TABLE 8.3: Expected correlations between GR and LGR or FCE and LFCE in cattle, sheep and pigs.

Source	Species	Feeding regime	End-point	Correlation between GR & LGR			Correlation between FCE & LFCE			Comments
				formula 1	formula 2	observed	formula 1	formula 2	observed	
Hereford experiment	cattle	*ad lib.*	age	0.96	0.97	0.96	0.96	0.96	0.97	^{1}Animals with low LW rejected for analysis to fixed LW.
			LW^1	0.83	0.89	-	0.95	0.96	-	
Swiger *et al.*, 1965	cattle	*ad lib?*	age	0.94	-	-	-	-	-	Postweaning GR; % retail product.
Andersen *et al.*, 1977b	cattle	*ad lib.*	LW^1	0.93	0.80	-	(0.96)	(0.86)	-	^{1}250 and 450 kg; (FCR).
Koch *et al.*, 1982b	cattle	*ad lib.*	age	0.91	-	-	-	-	-	Avg. pre- and postweaning GR; % retail cuts.
Olson *et al.*, 1976	sheep	*ad lib.*	age	0.99	0.95	-	-	-	-	Predicted % trimmed cuts.
More O'Ferrall and Timon, 1977a,b	sheep	grazing	LW	0.95	-	-	-	-	-	Lean % estimated from sample joint.
Wolf *et al.*, 1980, 1981 Wolf, 1981	sheep	grazing	LW	0.96	-	0.94	-	-	-	
Fowler *et al.*, 1976	pigs	semi *ad lib.*	LW	0.82	-	0.79	(0.88)	-	(0.82)	(FCR); two trials.
				0.80	-	0.77	(0.84)	-	(0.82)	
Pedersen, 1979	pigs	semi *ad lib.*	LW	0.90	-	0.85	(0.92)	-	(0.85)	Original data on % meat, meat gain, FCR and *efficiency* of meat gain.
		ad lib.		0.94	-	0.77	(0.89)	-	(0.72)	

Calculations based on data presented in Table 8.2.

cattle, sheep and pigs. Data include both estimated and dissected carcass lean %. The CVs of estimated lean % and estimated killing-out % could be considerably lower than CVs from slaughter data, depending on the precision of *in vivo* estimation. There were marked differences in the CVs, the ratio of CVs, and the correlations among component traits in different experiments. These may be species or breed differences, or differences due to the various feeding regimes and end-points of experiments. In the ABRO Hereford data the CV of GR was lower at a constant live weight than at a constant age (6% versus 10%). This may be partly due to the exclusion of some slow-growing bulls from analysis of data at a constant live weight (see Chapter VII). In the pig data of Pedersen (1979) and of Evans and Kempster (1982), restricted feeding reduced the CV of GR. In Pedersen's data restricted feeding increased the ratio [CV lean % : CV GR].

The expected phenotypic correlations between GR and LGR or FCE and LFCE were calculated for ABRO data, and for literature data where the necessary parameters were available (Table 8.3). All literature data referred to food conversion ratio (FCR) rather than FCE. In calculating expected correlations it was assumed that the CVs of FCR and FCE were equal, and the signs of correlations involving FCR were changed.

The observed phenotypic correlations and the expected correlations calculated from formulae 1 or 2, were in close agreement for ABRO Hereford data, for the sheep data of Wolf (1981) and colleagues, and for the pig data of Fowler *et al*. (1976). Pedersen (1979) did not present phenotypic correlations between killing-out % and other traits, so the expected phenotypic correlation between component and product traits was calculated from formula 1. Expected correlations were higher than the observed phenotypic correlations, probably because of the assumption that killing-out % was constant. When the CV of killing-out % is high, it may be worth attempting *in vivo* estimation of killing-out % rather than assuming a constant value in estimating LGR or LFCE.

Before starting a selection programme for LGR or LFCE in any livestock species, it would be useful to examine the expected response to selection. Neither LGR nor LFCE can be measured directly in the live animal. To estimate either of these traits in the live animal *in vivo* estimates of killing-out % and carcass lean % are required, and the accuracy of these measurements may be very variable. Here the expected response in LGR or LFCE from selection on GR or FCE should be compared to the expected response from selection on *in vivo* estimates of LGR or LFCE ($L\hat{G}R$, $LF\hat{C}E$). For example:

$$\frac{\text{Response in LGR from selection on GR}}{\text{Response in LGR from selection on L}\hat{\text{G}}\text{R}} = \left(\frac{h_{GR}}{h_{L\hat{G}R}}\right)\left(\frac{r_{G_{GR,LGR}}}{r_{G_{L\hat{G}R,LGR}}}\right)$$

When parameters for estimated LGR or LFCE are unavailable, the assumption of perfect accuracy of measurement will provide an estimate of the *minimum* relative response from indirect selection on GR or FCE. In cattle, literature estimates of the heritability of carcass lean %, killing-out %, GR and FCE are very similar (about 0.4; see Chapter V). Also, genetic correlations between pairs of these traits tend to be similar to the phenotypic correlations. In this case, the expected phenotypic correlation between GR and LGR, or FCE and LFCE should give a reasonable prediction of the *minimum* response from indirect selection on GR or FCE, as a proportion of response from direct selection on LGR or LFCE. In cases where there is little loss in response from indirect selection, the expense of estimating body composition may not be justified.

Wolf (1981) estimated the heritabilities of GR, killing-out % and carcass lean % in sheep as 0.10, 0.16 and 0.41. If killing-out % and lean % could be estimated *in vivo* with perfect accuracy, there would be considerable loss in response in LGR from selection on GR in this case, because of the relatively high heritability for lean %.

Pedersen (1979) presented phenotypic and genetic parameters for growth traits, including rate and efficiency of meat gain, of pigs on semi *ad libitum* or *ad libitum* feeding. From this data the expected correlated response in LGR from selection on GR would be *at least* 0.59 and 0.98 of the direct response, on semi *ad libitum* and *ad libitum* regimes. The expected correlated response in LFCE would be *at least* 0.70 of the direct response on either feeding regime. This shows that there may be large differences in the weighting given to components of product traits in selection, under different conditions of testing. Estimates of phenotypic and genetic parameters in different systems are needed, to predict when indirect selection will be useful.

8.2 Comparison of Biological and Economic Selection Indices

8.2.1 Introduction

In the classical economic selection index, the aggregate breeding value (H) can be expressed as a linear function of the animal's breeding value for each component trait (G), weighted by the relative economic value of the trait (a). For example, when the aggregate breeding value is a function of two traits x and y:

$$H = a_x G_x + a_y G_y$$

If phenotypic measurements (P) of the traits in the aggregate breeding value are used, then the index (I) is:

$$I = b_x P_x + b_y P_y$$

Index coefficients (b) are calculated for each of the traits actually measured, so that the correlation (r_{HI}) between the index (I) and the aggregate breeding value (H) is maximised (Hazel, 1943).

The following assumptions (summarised by Fowler *et al.*, 1976) are implicit in selection index theory in its most rigorous form:

1. All characters affecting the profitability of production which have a genetic component should be incorporated in the aggregate breeding value (discussed further by James, 1980).
2. The proportioning of importance between the measured traits should be determined solely by index calculations, using the best available estimates of the necessary parameters.
3. The precise conditions of testing are important only insofar as they affect accuracy in the estimation of breeding values and the phenotypic variances of the selection objectives.

Fowler *et al.* (1976) listed the main criticisms of the economic selection index as:

1. Economic relativities may not remain stable.
2. The choice and weighting of the objectives may relate only to a restricted set of conditions.
3. Many problems of production can have both genetic and non-genetic solutions; the proportioning of effort between these may require a deeper insight than just allowing the current monetary value of given improvement to weight the index.

4. Genetic and phenotypic parameters vary with the conditions of testing, breed and strain.
5. The value of a unit increase in a desirable character may not be linear.
6. The economic model is mathematically elegant but it does not take into account wider issues such as the physiological background of the measured traits.

There are several responses to these criticisms. Firstly, there is some evidence that selection indices are relatively insensitive to small changes in economic weights and genetic parameters (including evidence presented by Fowler *et al.*, 1976; see also Chapter IX). If the economic weights or genetic parameters differ considerably from one breed or production system to the next, then it is relatively simple to derive a different index for each breed or system. If the value of a unit increase in a desirable character is not linear, then quadratic functions may be used. However, in most cases it is probably adequate to take a linear approximation to overall merit, since genetic change is likely to be slow. Also, a linear index will be the most efficient way to move the progeny mean towards the overall optimum (James, 1982). Finally, it is not clear what the 'wider issues' ignored by index selection are.

The biological indices LGR and LFCE (product traits) do not involve economic calculations, and were supposed to overcome many of the criticisms of economic indices. However, the component traits of biological indices are still weighted in selection, according to their heritabilities, their CVs and the correlations between traits (Smith, 1967). The biological index is therefore an economic index with an implied set of economic weights. If there is large imbalance in the coefficients of variation of component traits, the most variable trait will tend to dominate the biological index. Unless the most variable trait also has the highest economic value, then selection on an economic index will be more effective than selection on the product trait. Biological and economic selection indices were therefore compared, for a range of heritabilities, CVs and correlations between component traits, to see when selection on the different indices is likely to be equally efficient for improving net economic merit.

8.2.2 Materials and methods

A formula was derived for estimating the correlation (r_{HJ}) between a product trait (J) (such as the biological indices LGR and LFCE) and the aggregate breeding value (H) of an economic index. For simplicity only two traits, x and y, were considered. In addition to the notation used previously:

a_x, a_y = economic values per unit x or y;

a^*_x, a^*_y = $a_x SD_x$ or $a_y SD_y$ = economic values per phenotypic SD unit x or y;

a = a^*_y / a^*_x

Then:

$$H = a_x G_x + a_y G_y$$

$$J = xy$$

$$r_{HJ} = \frac{COV_{HJ}}{\sqrt{(V_H V_J)}}$$

$$COV_{HJ} = COV_{a_x G_x, xy} + COV_{a_y G_y, xy}$$

Substituting equation [a] from Section 8.1.2:

$$r_{HJ} \doteq \frac{a_x\bar{y}V_{Gx} + a_y\bar{x}V_{Gy} + (a_x\bar{x} + a_y\bar{y})COV_{Gx,y}}{\sqrt{[(a^2{}_xV_{Gx} + a^2{}_yV_{Gy} + 2a_xa_yCOV_{Gx,y})(\bar{x}^2V_y + \bar{y}^2V_x + 2\bar{x}\bar{y}COV_{x,y})]}}$$

Expressing all traits and economic values in SD units, and simplifying:

$$r_{HJ} \doteq \frac{h^2{}_x(\frac{CV_x}{CV_y}) + ah^2{}_y + [1 + a(\frac{CV_x}{CV_y})]r_{Gx,y}h_xh_y}{\sqrt{[(h^2{}_x + a^2h^2{}_y + 2ar_{Gx,y}h_xh_y)(1 + (\frac{CV_x}{CV_y})^2 + 2(\frac{CV_x}{CV_y})r_{x,y})]}}$$

... *[Formula 7]*

Values of r_{HJ} were then computed for all combinations of:

$h^2{}_x$, $h^2{}_y$ = 0.10, 0.25, 0.50

$r_G = r$ = -0.5, 0, 0.5

a = 0.25, 0.50, 1.00, 2.00, 4.00

$\frac{CV_y}{CV_x}$ = 0.30, 0.65, 1.00

Values of r_{HI} were also computed for the same range of parameters by modifying Cunningham's (1970) Selind computer programme. The relative efficiency of selection on a biological index (r_{HJ}/r_{HI}) was then calculated for each combination of parameters (Table A8.2). Ranges and mean values of the relative efficiency are shown in Table 8.4.

Ignoring the term $V_xV_y(1+r^2{}_{x,y})$ in the expansion of V_{xy} in formula 7 had only a trivial effect on results, with CVs up to 20%. If CVs are much higher than this, and especially if traits are negatively correlated, formula 7 will tend to overestimate r_{HJ}.

TABLE 8.4: Relative efficiency of selection on biological and economic indices, for improving net economic merit.

CV_y/CV_x	Correlation between traits x and y	Relative efficiency (r_{HJ}/r_{HI}) Mean	Range
0.30	-0.5	0.61	0.02 - 1.00
	0	0.79	0.34 - 1.00
	0.5	0.86	0.46 - 1.00
0.65	-0.5	0.78	0.40 - 1.00
	0	0.88	0.59 - 1.00
	0.5	0.89	0.61 - 1.00
1.00	-0.5	0.83	0.69 - 0.99
	0	0.90	0.74 - 1.00
	0.5	0.90	0.70 - 1.00

Heritabilities of traits x and y = 0.10, 0.25, 0.50.

Relative economic weights a^*_y/a^*_x = 0.25, 0.50, 1.00, 2.00, 4.00

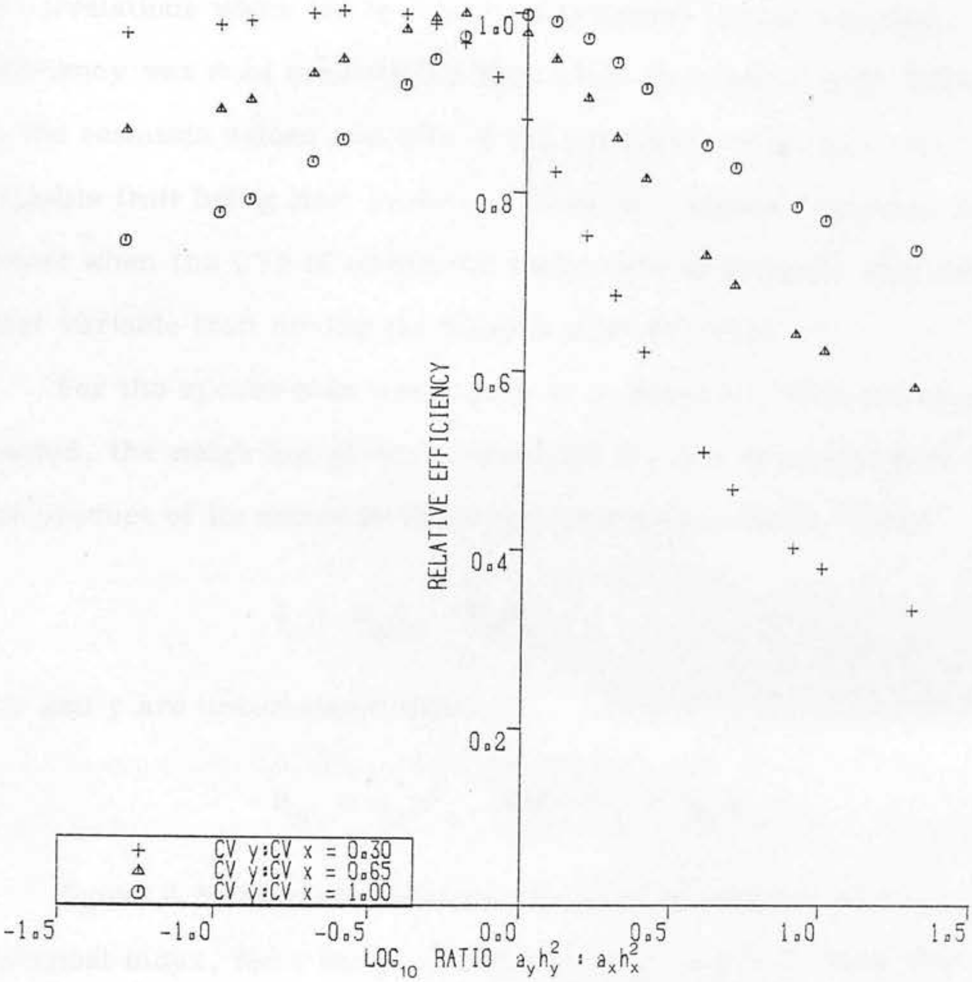

FIGURE 8.5: Relative efficiency of selection on biological and economic indices (r_{HJ}/r_{HI}), for different ratios of coefficients of variation, different economic values and different heritabilities for the two component traits (x and y). ($r_G = r \ = 0$).

8.2.3 Results

As expected from selection index theory, r_{HJ} was never greater than r_{HI}. However, for all ratios of economic values (a) and all ratios of CVs, there were specific combinations of heritabilities and of correlations which led to relative efficiencies approaching one. Efficiency was most consistently high when there was a large difference in the economic values and CVs of the two traits, with the most valuable trait being most variable. However, relative efficiency was lowest when the CVs of component traits were imbalanced, with the least variable trait having the highest economic value.

For the special case when traits in an economic index are uncorrelated, the weighting given to each trait is equal or proportional to the product of its economic value and heritability (Hazel, 1943):

$$I = b_x P_x + b_y P_y$$

if x and y are uncorrelated then:

$$b_x = a_x h^2{}_x \quad \text{and} \quad b_y = a_y h^2{}_y$$

Figure 8.5 shows the relative efficiency of selection on a biological index, for a range of ratios $[a_y h^2{}_y : a_x h^2{}_x]$, when the traits x and y are uncorrelated. When the economic value and heritability of the most variable trait are high, the greater the imbalance of CVs the higher the relative efficiency of selection on the biological index. Conversely, the lower the economic value and heritability of the most variable trait, the lower the relative efficiency of selection on the biological index.

It should be possible to exercise more control on the outcome of 'biological' selection by standardising the components in the biological index:

$$K = \frac{x-\bar{x}}{SD_x} + \frac{y-\bar{y}}{SD_y}$$

The correlation between this index and the aggregate breeding value (r_{HK}) is identical to r_{HJ} in formula 7, when the CVs of component traits are equal (see Appendix for proof). Such an index will tend to equalise the weighting given to traits with very different coefficients of variation.

8.3 Discussion and Conclusions

Product traits are frequently used as selection objectives in animal breeding. However, the cost and convenience of measuring different components of a product trait may vary widely. Before starting a selection programme for a product trait it would be useful to predict the phenotypic and genetic correlation between each component trait and the product, and the heritability of the product trait, using the formulae presented. In some cases, it may be possible to avoid expensive or difficult measurements, with little effect on response in the product trait. It appears that *in vivo* estimation of carcass composition in cattle and sheep, and to a lesser extent in pigs, could sometimes be disregarded with little effect on response in LGR or LFCE.

On the basis of criticisms of economic index selection, Fowler *et al*. (1976) proposed the biological indices, lean tissue growth rate and lean tissue food conversion, as objectives in pig breeding. The authors proposed that these biological indices avoided the 'black box' approach of the economic selection index. In fact, the biological index is more of a 'black box' than the economic index. The weighting given to traits in the biological index depends on the CVs and heritabilities of component traits, and the correlations between them. Thus, the weighting may vary from one breed or production system to another. This can be easily avoided by deriving different economic indices for the different breeds or systems. There are circumstances when selection on biological and economic indices will give very similar results. However, in most cases the classical selection index will be the most efficient way to improve the net economic merit of a population of animals, given reasonable estimates of economic weights, phenotypic and genetic parameters.

CHAPTER IX

Derivation of Beef Selection Indices

9.1 Introduction

In the previous chapter it was shown that selection on an economic index will usually be preferable to selection on a product trait. Only when the most variable trait has the highest economic weight will the relative efficiencies of selection on economic and 'biological' indices become similar. Selection indices suitable for terminal sire breeds were therefore derived, with efficiency of lean meat production as the objective for improvement. There is often a high incidence of calving difficulty in the progeny of terminal sire breeds with high GR (Chapter V). Within breeds there is a positive genetic correlation between GR and birth weight. For this reason, an index was also derived with a restriction on genetic change in birth weight, assuming that this would prevent an increase in the incidence of calving difficulty.

Lack of relevant economic and genetic parameters is often a limitation in deriving selection indices. Results presented depend on the accuracy of the assumptions made. However, there is some evidence that selection indices are relatively insensitive to small changes in genetic parameters (Fowler *et al.*, 1976) and economic weights (Fowler *et al.*, 1976; Vandepitte and Hazel, 1977; Smith, 1983). Sensitivity of indices to these changes was also examined in this chapter.

9.2 Materials and Methods

9.2.1 Genetic and phenotypic parameters

The efficiency of lean meat production has already been identified as a potential objective for improvement in terminal sire beef breeds. It may be defined as the weight of lean meat produced per unit of food consumed in a given age or live weight interval. However, there is relatively little genetic information on lean growth and food consumption.

The aggregate breeding value of selection indices in this chapter therefore comprised GR, FCE, killing-out % and carcass lean %. The mean literature estimates of heritability of these traits (and birth weight for the restricted index) were used in index calculations (Table 5.5).

The phenotypic correlations between traits in ABRO data corresponded well with literature estimates from experiments ending at a constant age (Tables 5.6 and 7.1). ABRO values were therefore included in calculating mean literature estimates of phenotypic correlations for use in indices. Where literature estimates of genetic correlations between pairs of traits were not available, these were assumed to be the same as phenotypic correlations at a constant age (Table 9.1). The only relevant literature estimate of the genetic correlation between GR and ultrasonic fat area was of opposite sign to that expected from the phenotypic correlation between the two traits, and from the phenotypic and genetic correlations between GR and lean %. The genetic correlation between GR and fat area was therefore assumed to be the same as the phenotypic correlation. There were no appropriate literature estimates for most genetic correlations with killing-out %. Phenotypic information on killing-out % at about 400 days of age was available for only 19 ABRO animals. However, Table 9.2 shows phenotypic correlations adjusted to a constant age, for a larger number of older ABRO animals. It was assumed that genetic correlations between killing-out % and other traits were the same as these phenotypic correlations. Since the data on killing-out % were less reliable than the data on other traits, special attention was paid to the sensitivity of indices to changes in correlations with killing-out %. The full matrix of correlations and heritabilities used in the indices is shown in Table 9.3.

TABLE 9.1: Phenotypic and genetic correlations used in index calculations.

Traits	Correlations Phenotypic	 Genetic
BW, GR	0.29	0.39
BW, FCE	0.10	0.11
BW, US	0.12	0.12[2]
BW, Lean %	0.08	0.05
GR, FCE	0.39	0.28
GR, US	0.30	0.30[2]
GR, Lean %	-0.25	-0.22
FCE, US	0.06	-0.14
FCE, Lean %	-0.06[1]	-0.06[2]
US, Lean %	-0.57	-0.57[2]

[1] 19 animals only.

[2] Assumed equal to phenotypic correlation. Other correlations from Tables 5.6, 7.1 and 7.4.

TABLE 9.2: Phenotypic correlations between killing-out % and other traits (from ABRO Hereford experiment).

Traits	Phenotypic correlation[1]
KO %, BW	0.04
KO %, GR from birth	0.45
KO %, FCE on test	0.20[2]
KO %, US	0.39
KO %, Lean %	-0.56

[1] Adjusted to constant age.

[2] 19 animals at about 400 days of age, FCE adjusted for initial weight on test.

All the other correlations from 82 animals at about 485 days of age.

TABLE 9.3: Phenotypic and genetic correlations and heritabilities used in index calculations.

		A	B	C	D	E	F
Birth weight	A	0.42	0.29	0.10	0.12	0.04	0.08
Growth rate	B	0.39	0.41	0.39	0.30	0.45	-0.25
FCE	C	0.11	0.28	0.42	0.06	0.20	-0.06
Ultrasonic fat	D	0.12	0.30	-0.14	0.19	0.39	-0.57
Killing-out %	E	0.04	0.45	0.20	0.39	0.39	-0.56
Carcass lean %	F	0.05	-0.22	-0.06	-0.57	-0.56	0.39

Heritabilities on the diagonal, phenotypic correlations above, genetic correlations below the diagonal.

Hill and Thompson (1978) showed that with a large number of traits, the sample estimate of the genetic covariance matrix has a high probability of not being positive definite. This implies that some heritabilities, genetic correlations or partial genetic correlations have impossible values. In the present study the matrix of covariances between traits in the index and those in the aggregate breeding value was not square, so could not be examined directly to see if it was positive definite. However, canonical analysis of the covariance matrices (by R. Thompson) showed that all linear combinations of phenotypic measurements had positive heritabilities.

Results in the literature and in Chapters VI and VII show that compensatory growth can affect the results of performance tests. For this reason it may be misleading to assume that measurements of GR and FCE over a short age (or live weight) interval reflect the animal's genotype. In practice, GR can be measured from birth to the end of test, but FCE is usually measured from 150 or 200 days of age. Regardless of feeding regime and end-point, most authors report a positive correlation between GR and FCE measured in the same period. However, the phenotypic correlation between GR *from birth* to the end of test and FCE *on test* may be negative due to compensatory growth (-0.10 in ABRO data). Adjusting FCE for bulls' initial weight on test may reduce this environmental effect, and lead to a positive correlation with GR from birth (0.36 in ABRO data). However, this will also remove the genetic variation in FCE on test due to genetic covariance with initial live weight. Indices derived in this chapter are appropriate to performance tests where there is no evidence of compensatory growth, or where FCE has been adjusted to reduce pre-test environmental effects.

9.2.2 Relative economic values

Economic values of genetic improvement in animal performance can be calculated from at least three viewpoints (Moav, 1973). In the first case economic values may be calculated in the interests of long-term national economy. Here the total volume of produce might be regarded as fixed, so improvement reduces the cost of production without increasing the total volume. If genetic improvement increases the output from each animal, the total number of animals must be reduced. This may be achieved if: (1) each producer keeps fewer animals, or more likely (2) the least efficient producers cease to operate. If some producers cease to operate there is a national saving in the costs of buildings (investment, repairs, renewal, etc.), machinery and labour, and land is released for other purposes. However, this may not directly benefit the remaining producers.

In the second case, economic values of genetic improvement may be calculated from the individual producer's short-term viewpoint. An individual producer (who forms a very small part of the whole market) can generally sell all produce with very little effect on the total market. Genetic improvement in a relatively small part of the total market may increase the volume of produce without a reduction in profit per unit of produce. However, if the producer's profit is increased by increasing output, he could simply keep more animals without considering genetic improvement.

Thirdly, economic values may be calculated from a new investor's viewpoint. In this case, the objective is to maximise profit per unit of investment (Moav, 1973).

In this chapter, economic values for selection indices were calculated in the interests of long-term national economy, as this seemed most appropriate to a national beef improvement programme. For comparison with the 'national interest' method, economic values were also calculated from the individual producer's viewpoint (see Appendix). Results are shown in Table A9.1, but were not used in selection indices.

Relative economic values used in selection indices are partial regressions of overall economic merit on each trait in the aggregate breeding value (Hazel, 1943; James, 1980). Economic values were therefore calculated separately for each trait, assuming other traits in the aggregate breeding value to be constant. Partial regressions of economic merit on breeding value may depend on the absolute level of performance (Moav, 1973). For simplicity, it was assumed that the relative economic values of traits in the aggregate breeding value remain constant as the level of performance increases. This assumption may be valid in the short term, but economic weights should be re-evaluated periodically.

Economic values of genetic improvement were calculated from physical and financial performance data for cereal beef and 18/20 month beef production systems, for comparison (Table 9.4). However, only values from the 18/20 month system were used in indices, as cereal beef accounts for less than 5% of the current British beef supply (Allen and Kilkenny, 1980; D.M. Allen, personal communication). All calculations assumed a fixed age at slaughter. Coefficients of variation in performance traits were assumed to be the same as in the ABRO Hereford data (Table 9.5), which agreed well with literature estimates (Table 8.2).

Total production costs were allocated to:

1. cost of a newborn calf;
2. variable costs of production (calf food costs, postweaning food costs, veterinary, haulage and bedding costs);

TABLE 9.4: Physical and financial performance data for two beef production systems.

Data		Source	Cereal beef	18/20 month beef
Breed		1	Friesian (Fr)	Fr or He x Fr
Sex		1	bulls	steers
Birth weight (kg)		1	45	45
Weaning age (days)		1	84	84
Weaning weight (kg)		1	100	100
Slaughter age (days)		1	360	580
Slaughter weight (kg)		1	441	482
Growth rate (g/day)		1	1100	753
SD growth rate		2	110	75
Postweaning food consumption (kg, wet)		1	1855	6395
Postweaning gross FCE (g gain/kg food)		3	183.8	59.7
SD FCE		2	18.38	5.97
Carcass weight (kg)		1,3	234	256
Killing-out %		3	53.1	53.1
SD killing-out %		2	2.27	2.27
Carcass lean %		2	59.0	59.0
SD carcass lean %		2	2.56	2.56
Cost of newborn calf (£/head)	*a*	1,4	95	95
Preweaning variable costs (£/head):		1		
food	*b*		38	38
veterinary	*c*		3	3
other	*d*		4	4
Postweaning variable costs (£/head):		1		
food	*e*		205	150[1]
veterinary	*f*		5	6
haulage and bedding	*g*		12	19
Estimated fixed costs (excl. rent) (£/head)	*h*	1,4,5	54	91
Rent for land (£/head)	*i*	1,4,5	-	19
Total food costs (b+e(+i)) (£/head)			243	207
Total non-food costs (excl. rent) (a + c + d + f + g + h)			173	218
Total production costs (£/head)			416	425

All costs adjusted to 1982 prices; [1]includes forage variable costs, see text for explanation.

Sources:
1. Scottish Agricultural Colleges (1982).
2. Assumed (after examining ABRO and literature estimates).
3. Calculated from 1 or 1 and 2.
4. Calculated from MLC 3 year average ratio of estimated calf : variable : fixed costs (J.B. Kilkenny, pers. comm.).
5: MLC, 1981.

TABLE 9.5: Performance data on ABRO Hereford bulls.

Trait[1]	Mean	Standard deviation	Coefficient of variation (%)
Birth weight (kg)	33.9	4.20	12
Growth rate from birth to 400 days (g/day)	890.0	88.70	10
Food conversion efficiency on test (g gain/kg food)	153.0	14.62	10
Dissectible carcass lean % (at 400 days of age)	64.2	2.56	4
Killing-out % (at 485 days of age)	57.7	2.47	4

[1] Ultrasonic fat areas were standardised within years, so data are not presented.

3. fixed costs of production (costs of buildings, machinery, equipment, labour, contractor charges, insurance and finance charges, etc.);
4. rent for land in the 18/20 month beef system (normally included as a fixed cost).

(1) Growth rate

Genetic improvement in GR leads to increased output per animal (i.e. weight of lean meat) at a fixed age. Consequently, fewer improved animals are needed in total, to produce the original national output of lean meat. Assuming that birth weight, FCE, killing-out % and carcass lean % are constant, a genetic improvement in GR to a fixed age at slaughter means that the total number of animals (n_1) is reduced by a proportion G (to n_2).

$$(n_1)(\text{original slaughter weight}) = (n_2)(\text{new slaughter weight})$$

$$G = 1 - \left(\frac{n_2}{n_1}\right)$$

$$G = 1 - \left(\frac{(\text{original GR x days to slaughter}) + \text{birth weight}}{(\text{new GR x days to slaughter}) + \text{birth weight}}\right)$$

This leads to a saving in non-food costs (i.e. cost of the calf, veterinary, haulage and bedding expenses and fixed costs) in the whole beef industry of:

$$(n_1)\ (G)\ (\text{non-food costs/head})$$

Individual animals' FCE is assumed constant, so each improved animal's total food consumption increases by a factor of C:

$$\text{FCE} = \frac{\text{original gain to slaughter}}{\text{original total food consumption}} = \frac{\text{new gain to slaughter}}{\text{new total food consumption}}$$

At a fixed age at slaughter:

$$\frac{\text{new total food consumption}}{\text{original total food consumption}} = \frac{\text{new GR}}{\text{original GR}} = C$$

With fewer animals, proportionately more of the total final slaughter weight comes from weight gained after birth, and less from birth weight. Thus, the food costs for the whole industry will *increase* by:

$(n_2)(C)$(original food costs/head) - (n_1)(original food costs/head)

Substituting $(n_2) = (n_1)(1-G)$, this is:

(n_1)(original food costs/head)$([C-CG]-1)$

The total saving in the whole beef industry will then be:

(n_1) [(G)(non-food costs/head)-([C-CG]-1)(food costs/head)]

In the cereal beef system it is assumed that all food is purchased. In this case, a genetic improvement in GR simply requires more food to be purchased. In the 18/20 month beef system much of the food used is home-grown. In this case, enterprises with improved animals may not have sufficient land to meet the increased food requirements. For this reason, rent of land was added to the forage variable costs plus purchased food costs, to calculate total food costs for the 18/20 month system. It was assumed that a small increase in GR would not increase the costs per animal for buildings, machinery or labour.

Could also apply
to pasture area
more efficient utilization
or more fertilizer

(2) Food conversion efficiency

Calculations of the relative economic value of a unit improvement in FCE refer to the postweaning period, as there were no genetic or phenotypic parameters available for FCE from birth. Gross FCE was calculated from total postweaning 'wet' food consumption as food prices referred to wet weights. The low FCE in the 18/20 month system is due to the large quantity of low dry matter forage consumed.

Improving postweaning FCE reduces the total postweaning food consumption by a factor of F:

$$F = 1 - \left(\frac{\text{(new total food consumption)}}{\text{(original total food consumption)}}\right)$$

Assuming slaughter age, GR etc. are constant:

(original FCE)(original consumption) = (new FCE)(new consumption),

thus,

$$F = 1 - \left(\frac{\text{original FCE}}{\text{new FCE}}\right)$$

If it is assumed that correlated improvements in preweaning FCE lead to about half this saving (i.e. 0.5F[preweaning food costs]), then this increases the relative economic value of improved FCE (Table 9.6). Thus, the saving in the whole beef industry is:

$$n_1[F(\text{postweaning food costs per head}) + 0.5F(\text{preweaning food costs per head})]$$

(3) Killing-out %

Assuming birth weight, GR, FCE (and therefore food consumption per animal) and carcass lean % are constant, a percentage unit increase in killing-out reduces the total number of animals required by a factor of K:

$$K = 1 - \left(\frac{\text{KO }\%}{(\text{KO }\% + 1)}\right)$$

where KO is the original killing out % (53.1%). This represents a saving in the whole beef industry of:

(n_1) (K) (total production costs/head).

(4) Carcass lean %

Assuming birth weight, GR, FCE and killing-out % are constant, a percentage unit increase in carcass lean reduces the total number of animals required to produce the fixed output by a factor of L:

$$L = 1 - \left(\frac{\text{lean }\%}{(\text{lean }\% + 1)}\right)$$

This represents a saving in the whole beef industry of:

(n_1) (L) (total production costs/head).

The relative economic values of all traits are expressed in terms of n_1, so this term can be ignored in calculations.

Table 9.6 shows the economic values of genetic improvement in GR, FCE, killing-out % and carcass lean %. In the cereal beef system, FCE had the highest relative economic value per standard deviation improvement. Killing-out % and lean % had similar economic values, and GR had the lowest value per standard deviation improvement. This reflects the

TABLE 9.6: Relative economic values of genetic improvement in beef performance traits, assuming fixed output.

	Cereal beef		18/20 month beef	
Value of improvement:	per unit	per SD	per unit	per SD
Growth rate (g/day)	£0.12	£13.04	£0.24	£17.81[2]
FCE (g gain/kg food)	£1.21 *(£1.11)*[1]	£22.28 *(£20.39)*	£3.10 *(£2.78)*	£18.48[2] *(£16.61)*
Killing-out %	£7.69	£17.46	£7.86	£17.83[2]
Carcass lean %	£6.93	£17.75	£7.08	£18.13[2]
Relative economic values				
Growth rate		1.00		1.00
FCE		1.71		1.04
Killing-out %		1.34		1.00
Carcass lean %		1.36		1.02

[1] Figures in parentheses exclude the estimated value of correlated improvement in preweaning FCE.

[2] Values used in index calculations (Section 9.2.3).

high ratio of variable to fixed costs in the cereal beef system (4.9 : 1), due to the dependence on expensive, purchased food. In the 18/20 month beef system all traits had similar relative economic values per standard deviation improvement. This reflects a low ratio of variable to fixed costs (2.6 : 1), because of the dependence on home-grown forage, with a concomitant high labour requirement.

Economic values calculated from the producer's viewpoint, allowing increased output, are shown in Table A9.1. The *absolute* economic values of all traits were slightly higher than values calculated from the national viewpoint. The *relative* economic value of GR calculated from the producer's viewpoint was higher than that calculated in the interests of national economy. It has been shown (E.W. Brascamp, personal communication) that different methods of calculating relative economic values tend to give the same results when profit (after subtracting a labour and management fee) tends to zero. In the UK, profit margins for beef production have been low in recent years, which may explain the broadly similar results for economic values calculated from the national interest and the producer's interest. If profit margins increase, there may be greater disparity between economic weights calculated in different ways.

In a national beef improvement programme different economic values for improvement in the various traits should be derived for different breeds and husbandry systems.

9.3 Results

9.3.1 *Index calculations*

Two selection indices were calculated using Cunningham's (1970) Selind computer programme. The economic weights derived for the 18/20 month beef system were used. In each case the aggregate breeding value included GR, FCE, killing-out % and carcass lean % (Table 9.7). Genetic increases in birth weight were completely restricted in index 1. In practice, a partial restriction may be sufficient to prevent a serious increase in calving difficulty. (The theoretical background to the method of restriction used here was discussed by Cunningham, Moen and Gjedrem [1970]).

Correlations between the two selection indices and individual traits in the aggregate breeding value are shown in Table 9.8. There was a small negative correlation between each index and carcass lean %. This indicates that selection on either index will actually lead to a genetic decrease in carcass leanness. However, this decrease in leanness is less than that expected from selection on GR alone. Growth rate, FCE, and to a lesser extent killing-out %, were all positively correlated with the aggregate breeding value. As expected, correlations between GR and the aggregate breeding value were lowest when changes in birth weight were restricted. Index coefficients (b-values) are shown in Table 9.9.

Correlations between combinations of index measurements and the aggregate breeding value are shown in Table 9.10. The expected economic response from one standard deviation of selection on any index is the product of the standard deviation of the aggregate breeding value (£23.57) and the correlation between the index and the aggregate breeding value. Direct comparison of indices 1 and 2 is not valid, as

TABLE 9.7: Traits in the index and in the aggregate breeding value of the two selection indices.

	Index	
	1	2
Birth weight restricted	✓	
Traits in the index:		
Birth weight	✓	
Growth rate	✓	✓
Food conversion efficiency	✓	✓
Ultrasonic fat area	✓	✓
Traits in the aggregate breeding value:		
Birth weight	✓	
Growth rate	✓	✓
Food conversion efficiency	✓	✓
Killing-out %	✓	✓
Carcass lean %	✓	✓

TABLE 9.8: Correlations between the two selection indices and individual traits in the aggregate breeding value.

Index:	1	2
Trait:		
Birth weight	0	-
Growth rate	0.41	0.50
Food conversion efficiency	0.51	0.49
Killing-out %	0.22	0.22
Carcass lean %	-0.06	-0.06

TABLE 9.9: Index coefficients for the two selection indices.

Index:	1	2
Trait:	*Index coefficient (b)*[1]	
Birth weight	-3.675	-
Growth rate	7.973	9.159
Food conversion efficiency	7.684	7.463
Ultrasonic fat area	-3.004	-3.356

[1] Index coefficients refer to standardised traits.

TABLE 9.10: Correlations between combinations of index measurements and the aggregate breeding value (r_{HI}).

Index:	1	2
SD of aggregate breeding value (£):	23.57	23.57
Traits in the index[1]:	r_{HI}	
(BW), GR, FCE, US[2]	0.53	0.57
(BW), GR, FCE	0.52	0.56
(BW), GR, US	0.44	0.49
(BW), FCE, US	0.44	0.46
(BW), GR	0.41	0.47
(BW), FCE	0.44	0.46
(BW), US	0.02	0.01

[1] Index 1 had a restriction on genetic change in birth weight (BW), so this was measured in each case. BW was not measured in index 2.

[2] US = ultrasonic fat area.

the cost of a genetic increase in birth weight is ignored in index 2. However, the maximum reduction in expected economic response due to complete restriction of changes in birth weight was about 8%. Dropping ultrasonic measurements from the index reduced the correlation with the aggregate breeding value by less than 3%. Measuring animals' food consumption in central test stations is very expensive. However, dropping FCE measurements from the index reduced the correlation with the aggregate breeding value by 14 to 18%.

Tables 9.11 and 9.12 show phenotypic correlations between biological selection indices, standardised biological indices, economic indices and performance traits, for the 235 ABRO bulls. All food intake, FCE and LFCE measurements were adjusted for bulls' initial weight on test. As mentioned previously, this adjustment may be justified to avoid selection of animals with low initial weight and very high FCE on test, due to compensatory growth. All indices, except the standardised index of lean and FCE, and economic index 1, showed positive phenotypic correlations with birth weight. Both biological indices involving FCE showed negative correlations with food intake (unadjusted or adjusted for initial weight). Economic indices had small negative correlations with adjusted total food intake, and slightly higher positive correlations with unadjusted food intake. All indices except LGR showed positive correlations with unadjusted and adjusted FCE. LGR and economic indices 1 and 2 were negatively correlated with estimated lean %. This is due to the imbalance of coefficients of variation of lean and GR in the biological index (LGR), and to the relatively low importance of lean % in the economic index.

TABLE 9.11: Correlations between different selection indices on 235 performance tested bulls.

		A	B	C	D	E	F
Lean growth rate	A	1.00	0.39	0.72	0.12	0.76	0.84
Lean food conversion efficiency [1]	B		1.00	0.50	0.84	0.80	0.80
Standardised lean % + standardised GR	C			1.00	0.60	0.62	0.66
Standardised lean % + standardised FCE[1]	D				1.00	0.54	0.50
Index 1 (birth weight restricted) [1]	E					1.00	0.95
Index 2 (no restriction) [1]	F						1.00

[1] FCE and LFCE adjusted to constant initial weight on test.

TABLE 9.12: Correlations between selection indices and other performance traits for 235 tested bulls.

Index	Correlation with: Birth weight	GR 0-400 days	Food intake 200-400 days	Adjusted food intake[1]	FCE 200-400 days	Adjusted FCE[1]	Estimated lean %
Lean growth rate	0.25	0.96	0.67	0.28	-0.07	0.39	-0.22
Lean food conversion efficiency[1]	0.17	0.29	-0.32	-0.39	0.82	0.97	0.22
Standardised lean % + standardised GR	0.12	0.50	0.23	-0.02	0.05	0.33	0.51
Standardised lean % + standardised FCE[1]	0.02	-0.09	-0.54	-0.49	0.72	0.70	0.70
Index 1 (birth weight restricted)[1]	-0.06	0.70	0.14	-0.08	0.50	0.81	-0.07
Index 2 (no restriction)[1]	0.24	0.79	0.26	-0.02	0.44	0.81	-0.12

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[1] Cumulated food intake, FCE and LFCE adjusted to constant initial weight on test.

9. 3. 2 *Sensitivity to changes in parameters*

Economic selection indices are often criticised when they involve assumptions about economic or genetic parameters. Selection indices must be fairly robust to be used confidently in practical animal production. For these reasons, an examination was made of the effects of changes in the economic weights and genetic parameters on the correlation between the index and the aggregate breeding value.

Using matrix notation, the correlation between a selection index and the aggregate breeding value is (e.g. Cunningham, 1970):

$$r_{HI} = \frac{b'Ga}{\sqrt{[(b'Pb)(a'Ca)]}}$$

where:

b = vector of index weights;

a = vector of economic values of traits in the breeding value;

P = variance-covariance matrix of measurements in the index;

C = variance-covariance matrix of traits in the aggregate breeding value;

G = covariance matrix of measurements in the index with traits in the aggregate breeding value.

Different economic parameters (a*) or genetic parameters (C*, G*) will lead to different index weights (b*) and a different index (I*). How do changes in parameters affect selection for the current aggregate breeding value (H)? The response to selection on an index depends on the selection intensity, the correlation between the index and the aggregate breeding value, and the standard deviation of the aggregate breeding value (e.g. Falconer, 1981). Thus, the predicted efficiency of selection on a new index (I*) compared to selection on the original index (I) depends on the correlation between the new index and the original breeding value, and may be defined (e.g. Smith, 1983):

$$\frac{r_{HI*}}{r_{HI}}$$

where $r_{HI*} = \dfrac{b^{*\prime}Ga}{\sqrt{[(b^{*\prime}Pb^{*})(a'Ca)]}}$

The efficiency of selection (r_{HI*}/r_{HI}) was calculated for indices 1 and 2, with a 50% increase or decrease in the relative economic value of each trait in the aggregate breeding value. Changes in the value of GR or FCE had most effect on the predicted efficiency of selection (Table 9.13). However, efficiency was never reduced by more than 3.3% when relative economic values were changed one at a time. Decreasing the economic value of FCE by 50% and simultaneously increasing the value of GR by 50%, or *vice versa*, led to a 6 to 7% drop in efficiency for selection on I* compared to I.

Similarly, individual genetic correlations in the two indices were increased or decreased by 0.2. Changes in single correlations never reduced efficiency by more than 1% (Table 9.14). Even with simultaneous changes of -0.2 in all genetic correlations, selection on I* was 91 to 92% as efficient as selection on I. Correlations between killing-out % and other traits were from a relatively small data set, so larger changes were examined. Changes of 0.4 in these correlations only reduced the predicted efficiency of selection by 0 to 3%.

Individual reductions of 0.1 in heritability estimates never reduced the predicted efficiency of selection by more than 1.5% (Table 9.15). Reductions of 0.2 caused a 0 to 7% drop in efficiency. Efficiency of selection was most sensitive to changes in the heritabilities of GR or FCE. Simultaneous reduction of the heritabilities of all traits in the aggregate breeding value had only a trivial effect on efficiency of selection.

TABLE 9.13: Effects of changes in economic weights on the predicted efficiency of selection.

Index:	1		2	
Change in economic weight:	+50%	-50%	+50%	-50%
Trait changed:	*Efficiency (r_{HI*}/r_{HI})*			
Growth rate	0.989	0.977	0.990	0.977
Food conversion efficiency	0.988	0.967	0.988	0.971
Killing-out %	0.996	0.994	0.997	0.996
Carcass lean %	0.993	0.993	0.994	0.995
GR and FCE + 50%	1.000		1.000	
GR and FCE - 50%	0.997		0.997	
GR + 50%, FCE - 50%	0.930		0.939	
GR - 50%, FCE + 50%	0.942		0.941	

TABLE 9.14: Effects of changes in genetic correlations on the predicted efficiency of selection.

Index:		1		2	
Change in correlation:		+0.2	-0.2	+0.2	-0.2
Correlation changed		*Efficiency* (r_{HI^*}/r_{HI})			
Birth weight,	GR	0.999	1.000		
	FCE	0.999	0.999		
	Ultrasonic fat	1.000	1.000		
	Killing-out %	1.000	1.000		
	Lean %	0.999	1.000		
GR,	FCE	1.000	1.000	1.000	1.000
	Ultrasonic fat	0.997	0.997	0.997	0.997
	Killing-out %	0.995	0.993	0.996	0.995
	Lean %	0.994	0.993	1.000	0.994
FCE,	Ultrasonic fat	0.996	0.997	0.997	0.997
	Killing-out %	0.995	0.994	0.996	0.994
	Lean %	0.995	0.994	0.995	0.994
Ultrasonic fat,	Killing-out %	0.997	0.997	0.997	0.997
	Lean %	0.997	0.997	0.997	0.997
All correlations changed		0.965	0.918	0.974	0.910

TABLE 9.15: Effects of changes in heritability estimates on the predicted efficiency of selection.

Index:	1		2	
Change in heritability:	-0.1	-0.2	-0.1	-0.2
Trait changed	*Efficiency* (r_{HI*}/r_{HI})			
Birth weight	1.000	1.000		
Growth rate	0.986	0.931	0.989	0.942
Food conversion efficiency	0.988	0.936	0.989	0.944
Ultrasonic fat area	1.000	1.000	1.000	1.000
Killing-out %	1.000	0.998	1.000	0.999
Carcass lean %	1.000	0.998	1.000	0.998
All traits	1.000	1.000	1.000	1.000

9.4 Discussion and Conclusions

Economic index selection was originally examined because of the very low weighting often given to lean % in the biological indices LGR and LFCE (Chapters VII and VIII). However, lean % was also given a rather low weighting in the economic indices derived in this chapter. Ultrasonic measurements could be dropped from indices 1 and 2 with virtually no effect on the expected economic response to selection. Economic index selection will still be preferable to selection on LGR and LFCE, as the weightings given to each trait will be more stable from one cycle of selection to the next. Additionally, economic indices permit the restriction of genetic increase in birth weight, which is expected following selection on growth rate and related traits.

Economic evaluation of genetic improvement is a contentious area, but the two methods used in this chapter produced broadly similar results. Also, the indices examined appeared insensitive to quite wide changes in the relative economic value of traits in the aggregate breeding value. The variation in economic values considered here is likely to exceed variation between different production systems, and between different methods of calculation. Similarly, moderate fluctuations in the ratio of food costs to non-food costs (or the ratio of production costs to product value, for indices using economic weights calculated from the producer's viewpoint) should not significantly reduce the efficiency of selection. Indices were also insensitive to moderate changes in genetic correlations and heritabilities of traits in the aggregate breeding value. These results support those of Fowler *et al*. (1976), Vandepitte and Hazel (1977) and Smith (1983). Fowler *et al*. (1976) examined a pig selection index with seven traits in the aggregate breeding value. Changes of 50% in the economic value of individual traits never reduced the efficiency of selection by more than 2%. Similarly, changes of ±0.2 in genetic correlations, and -0.1 in heritability estimates reduced predicted efficiency of selection by less than 3.2% and 0.6%, respectively.

Thus, it appears that changes in economic and genetic parameters are likely to have only a trivial effect on the overall economic merit of selected animals, though the biological performance of animals selected by different indices may differ. The indices derived in this chapter may be sufficiently robust for use in a practical improvement programme. However, the use of selection indices does not avoid the problems of pre-test effects. If test performance, especially FCE, is influenced by pre-test environment, then the efficiency of selection may be reduced considerably.

CHAPTER X

Final Discussion and Conclusions

In vivo estimation of body composition has an important role in practical and experimental animal production. Ultrasonic techniques have been used quite successfully to evaluate the carcass composition of live cattle, for the past 20 years. During this time simple 'A'-mode machines have been largely replaced by more sophisticated 'B'-mode machines, with only a slight improvement in the precision of predicting carcass composition. Results of most modern pulse-echo scanners still require subjective interpretation. Consequently, best results are achieved by skilled operators, who are using the machines regularly. Marked improvements in the accuracy of these ultrasonic machines are unlikely, since correlations between ultrasonic fat area measurements and carcass composition are often as high as correlations between measurements on the carcass and total composition. Further improvements may come from techniques which respond to intermuscular and intramuscular fat, as well as subcutaneous fat. For example, direct measurement of the velocity of ultrasound through the hind limb of cattle has given promising results, and requires no subjective interpretation. Similarly, computerised tomography could be useful in future, especially if machines become less expensive.

Death rates from coronary heart disease in the UK are among the highest in the world. Several recent reports from the medical profession and from human nutritionists have recommended a reduction of fat in the diet, because of its association with heart disease. Already there is strong consumer discrimination against animal fat. However, further changes in public attitudes to the diet are expected in the next 15 years (New Scientist, 14th July, 1983).

In the mid to late 1970's it was estimated that there was considerable excess fat production in Britain - 48 000 tonnes from beef cattle in 1976 (Kempster and Harrington, 1979), 25 000 tonnes from sheep in 1977 (Kempster, 1979), and 140 000 tonnes of pig fat in 1978 (Chadwick and Kempster, 1980). There may have been some improvement in reducing excess fat since these estimates were made, especially in pigs, but further reductions in the average level of fatness of all species are still required. Fallows (1983) suggested that producer attitudes, current payment schemes, inconsistent grading of carcasses, and poor communication between buyers and suppliers were barriers to the production of leaner meat. The lack of a financial incentive to producers is probably the greatest barrier, but this is a political rather than a scientific problem.

Assuming this incentive for leaner meat is provided, are genetic changes in carcass composition desirable? At least in ruminants, it may be a waste of selection pressure to select for leanness *per se*. If production of lean meat becomes financially attractive, producers could respond very rapidly, simply by slaughtering animals at a younger age, or restricting their food intake. These changes in management would be flexible, and avoid unfavourable correlated genetic changes. For example, selection for leanness in pigs may have led to reduced fertility and meat quality, and increased stress susceptibility, though a single gene may be responsible for these deleterious effects (Chapter V). It has also been suggested that selection for leanness in grazing animals may increase the maintenance costs of the breeding population (Webster, 1977, 1980a). However, this argument was based on a comparison of breeds and crosses, and may not hold within a breed. It also seems unlikely that carcass composition will become an important objective for suckler herds. Carter (1982) suggested that selection for LGR may reduce tolerance to changes in forage supply, though no experimental evidence was presented. If this suggestion proves to be correct it would influence selection decisions in terminal sire breeds in the UK, as most progeny are reared extensively. Much more information is needed on energy partition and efficiency in beef cattle. Comparison of selected and control lines of ABRO Hereford cattle may provide some information in several years time.

At first sight, the biological indices LGR and LFCE appear to be useful selection criteria for increasing the efficiency of lean meat production in terminal sire breeds. However, results in Chapter VIII show that there may be little loss in expected response in LGR or LFCE from indirect selection on their most variable components (GR or FCE). In this case, *in vivo* estimation of carcass composition may not be cost-effective. This result has implications for selection on other product traits. In some circumstances, it may be possible to drop expensive or difficult measurements of a component trait, with little effect on response in the product trait.

Economic index selection was examined as an alternative to selection on LGR and LFCE in terminal sire beef breeds. There was a low negative correlation between the two selection indices derived and carcass lean % (-0.06). Selection on these indices would therefore slightly decrease lean %, but improve the economic efficiency of lean meat production. Ultrasonic measurements could be dropped with only a trivial effect on expected economic response. The indices were fairly insensitive to considerable changes in the relative economic values of GR, FCE, killing-out % and lean %. Thus, the indices could be useful in improving efficiency of beef production, both from the national viewpoint, and from the individual producers' viewpoint. Many terminal sire breeders have concentrated on GR as a selection objective. This may lead to correlated improvements in FCE, but selection indices would weight the two traits to achieve the maximum economic response to selection. Additionally, genetic increases in birth weight may be restricted in selection indices. This may prevent an increase in the incidence of calving difficulty, which is expected following selection on GR or related traits. Indices similar to those derived may be attractive to breeders of the smaller terminal sire breeds. It may be in their long-term interest to exploit easy calving and efficiency of growth, rather than trying to compete with larger breeds by selecting solely for increased growth rate.

There is a marked deficiency of genetic information on GR, FCE, ultrasonic measurements and carcass composition for beef cattle in Britain. Though the selection indices derived were fairly insensitive to changes in genetic parameters, it would still be preferable to have comprehensive sets of parameters for the most important terminal sire breeds and production systems. However, it seems unlikely that funds will be available to obtain such data.

There may be little advantage in using selection indices if the central test performance is dominated by environmental effects. There is growing evidence of a weak relationship between the performance of bulls centrally tested from a late age, and the performance of their progeny. In New Zealand, where bulls are tested under pastoral conditions from a late age, growth traits had a very low effective heritability (Baker *et al*., 1982). In contrast, De Roo and Fimland (1983) reported quite a high genetic correlation between the growth rate of dairy and dual-purpose bulls tested from 90 days of age, and the slaughter weight of their progeny. It appears that testing bulls from a young age may reduce environmental effects on performance and increase the accuracy of identifying bulls with genetically superior performance on test. However, there may still be a weak relationship between bulls' test performance and the performance of progeny on commercial farms. In pigs, for example, Bampton, Curran and Kempson (1977) and Standal (1977) reported rather low genetic correlations between performance on central testing stations and 'on-farm' performance. The situation could be worse in the beef industry, as station and farm environments are probably less similar than in the pig industry. In Britain, MLC central tests for beef bulls start at 150 to 190 days of age. Here there may be large pre-test environmental effects and genotype x test environment interactions. The efficacy of these tests for identifying genetically superior bulls for commercial production therefore needs to be checked urgently.

In the present study, artificial rearing of beef bulls was not effective in reducing environmental variation in performance. Artificially reared bulls had poor pre-test GR, which led to compensatory growth on test. This reduces the accuracy of selection, especially for traits such as FCE which are only measured from 200 days of age. The poor performance of artificially reared bulls may be specific to the ABRO herd, or it may apply more generally to beef breeds. Weaning bulls at 84 days of age, rather than 168 days of age, reduced the effects of dam age and season of birth on most performance traits in the present study. There was no detrimental effect of early weaning on bull performance. These results indicate that central performance tests of beef bulls could start at 2 to 3 months of age - earlier than current MLC tests, and much earlier than the upper age limit of 7 months recommended by the European Association for Animal Production (Andersen *et al*., 1981). This would also reduce the herd effects which tend to dominate central tests (Chapter V).

Within each of the rearing treatments examined in this study, some bulls showed compensatory growth on test. In national tests this may be reduced by rejecting bulls below a given weight at the start of test. In the results presented there was no evidence that measuring performance over a weight interval rather than an age interval, or extending the test period, significantly reduced pre-test environmental effects.

At present, animal breeding advice and technical services of government organisations are spread rather thinly over many beef breeding herds. Many breeders may not be fully using the information provided. It may be more effective to concentrate services on groups of innovative breeders. If the starting age for central performance tests was greatly reduced, many breeders may refuse to submit bulls. However, this would leave those breeders most interested in genetic improvement.

Group Breeding Schemes or Sire Referencing Schemes may be useful alternatives to central testing in future genetic improvement programmes. They permit clearer definition of objectives to suit individual breeds, or groups of breeders, and animals are tested under commercial conditions. It is possible that the financial resources and manpower currently devoted to central testing would be more effective in providing advice, financial support, and a high standard of recording (including FCE where appropriate) for participants in Group Breeding Schemes (especially nucleus herds) and Sire Referencing Schemes. Genetic improvement in these co-operatives could be boosted by using superovulation and embryo transfer or, in future, techniques such as embryo splitting. With the current recession in the beef industry, there may be many groups of breeders who would be receptive to a new approach.

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APPENDIX

TABLE A3.1: Nutritional information on the dried grass/ barley complete diet.

Dry matter (DM) (g/kg)	910.1
Crude protein (g/kg DM)	154.7
Fibre (g/kg DM)	155.7
Digestibility of organic matter in DM (*in vitro*) (g/kg)	745.5
Metabolisable energy (derived)(MJ/kg DM)	11.7

Based on 14 samples.

Information kindly supplied by
Dr. M. Lewis, ESCA.

TABLE A3.2: Chi-squared test on interpretation of Danscanner scans - trial 1 (40 animals, 3 scans per animal on each occasion).

	Repeat measurement of DFA	
Interpretation	discordant	concordant
Difficult	34	118
Easy	7	81

$\chi^2 = 8.19$ ($P < 0.01$)

TABLE A4.1: Precision of predicting carcass composition from Danscanner ultrasonic measurements.

Model	Independent variables	No.	% lean		% fat	
			R^2	RSD	R^2	RSD
A1	Age, LW, DFA 10, 13, 3, DMA 10, 13, 3	54	0.69	2.18	0.75	2.49
A2	Age, LW, DFA 10, 13, DMA 10, 13, 3		0.69	2.15	0.75	2.45
A3	Age, LW, DFA 10, 13, 3, DMA 10, 13		0.69	2.16	0.74	2.51
A4	Age, LW, DFA 10, 13, 3, DMA 10		0.69	2.14	0.74	2.48
A5	Age, LW, DFA 10, 13, 3		0.67	2.17	0.73	2.49
A6	Age, LW, DFA 10, 13		0.67	2.15	0.73	2.47
A7	Age, LW, DFA 13, 3		0.65	2.21	0.72	2.50
A8	Age, LW, DFA 10, 3		0.64	2.23	0.70	2.58
A9	Age, LW, DFA 13		0.64	2.19	0.71	2.50
A10	Age, LW		0.35	2.92	0.43	3.48
A11	Age		0.33	2.92	0.37	3.60
A12	LW		0.34	2.91	0.43	3.43
A13	LW, DFA 10, 13, 3		0.65	2.21	0.73	2.47
A14	LW, DFA 10, 13		0.65	2.18	0.72	2.46
A15	LW, DFA 13, 3		0.61	2.28	0.71	2.50
A16	LW, DFA 10, 3		0.63	2.24	0.70	2.55
A17	LW, DFA 13		0.61	2.26	0.71	2.50
A18	LW, DFA 10		0.59	2.31	0.65	2.74
A19	LW, DFA 3		0.56	2.41	0.66	2.68
A20	Age^1, LW^a, DFA 10^a, 13^a, 3^a		0.72	2.12	0.80	2.29
A21	Age^1, LW^a, DFA 10^a, 13, 3^a		0.72	2.08	0.80	2.26
A22	Age^1, LW^a, DFA 10^a, 13^a		0.67	2.23	0.74	2.54
A23	Age^1, LW^a, DFA 13^a, 3^a		0.67	2.23	0.76	2.40
A24	Age^1, LW^a, DFA 13, 3^a		0.67	2.21	0.75	2.41
A25	Age^1, LW^a, DFA 10^a, 3^a		0.71	2.11	0.78	2.32
A26	Age^1, LW^a, DFA 10^a		0.60	2.40	0.66	2.82
A27	Age^1, LW^a, DFA 13^a		0.63	2.29	0.72	2.56
A28	Age^1, LW^a, DFA 3^a		0.61	2.36	0.70	2.62
A29	Age^1, LW, DFA 10		0.59	2.34	0.65	2.77
A30	Age^1, LW, DFA 13		0.61	2.28	0.71	2.53
A31	Age^1, LW, DFA 3		0.57	2.41	0.66	2.71
A32	Age^1, DFA 10		0.59	2.32	0.62	2.82
A33	Age^1, DFA 13		0.61	2.25	0.70	2.54
A34	Age^1, DFA 3		0.57	2.38	0.66	2.69
A35	Age^1, LW^a, DFA 13^a, 3^a	78	0.67	2.48	0.74	2.87
A36	Age^1, LW^a, DFA 13, 3^a		0.66	2.47	0.73	2.88
A37	Age^1, LW^a, DFA 13, 3		0.63	2.55	0.70	2.99
A38	Age^1, LW, DFA 13, 3		0.63	2.53	0.70	2.97
A39	Age^1, LW^a, DFA 13^a		0.62	2.60	0.68	3.07
A40	Age^1, LW, DFA 13		0.61	2.59	0.68	3.05
A41	Age^1, LW^a		0.41	3.17	0.50	3.81

^{1} = Main effect.

a = Partial regression within age-class.

Variables without a superscript are partial regressions over both age classes.

All models include day of slaughter.

TABLE A4.2: Precision of predicting carcass composition from Scanogram ultrasonic measurements.

Model	Independent variables	No.	% lean		% fat	
			R^2	RSD	R^2	RSD
A42	Age, LW, SFA 10, 13, 3	29	0.66	2.46	0.74	3.11
A43	LW, SFA 10, 13, 3		0.64	2.45	0.73	3.09
A44	Age, LW, SFA 13, 3		0.65	2.42	0.74	3.04
A45	Age, LW, SFA 10, 13		0.61	2.55	0.71	3.22
A46	LW, SFA 13, 3		0.63	2.40	0.73	3.02
A47	LW, SFA 10, 13		0.61	2.50	0.71	3.16
A48	LW, SFA 10, 3		0.52	2.76	0.66	3.42
A49	LW, SFA 10		0.46	2.84	0.61	3.53
A50	LW, SFA 13		0.60	2.44	0.71	3.09
A51	LW, SFA 3		0.46	2.84	0.61	3.55
A52	Age^1, LW^a, SFA 13^a, 3^a	39	0.77	2.28	0.79	2.83
A53	Age^1, LW^a, SFA 13^a, 3		0.77	2.25	0.79	2.79
A54	Age^1, LW^a, SFA 13^a		0.75	2.31	0.77	2.89
A55	Age^1, LW^a, SFA 3		0.67	2.59	0.70	3.20
A56	Age^1, SFA 13		0.68	2.44	0.72	2.99
A57	Age^1, SFA 3^a		0.61	2.75	0.66	3.34
A58	Age^1, LW^a		0.47	3.22	0.50	4.06
A59	Age^1, LW^a, SFA 13^a, 10^a	38	0.76	2.43	0.77	3.07
A60	Age^1, LW, SFA 13^a, 10		0.75	2.37	0.75	3.05
A61	Age^1, LW, SFA 13^a		0.75	2.34	0.75	3.00
A62	Age^1, LW, SFA 10		0.59	2.95	0.60	3.75
A63	Age^1, SFA 13		0.66	2.60	0.70	3.15
A64	Age^1, SFA 10		0.58	2.92	0.60	3.68
A65	Age^1, LW		0.37	3.57	0.40	4.51

^{1} = Main effect.

^{a} = Partial regression within age-class.

Variables without superscripts are partial regressions over both age classes.

All models include day of slaughter.

TABLE A4.3: Precision of predicting carcass composition from Scanogram ultrasonic measurements, Weighband and skinfold thickness measurements (42 animals).

Model	Independent variables	% lean		% fat	
		R^2	RSD	R^2	RSD
A66	Age, LW, WB, SFT, AFT, SFA 10, 13, 3	0.68	2.40	0.80	2.74
A67	Age, LW, WB, SFT, AFT, SFA 10, 13	0.68	2.36	0.80	2.70
A68	LW, WB, SFT, AFT, SFA 10, 13	0.68	2.32	0.80	2.65
A69	LW, WB, AFT, SFA 10, 13	0.68	2.29	0.79	2.64
A70	LW, WB, SFT, SFA 10, 13	0.68	2.29	0.80	2.63
A71	LW, WB, SFA 10, 13	0.68	2.26	0.79	2.60
A72	LW, SFA 10, 13	0.67	2.25	0.78	2.64
A73	LW, SFA 13, 3	0.66	2.27	0.78	2.66
A74	LW, SFA 10, 3	0.63	2.39	0.75	2.81
A75	WB, SFA 10, 13	0.66	2.29	0.78	2.66
A76	WB, SFA 13, 3	0.65	2.31	0.77	2.70
A77	WB, SFA 10, 3	0.62	2.41	0.75	2.80
A78	LW, WB, SFA 13	0.67	2.25	0.79	2.60
A79	LW, WB, SFA 10	0.64	2.33	0.77	2.70
A80	LW, WB, SFA 3	0.58	2.53	0.73	2.96
A81	LW, SFA 13	0.66	2.24	0.78	2.63
A82	LW, SFA 10	0.62	2.36	0.75	2.79
A83	LW, SFA 3	0.56	2.57	0.70	3.06
A84	Age, LW, WB, SFT, AFT	0.50	2.87	0.64	3.47
A85	LW, WB, SFT, AFT	0.49	2.83	0.64	3.42
A86	LW, WB, SFT	0.49	2.79	0.64	3.37
A87	LW, WB, AFT	0.48	2.82	0.64	3.38
A88	LW, WB	0.48	2.78	0.64	3.33
A89	LW	0.42	2.89	0.58	3.55
A90	WB	0.45	2.82	0.62	3.39
A91	SFT	0.44	2.85	0.58	3.54
A92	AFT	0.41	2.91	0.57	3.61
A93	Age^1, LW^a, WB^a, SFT^a, AFT^a, SFA 10^a, 13^a, 3^a	0.66	2.59	0.82	2.71
A94	Age^1, LW^a, WB^a, SFT, AFT, SFA 10^a, 13^a, 3^a	0.66	2.49	0.82	2.63
A95	Age^1, LW^a, WB, SFT, AFT, SFA 10^a, 13^a, 3^a	0.66	2.45	0.82	2.59
A96	Age^1, LW^a, WB, SFT, SFA 10^a, 13^a, 3^a	0.65	2.41	0.81	2.56
A97	Age^1, LW^a, WB, SFT, SFA 10, 13	0.63	2.35	0.80	2.48
A98	Age^1, LW^a, WB, SFA 10, 13	0.62	2.34	0.80	2.45
A99	Age^1, LW^a, SFT, SFA 10, 13	0.62	2.34	0.79	2.51
A100	Age^1, LW^a, SFA 10^a, 13^a, 3^a	0.63	2.41	0.80	2.58
A101	Age^1, LW^a, SFA 10, 13^a, 3^a	0.63	2.38	0.80	2.54
A102	Age^1, LW^a, SFA 10, 13^a, 3	0.62	2.37	0.79	2.52
A103	Age^1, LW^a, SFA 10, 3	0.60	2.36	0.77	2.60
A104	Age^1, LW^a, SFA 10, 13^a	0.62	2.33	0.79	2.51
A105	Age^1, LW^a, SFA 10, 13	0.61	2.33	0.79	2.49
A106	Age^1, LW, SFA 10, 13	0.58	2.39	0.76	2.58
A107	Age^1, LW^a, SFA 10	0.60	2.34	0.74	2.70
A108	Age^1, LW^a, SFA 13	0.57	2.42	0.77	2.56

^{1} = Main effect.

a = Partial regression within age-class.

Variables without superscripts are partial regressions over both age classes.

Models 62 to 88 include day of slaughter.

TABLE A6.1: Variation in live weight and food intake accounted for by year-season of birth.

Age at weaning (days)		0			84			168		
No. bulls		69			80			86		
Trait	Age (days)	R^2	RSD	P	R^2	RSD	P	R^2	RSD	P
Live weight (kg)	0	0.28	4.8	**	0.17	3.9	*	0.10	5.0	
	56	0.25	14.8	*	0.23	11.9	**	0.18	13.1	*
	113	0.31	20.8	**	0.29	17.6	***	0.20	17.6	*
	170	0.23	28.0	*	0.19	24.5	*	0.23	23.5	**
	198	0.19	31.0		0.12	27.7		0.20	25.2	*
	225	0.16	34.5		0.08	30.0		0.12	27.5	
	253	0.13	37.7		0.08	32.5		0.04	30.8	
	281	0.14	38.4		0.10	34.2		0.07	35.3	
	309	0.16	36.9		0.10	34.6		0.05	35.4	
	337	0.17	37.5		0.14	37.1		0.07	37.5	
	365	0.20	39.5	*	0.18	40.0	*	0.08	39.3	
	393	0.25	37.4	*	0.18	40.6	*	0.11	40.1	
Cumulated food intake from 200 days (kg)	225	0.08	32.4		0.14	31.2		0.05	25.3	
	253	0.16	59.9		0.07	58.0		0.03	52.4	
	281	0.24	79.1	*	0.11	84.5		0.07	73.8	
	309	0.26	101.9	**	0.15	108.0		0.11	96.7	
	337	0.25	119.6	*	0.17	133.3	*	0.12	114.0	
	365	0.26	136.0	**	0.17	160.0		0.13	140.4	
	393	0.29	154.8	**	0.14	185.1		0.14	160.9	
Cumulated FCE from 200 days (g/kg food)	225	0.09	57.4		0.07	76.9		0.17	78.6	*
	253	0.26	47.0	**	0.20	45.8	*	0.16	49.1	
	281	0.30	29.6	**	0.21	33.0	*	0.18	30.9	*
	309	0.18	29.3		0.21	25.1	*	0.21	24.2	**
	337	0.22	25.8	*	0.15	23.3		0.18	21.0	*
	365	0.15	23.7		0.13	20.2		0.22	20.6	**
	393	0.12	21.5		0.20	17.7	*	0.36	15.5	***

TABLE A6.2: Variation in live weight and food intake accounted for by dam age.

Age at weaning (days)		0			84			168		
No. bulls		69			80			86		
Trait	Age (days)	R^2	RSD	P	R^2	RSD	P	R^2	RSD	P
Live weight (kg)	0	0.26	4.7	***	0.21	3.8	**	0.24	4.5	***
	56	0.08	16.0		0.20	11.9	**	0.37	11.3	***
	113	0.12	22.9		0.26	17.6	***	0.34	15.7	***
	170	0.05	30.4		0.11	25.2		0.22	23.2	***
	198	0.04	32.9		0.09	27.5		0.19	24.9	**
	225	0.01	36.5		0.06	29.6		0.22	25.4	***
	253	0.02	39.2		0.04	32.4		0.25	26.7	***
	281	0.02	40.1		0.04	34.7		0.24	31.2	***
	309	0.02	38.9		0.04	35.0		0.29	30.2	***
	337	0.01	40.0		0.04	38.4		0.29	32.1	***
	365	0.01	42.8		0.07	41.3		0.26	34.7	***
	393	0.01	41.8		0.09	41.9		0.28	35.5	***
Cumulated food intake from 200 days (kg)	225	0.02	32.6		0.04	32.4		0.03	25.1	
	253	0.00	63.6		0.03	58.2		0.10	49.3	
	281	0.01	88.3		0.02	87.1		0.11	70.7	*
	309	0.02	114.5		0.03	113.4		0.14	93.2	*
	337	0.01	133.6		0.05	140.4		0.18	108.3	**
	365	0.01	154.6		0.04	168.4		0.19	132.6	**
	393	0.02	176.8		0.04	191.8		0.19	153.6	**
Cumulated FCE from 200 days (g/kg food)	225	0.12	55.0		0.06	76.0		0.09	80.8	
	253	0.03	52.4		0.07	48.6		0.03	51.6	
	281	0.03	34.0		0.06	35.3		0.02	33.2	
	309	0.06	30.6		0.07	26.7		0.06	26.0	
	337	0.05	27.9		0.09	23.6		0.05	22.2	
	365	0.03	24.8		0.10	20.1		0.07	22.1	
	393	0.03	22.0		0.04	19.1		0.17	17.4	**

TABLE A6.3: Calf mortality according to year of birth, sex and weaning age.

		Male			Female
Weaning age (days)		0	84	168	168
Year[1]					
1980	No. born alive	32	31	40	85
	No. dead 0-3 months	7 *(22%)*	1 *(3%)*	3 *(8%)*	4 *(5%)*
	No. dead 0-6 months	9 *(28%)*	2 *(6%)*	5 *(13%)*	5 *(6%)*
1981	No. born alive	24	23	35	92
	No. dead 0-3 months	3 *(13%)*	5 *(22%)*	1 *(3%)*	2 *(2%)*
	No. dead 0-6 months	5 *(21%)*	6 *(26%)*	1 *(3%)*	6 *(7%)*
1982	No. born alive	25	27	26	83
	No. dead 0-3 months	3 *(12%)*	0	0	2 *(2%)*
	No. dead 0-6 months	4 *(16%)*	1 *(4%)*	1 *(4%)*	3 *(4%)*
1980-1982	No. born alive	81	81	101	260
	No. dead 0-3 months	13 *(16%)*	6 *(7%)*	4 *(4%)*	8 *(3%)*
	No. dead 0-6 months	18 *(22%)*	9 *(11%)*	7 *(7%)*	14 *(5%)*

[1] Reliable data were not available for 1978 and 1979.

TABLE A8.1: Expected phenotypic correlation between a product trait (xyz) and one component (x) for different ratios of coefficients of variation of component traits, and different phenotypic correlations between components (x, y and z).[1]

CV_y/CV_x	CV_z/CV_x	$r_{x,y}$	$r_{x,z}$	$r_{y,z}$	Expected $r_{x,xyz}$
0.30	0.30	−0.5	−0.5	−0.5	1.00
0.30	0.30	−0.5	−0.5	0	0.92
0.30	0.30	−0.5	−0.5	0.5	0.86
0.30	0.30	−0.5	0	−0.5	0.96
0.30	0.30	−0.5	0	0.0	0.91
0.30	0.30	−0.5	0	0.5	0.86
0.30	0.30	−0.5	0.5	−0.5	0.96
0.30	0.30	−0.5	0.5	0	0.92
0.30	0.30	0	−0.5	−0.5	0.96
0.30	0.30	0	−0.5	0.0	0.91
0.30	0.30	0	−0.5	0.5	0.86
0.30	0.30	0	0.0	−0.5	0.96
0.30	0.30	0	0.0	0.0	0.92
0.30	0.30	0	0.0	0.5	0.89
0.30	0.30	0	0.5	−0.5	0.98
0.30	0.30	0	0.5	0.0	0.95
0.30	0.30	0	0.5	0.5	0.92
0.30	0.30	0.5	−0.5	−0.5	0.96
0.30	0.30	0.5	−0.5	0	0.92
0.30	0.30	0.5	0	−0.5	0.98
0.30	0.30	0.5	0	0.0	0.95
0.30	0.30	0.5	0	0.5	0.92
0.30	0.30	0.5	0.5	0	0.97
0.30	0.30	0.5	0.5	0.5	0.95
0.30	0.65	−0.5	−0.5	−0.5	0.87
0.30	0.65	−0.5	−0.5	0	0.70
0.30	0.65	−0.5	−0.5	0.5	0.60
0.30	0.65	−0.5	0	−0.5	0.84
0.30	0.65	−0.5	0	0.0	0.77
0.30	0.65	−0.5	0	0.5	0.72
0.30	0.65	−0.5	0.5	−0.5	0.91
0.30	0.65	−0.5	0.5	0	0.86
0.30	0.65	0	−0.5	−0.5	0.83
0.30	0.65	0	−0.5	0.0	0.73
0.30	0.65	0	−0.5	0.5	0.66
0.30	0.65	0	0.0	−0.5	0.87
0.30	0.65	0	0.0	0.0	0.81
0.30	0.65	0	0.0	0.5	0.77
0.30	0.65	0	0.5	−0.5	0.94
0.30	0.65	0	0.5	0.0	0.90
0.30	0.65	0	0.5	0.5	0.86
0.30	0.65	0.5	−0.5	−0.5	0.84
0.30	0.65	0.5	−0.5	0	0.77
0.30	0.65	0.5	0	−0.5	0.90
0.30	0.65	0.5	0	0.0	0.85
0.30	0.65	0.5	0	0.5	0.81
0.30	0.65	0.5	0.5	0	0.94
0.30	0.65	0.5	0.5	0.5	0.90
0.30	0.95	−0.5	−0.5	−0.5	0.55
0.30	0.95	−0.5	−0.5	0	0.44
0.30	0.95	−0.5	−0.5	0.5	0.37
0.30	0.95	−0.5	0	−0.5	0.72
0.30	0.95	−0.5	0	0.0	0.65
0.30	0.95	−0.5	0	0.5	0.60
0.30	0.95	−0.5	0.5	−0.5	0.86
0.30	0.95	−0.5	0.5	0	0.82
0.30	0.95	0	−0.5	−0.5	0.60
0.30	0.95	0	−0.5	0.0	0.51
0.30	0.95	0	−0.5	0.5	0.46
0.30	0.95	0	0.0	−0.5	0.77
0.30	0.95	0	0.0	0.0	0.71
0.30	0.95	0	0.0	0.5	0.66
0.30	0.95	0	0.5	−0.5	0.90
0.30	0.95	0	0.5	0.0	0.86
0.30	0.95	0	0.5	0.5	0.82
0.30	0.95	0.5	−0.5	−0.5	0.66
0.30	0.95	0.5	−0.5	0	0.58
0.30	0.95	0.5	0	−0.5	0.81
0.30	0.95	0.5	0	0.0	0.76
0.30	0.95	0.5	0	0.5	0.72
0.30	0.95	0.5	0.5	0	0.90
0.30	0.95	0.5	0.5	0.5	0.87

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[1] All combinations of the correlations [-0.5, 0.5, 0.5] produced impossible partial correlations, so are excluded from the table.

TABLE A8.1 (continued):

CV_y/CV_x	CV_z/CV_x	$r_{x,y}$	$r_{x,z}$	$r_{y,z}$	Expected $r_{x,xyz}$
0.65	0.30	−0.5	−0.5	−0.5	0.87
0.65	0.30	−0.5	−0.5	0	0.70
0.65	0.30	−0.5	−0.5	0.5	0.60
0.65	0.30	−0.5	0	−0.5	0.83
0.65	0.30	−0.5	0	0.0	0.73
0.65	0.30	−0.5	0	0.5	0.66
0.65	0.30	−0.5	0.5	−0.5	0.84
0.65	0.30	−0.5	0.5	0	0.77
0.65	0.30	0	−0.5	−0.5	0.84
0.65	0.30	0	−0.5	0.0	0.77
0.65	0.30	0	−0.5	0.5	0.72
0.65	0.30	0	0.0	−0.5	0.87
0.65	0.30	0	0.0	0.0	0.81
0.65	0.30	0	0.0	0.5	0.77
0.65	0.30	0	0.5	−0.5	0.90
0.65	0.30	0	0.5	0.0	0.85
0.65	0.30	0	0.5	0.5	0.81
0.65	0.30	0.5	−0.5	−0.5	0.91
0.65	0.30	0.5	−0.5	0	0.86
0.65	0.30	0.5	0	−0.5	0.94
0.65	0.30	0.5	0	0.0	0.90
0.65	0.30	0.5	0	0.5	0.86
0.65	0.30	0.5	0.5	0	0.94
0.65	0.30	0.5	0.5	0.5	0.90
0.65	0.65	−0.5	−0.5	−0.5	1.00
0.65	0.65	−0.5	−0.5	0	0.47
0.65	0.65	−0.5	−0.5	0.5	0.36
0.65	0.65	−0.5	0	−0.5	0.77
0.65	0.65	−0.5	0	0.0	0.62
0.65	0.65	−0.5	0	0.5	0.53
0.65	0.65	−0.5	0.5	−0.5	0.84
0.65	0.65	−0.5	0.5	0	0.74
0.65	0.65	0	−0.5	−0.5	0.77
0.65	0.65	0	−0.5	0.0	0.62
0.65	0.65	0	−0.5	0.5	0.53
0.65	0.65	0	0.0	−0.5	0.84
0.65	0.65	0	0.0	0.0	0.74
0.65	0.65	0	0.0	0.5	0.66
0.65	0.65	0	0.5	−0.5	0.92
0.65	0.65	0	0.5	0.0	0.84
0.65	0.65	0	0.5	0.5	0.78
0.65	0.65	0.5	−0.5	−0.5	0.84
0.65	0.65	0.5	−0.5	0	0.74
0.65	0.65	0.5	0	−0.5	0.92
0.65	0.65	0.5	0	0.0	0.84
0.65	0.65	0.5	0	0.5	0.78
0.65	0.65	0.5	0.5	0	0.93
0.65	0.65	0.5	0.5	0.5	0.87
0.65	0.95	−0.5	−0.5	−0.5	0.61
0.65	0.95	−0.5	−0.5	0	0.23
0.65	0.95	−0.5	−0.5	0.5	0.17
0.65	0.95	−0.5	0	−0.5	0.66
0.65	0.95	−0.5	0	0.0	0.52
0.65	0.95	−0.5	0	0.5	0.45
0.65	0.95	−0.5	0.5	−0.5	0.81
0.65	0.95	−0.5	0.5	0	0.71
0.65	0.95	0	−0.5	−0.5	0.60
0.65	0.95	0	−0.5	0.0	0.45
0.65	0.95	0	−0.5	0.5	0.37
0.65	0.95	0	0.0	−0.5	0.77
0.65	0.95	0	0.0	0.0	0.66
0.65	0.95	0	0.0	0.5	0.58
0.65	0.95	0	0.5	−0.5	0.90
0.65	0.95	0	0.5	0.0	0.82
0.65	0.95	0	0.5	0.5	0.75
0.65	0.95	0.5	−0.5	−0.5	0.72
0.65	0.95	0.5	−0.5	0	0.60
0.65	0.95	0.5	0	−0.5	0.86
0.65	0.95	0.5	0	0.0	0.77
0.65	0.95	0.5	0	0.5	0.70
0.65	0.95	0.5	0.5	0	0.91
0.65	0.95	0.5	0.5	0.5	0.84

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[1] All combinations of the correlations [−0.5. 0.5. 0.5] produced impossible partial correlations. so are excluded from the table.

TABLE A8.1 (continued):

CV_y/CV_x	CV_z/CV_x	$r_{x,y}$	$r_{x,z}$	$r_{y,z}$	Expected $r_{x.xyz}$
1.00	0.30	−0.5	−0.5	−0.5	0.50
1.00	0.30	−0.5	−0.5	0	0.39
1.00	0.30	−0.5	−0.5	0.5	0.34
1.00	0.30	−0.5	0	−0.5	0.56
1.00	0.30	−0.5	0	0.0	0.48
1.00	0.30	−0.5	0	0.5	0.42
1.00	0.30	−0.5	0.5	−0.5	0.62
1.00	0.30	−0.5	0.5	0	0.55
1.00	0.30	0	−0.5	−0.5	0.70
1.00	0.30	0	−0.5	0.0	0.64
1.00	0.30	0	−0.5	0.5	0.59
1.00	0.30	0	0.0	−0.5	0.75
1.00	0.30	0	0.0	0.0	0.69
1.00	0.30	0	0.0	0.5	0.65
1.00	0.30	0	0.5	−0.5	0.80
1.00	0.30	0	0.5	0.0	0.74
1.00	0.30	0	0.5	0.5	0.70
1.00	0.30	0.5	−0.5	−0.5	0.86
1.00	0.30	0.5	−0.5	0	0.81
1.00	0.30	0.5	0	−0.5	0.90
1.00	0.30	0.5	0	0.0	0.85
1.00	0.30	0.5	0	0.5	0.81
1.00	0.30	0.5	0.5	0	0.90
1.00	0.30	0.5	0.5	0.5	0.86
1.00	0.65	−0.5	−0.5	−0.5	0.50
1.00	0.65	−0.5	−0.5	0	0.20
1.00	0.65	−0.5	−0.5	0.5	0.15
1.00	0.65	−0.5	0	−0.5	0.57
1.00	0.65	−0.5	0	0.0	0.42
1.00	0.65	−0.5	0	0.5	0.35
1.00	0.65	−0.5	0.5	−0.5	0.69
1.00	0.65	−0.5	0.5	0	0.57
1.00	0.65	0	−0.5	−0.5	0.64
1.00	0.65	0	−0.5	0.0	0.51
1.00	0.65	0	−0.5	0.5	0.43
1.00	0.65	0	0.0	−0.5	0.75
1.00	0.65	0	0.0	0.0	0.64
1.00	0.65	0	0.0	0.5	0.57
1.00	0.65	0	0.5	−0.5	0.85
1.00	0.65	0	0.5	0.0	0.76
1.00	0.65	0	0.5	0.5	0.69
1.00	0.65	0.5	−0.5	−0.5	0.81
1.00	0.65	0.5	−0.5	0	0.71
1.00	0.65	0.5	0	−0.5	0.90
1.00	0.65	0.5	0	0.0	0.81
1.00	0.65	0.5	0	0.5	0.74
1.00	0.65	0.5	0.5	0	0.90
1.00	0.65	0.5	0.5	0.5	0.84
1.00	0.95	−0.5	−0.5	−0.5	0.50
1.00	0.95	−0.5	−0.5	0	0.03
1.00	0.95	−0.5	−0.5	0.5	0.02
1.00	0.95	−0.5	0	−0.5	0.51
1.00	0.95	−0.5	0	0.0	0.36
1.00	0.95	−0.5	0	0.5	0.30
1.00	0.95	−0.5	0.5	−0.5	0.71
1.00	0.95	−0.5	0.5	0	0.58
1.00	0.95	0	−0.5	−0.5	0.52
1.00	0.95	0	−0.5	0.0	0.38
1.00	0.95	0	−0.5	0.5	0.31
1.00	0.95	0	0.0	−0.5	0.72
1.00	0.95	0	0.0	0.0	0.59
1.00	0.95	0	0.0	0.5	0.51
1.00	0.95	0	0.5	−0.5	0.87
1.00	0.95	0	0.5	0.0	0.75
1.00	0.95	0	0.5	0.5	0.67
1.00	0.95	0.5	−0.5	−0.5	0.72
1.00	0.95	0.5	−0.5	0	0.60
1.00	0.95	0.5	0	−0.5	0.87
1.00	0.95	0.5	0	0.0	0.76
1.00	0.95	0.5	0	0.5	0.68
1.00	0.95	0.5	0.5	0	0.90
1.00	0.95	0.5	0.5	0.5	0.82

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[1] All combinations of the correlations [-0.5, 0.5, 0.5] produced impossible partial correlations, so are excluded from the table.

TABLE A8.2: Relative efficiency of selection on biological and economic selection indices for different ratios of coefficients of variation, different relative economic values (a^*_y/a^*_x) and different heritabilities for the two components.

					Relative efficiency (r_{HJ}/r_{HI})		
					CV_y/CV_x		
a^*_y/a^*_x	h^2_x	h^2_y	$r_G=r$	r_{HI}	0.03	0.06	0.10
0.25	0.10	0.10	0.50	0.316	0.999	0.976	0.943
0.25	0.10	0.10	0	0.316	0.999	0.944	0.855
0.25	0.10	0.10	−0.50	0.316	0.998	0.896	0.689
0.25	0.10	0.25	0.50	0.387	0.902	0.964	0.988
0.25	0.10	0.25	0	0.347	0.964	0.998	0.972
0.25	0.10	0.25	−0.50	0.307	0.999	0.930	0.747
0.25	0.10	0.50	0.50	0.548	0.712	0.825	0.886
0.25	0.10	0.50	0	0.442	0.822	0.948	0.991
0.25	0.10	0.50	−0.50	0.334	0.931	0.996	0.923
0.25	0.25	0.10	0.50	0.500	0.938	0.860	0.792
0.25	0.25	0.10	0	0.496	0.981	0.887	0.772
0.25	0.25	0.10	−0.50	0.517	0.999	0.919	0.727
0.25	0.25	0.25	0.50	0.500	0.999	0.976	0.943
0.25	0.25	0.25	0	0.500	0.998	0.944	0.855
0.25	0.25	0.25	−0.50	0.500	0.998	0.896	0.689
0.25	0.25	0.50	0.50	0.566	0.948	0.988	0.998
0.25	0.25	0.50	0	0.527	0.985	0.992	0.946
0.25	0.25	0.50	−0.50	0.488	0.999	0.912	0.715
0.25	0.50	0.10	0.50	0.731	0.880	0.781	0.699
0.25	0.50	0.10	0	0.704	0.971	0.863	0.740
0.25	0.50	0.10	−0.50	0.749	0.998	0.938	0.762
0.25	0.50	0.25	0.50	0.702	0.957	0.890	0.827
0.25	0.50	0.25	0	0.702	0.986	0.898	0.787
0.25	0.50	0.25	−0.50	0.726	0.999	0.912	0.716
0.25	0.50	0.50	0.50	0.707	0.999	0.976	0.943
0.25	0.50	0.50	0	0.707	0.999	0.944	0.855
0.25	0.50	0.50	−0.50	0.707	0.998	0.896	0.689
0.50	0.10	0.10	0.50	0.316	0.993	0.996	0.980
0.50	0.10	0.10	0	0.316	0.985	0.992	0.946
0.50	0.10	0.10	−0.50	0.316	0.974	0.982	0.861
0.50	0.10	0.25	0.50	0.424	0.816	0.905	0.949
0.50	0.10	0.25	0	0.397	0.822	0.948	0.991
0.50	0.10	0.25	−0.50	0.370	0.782	0.960	0.991
0.50	0.10	0.50	0.50	0.625	0.618	0.747	0.822
0.50	0.10	0.50	0	0.568	0.622	0.816	0.917
0.50	0.10	0.50	−0.50	0.565	0.506	0.798	0.952
0.50	0.25	0.10	0.50	0.488	0.959	0.893	0.831
0.50	0.25	0.10	0	0.486	0.995	0.928	0.830
0.50	0.25	0.10	−0.50	0.515	0.994	0.952	0.790
0.50	0.25	0.25	0.50	0.500	0.993	0.996	0.980
0.50	0.25	0.25	0	0.500	0.985	0.992	0.946
0.50	0.25	0.25	−0.50	0.500	0.974	0.982	0.861
0.50	0.25	0.50	0.50	0.607	0.878	0.948	0.979
0.50	0.25	0.50	0	0.577	0.880	0.977	0.998
0.50	0.25	0.50	−0.50	0.540	0.859	0.987	0.971
0.50	0.50	0.10	0.50	0.717	0.896	0.802	0.723
0.50	0.50	0.10	0	0.694	0.981	0.887	0.772
0.50	0.50	0.10	−0.50	0.748	0.994	0.952	0.790
0.50	0.50	0.25	0.50	0.684	0.978	0.925	0.872
0.50	0.50	0.25	0	0.687	0.999	0.944	0.855
0.50	0.50	0.25	−0.50	0.722	0.993	0.956	0.798
0.50	0.50	0.50	0.50	0.707	0.993	0.996	0.980
0.50	0.50	0.50	0	0.707	0.985	0.992	0.946
0.50	0.50	0.50	−0.50	0.707	0.974	0.982	0.861
1.00	0.10	0.10	0.50	0.316	0.955	0.991	0.998
1.00	0.10	0.10	0	0.316	0.880	0.977	0.998
1.00	0.10	0.10	−0.50	0.316	0.731	0.935	0.994
1.00	0.10	0.25	0.50	0.462	0.715	0.827	0.888
1.00	0.10	0.25	0	0.455	0.622	0.816	0.917
1.00	0.10	0.25	−0.50	0.481	0.386	0.711	0.906
1.00	0.10	0.50	0.50	0.685	0.539	0.680	0.764
1.00	0.10	0.50	0	0.658	0.469	0.698	0.830
1.00	0.10	0.50	−0.50	0.720	0.266	0.618	0.847
1.00	0.25	0.10	0.50	0.462	0.985	0.938	0.888
1.00	0.25	0.10	0	0.455	0.996	0.979	0.917
1.00	0.25	0.10	−0.50	0.481	0.946	0.994	0.906

TABLE A8.2 (continued):

					Relative efficiency (r_{HJ}/r_{HI})		
					CV_y/CV_x		
a^*_y/a^*_x	h^2_x	h^2_y	$r_G=r$	r_{HI}	0.03	0.06	0.10
1.00	0.25	0.25	0.50	0.500	0.955	0.991	0.998
1.00	0.25	0.25	0	0.500	0.880	0.977	0.997
1.00	0.25	0.25	−0.50	0.500	0.731	0.935	0.994
1.00	0.25	0.50	0.50	0.652	0.780	0.878	0.929
1.00	0.25	0.50	0	0.645	0.685	0.861	0.946
1.00	0.25	0.50	−0.50	0.670	0.454	0.761	0.934
1.00	0.50	0.10	0.50	0.685	0.921	0.837	0.764
1.00	0.50	0.10	0	0.658	0.995	0.928	0.830
1.00	0.50	0.10	−0.50	0.720	0.979	0.977	0.847
1.00	0.50	0.25	0.50	0.652	0.997	0.967	0.929
1.00	0.50	0.25	0	0.645	0.985	0.992	0.946
1.00	0.50	0.25	−0.50	0.670	0.920	0.997	0.934
1.00	0.50	0.50	0.50	0.707	0.955	0.991	0.998
1.00	0.50	0.50	0	0.707	0.880	0.977	0.998
1.00	0.50	0.50	−0.50	0.707	0.731	0.935	0.994
2.00	0.10	0.10	0.50	0.316	0.881	0.951	0.980
2.00	0.10	0.10	0	0.316	0.685	0.861	0.946
2.00	0.10	0.10	−0.50	0.316	0.292	0.638	0.861
2.00	0.10	0.25	0.50	0.488	0.631	0.759	0.831
2.00	0.10	0.25	0	0.486	0.469	0.698	0.830
2.00	0.10	0.25	−0.50	0.515	0.168	0.536	0.790
2.00	0.10	0.50	0.50	0.717	0.487	0.635	0.723
2.00	0.10	0.50	0	0.694	0.381	0.625	0.772
2.00	0.10	0.50	−0.50	0.748	0.167	0.535	0.790
2.00	0.25	0.10	0.50	0.424	1.000	0.980	0.949
2.00	0.25	0.10	0	0.397	0.927	0.994	0.991
2.00	0.25	0.10	−0.50	0.370	0.675	0.906	0.991
2.00	0.25	0.25	0.50	0.500	0.881	0.951	0.980
2.00	0.25	0.25	0	0.500	0.685	0.861	0.946
2.00	0.25	0.25	−0.50	0.500	0.292	0.638	0.861
2.00	0.25	0.50	0.50	0.684	0.689	0.807	0.872
2.00	0.25	0.50	0	0.687	0.511	0.731	0.855
2.00	0.25	0.50	−0.50	0.722	0.180	0.546	0.798
2.00	0.50	0.10	0.50	0.625	0.954	0.885	0.822
2.00	0.50	0.10	0	0.568	0.996	0.979	0.917
2.00	0.50	0.10	−0.50	0.565	0.895	0.995	0.952
2.00	0.50	0.25	0.50	0.607	0.994	0.996	0.979
2.00	0.50	0.25	0	0.577	0.880	0.977	0.998
2.00	0.50	0.25	−0.50	0.540	0.569	0.841	0.971
2.00	0.50	0.50	0.50	0.707	0.881	0.951	0.980
2.00	0.50	0.50	0	0.707	0.685	0.861	0.946
2.00	0.50	0.50	−0.50	0.707	0.292	0.638	0.861
4.00	0.10	0.10	0.50	0.316	0.805	0.897	0.943
4.00	0.10	0.10	0	0.316	0.511	0.731	0.855
4.00	0.10	0.10	−0.50	0.316	0.016	0.401	0.689
4.00	0.10	0.25	0.50	0.500	0.576	0.712	0.792
4.00	0.10	0.25	0	0.496	0.381	0.625	0.772
4.00	0.10	0.25	−0.50	0.517	0.070	0.450	0.727
4.00	0.10	0.50	0.50	0.731	0.457	0.608	0.699
4.00	0.10	0.50	0	0.704	0.335	0.585	0.740
4.00	0.10	0.50	−0.50	0.749	0.123	0.496	0.762
4.00	0.25	0.10	0.50	0.387	0.987	0.998	0.988
4.00	0.25	0.10	0	0.347	0.751	0.905	0.972
4.00	0.25	0.10	−0.50	0.307	0.100	0.476	0.747
4.00	0.25	0.25	0.50	0.500	0.805	0.897	0.943
4.00	0.25	0.25	0	0.500	0.511	0.731	0.855
4.00	0.25	0.25	−0.50	0.500	0.016	0.401	0.689
4.00	0.25	0.50	0.50	0.702	0.626	0.754	0.827
4.00	0.25	0.50	0	0.702	0.404	0.644	0.787
4.00	0.25	0.50	−0.50	0.726	0.053	0.435	0.716
4.00	0.50	0.10	0.50	0.548	0.984	0.936	0.886
4.00	0.50	0.10	0	0.442	0.927	0.994	0.991
4.00	0.50	0.10	−0.50	0.334	0.426	0.742	0.923
4.00	0.50	0.25	0.50	0.566	0.961	0.994	0.998
4.00	0.50	0.25	0	0.527	0.685	0.861	0.946
4.00	0.50	0.25	−0.50	0.488	0.052	0.434	0.715
4.00	0.50	0.50	0.50	0.707	0.805	0.897	0.943
4.00	0.50	0.50	0	0.707	0.511	0.731	0.855
4.00	0.50	0.50	−0.50	0.707	0.016	0.401	0.689

Derivation of correlation between a standardised biological index and the aggregate breeding value (r_{HK}, Section 8.2.3)

$$H = a_x G_x + a_y G_y$$

$$K = \frac{x-\bar{x}}{SD_x} + \frac{y-\bar{y}}{SD_y}$$

$$V_H = a^2{}_x V_{Gx} + a^2{}_y V_{Gy} + 2a_x a_y COV_{Gx,y}$$

$$V_K = 1 + 1 + 2COV_{\frac{x-\bar{x}}{SD_x},\,\frac{y-\bar{y}}{SD_y}}$$

$$= 2 + 2r_{x,y}$$

$$COV_{HK} = a_x COV_{Gx,\,\frac{x-\bar{x}}{SD_x}} + a_x COV_{Gx,\,\frac{y-\bar{y}}{SD_y}} + a_y COV_{Gy,\,\frac{y-\bar{y}}{SD_y}} + a_y COV_{Gy,\,\frac{x-\bar{x}}{SD_x}}$$

$$= a_x \frac{V_{Gx}}{SD_x} + a_x \frac{COV_{Gx,y}}{SD_y} + a_y \frac{V_{Gy}}{SD_y} + a_y \frac{COV_{Gx,y}}{SD_x}$$

$$r_{HK} = \frac{a_x h^2{}_x SD_x + a_x h_x h_y r_{Gx,y} SD_x + a_y h_x h_y r_{Gx,y} SD_y + a_y h^2{}_y SD_y}{\sqrt{[(a^2{}_x h^2{}_x V_x + a^2{}_y h^2{}_y V_y + 2a_x a_y h_x h_y r_{Gx,y} SD_x SD_y)(2 + 2r_{x,y})]}}$$

Simplifying and collecting terms:

$$r_{HK} = \frac{h^2{}_x + ah^2{}_y + (1+a)h_x h_y r_{Gx,y}}{\sqrt{[(h^2{}_x + a^2h^2{}_y + 2ah_x h_y r_{Gx,y})(2+2r_{x,y})]}}$$

Calculation of relative economic values of improvement in beef production traits, from the producer's viewpoint (Section 9.2.2)

In recent years, 48 to 56% of all cattle slaughtered in Britain were sold on a live weight basis (MLC, 1981). In this case there is no direct economic benefit from genetic improvement in killing-out % or lean %, unless the buyer pays a premium for the improved strain. For producers selling on a dead weight basis there is no consistent advantage for lean carcasses.

Assuming birth weight, FCE, killing-out % and carcass lean % are constant, a genetic increase in GR of 1 g/day from birth to slaughter would produce:

(0.001 x days at slaughter) kg extra live weight, or
(0.001 x days at slaughter x killing-out %) kg extra carcass weight.

As FCE is assumed constant, the improved animals will have higher total food consumption per head by a factor of C:

$$C = \frac{\text{new total food consumption}}{\text{original total food consumption}} = \frac{\text{new GR}}{\text{original GR}}$$

The cost of this extra food was subtracted from the value of the extra live or carcass weight.

A genetic improvement in postweaning gross FCE of 1 g gain/kg food would reduce postweaning food consumption by a factor of F as derived in Section 9.2.2. This may be evaluated as a saving in food costs. Alternatively, if the producer wishes to maximise output from the available food supply, then (1+F) times the original number of animals could be fed from weaning to slaughter. This would be worth:

F [(slaughter weight x price/kg live weight)
-(purchase and rearing costs for the calf)
-(non-food costs of production)].

This is an underestimate of the value of improved FCE, as the correlated improvement in preweaning FCE is ignored.

Assuming birth weight, GR, FCE and carcass lean % are constant, a percentage unit increase in killing-out % would be worth:

(0.01 x slaughter weight x price/kg carcass weight).

Relative economic values of genetic improvement calculated from the producer's viewpoint are shown in Table A9.1

TABLE A9.1: Relative economic values of genetic improvement in beef performance traits, from the producer's viewpoint.

	Cereal beef		18/20 month beef	
Value of improvement:	per unit	per SD	per unit	per SD
Growth rate (g/day)	£0.14 *(£0.14)*[1]	£15.34 *(£15.30)*	£0.31 *(£0.31)*	£23.04 *(£23.00)*
FCE (g gain/kg food)	£1.25 *(£1.24)*	£22.91 *(£22.87)*	£3.73 *(£3.72)*	£22.26 *(£22.22)*
Killing-out %	£8.31	£18.87	£9.09	£20.62
Relative economic values				
Growth rate		1.00		1.00
FCE		1.49		0.97
Killing-out %		1.23		0.89

Calculations based on dead weight price of £1.885 per kg.

[1] Figures in parentheses based on live weight price of £1.00 per kg.