Objectives and Strategies in Pig Improvement: An Applied Perspective

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ABSTRACT

Largely because of the influence of Charles Smith, simple performance testing of pigs over the previous 30 yr has been highly successful. With larger production units, current genetic objectives can be divided into two components: 1) to raise genetic potential for production traits and 2) to maximize the probability that this potential can be realized in practice. Faster improvement through increased accuracy and a more flexible nucleus structure are offered by BLUP methodology. Electronic measures of feed intake permit selection based on feeding behavior and the shape of the feed intake curve. After the elimination of the halothane gene, the next limiting factor for meat quality could be intramuscular fat. With more than 1500 mapped genes, the main constraints on marker-assisted selection are the high costs of DNA testing and the relatively small effects of this selection on performance. A combination of the possible effects of BLUP, the Meishan breed, and the ESR gene could give genetic improvements totaling 4 liveborn piglets per litter over the next 10 yr. There appear to be no limits on future improvement of lean growth, but risks are adverse changes in reproduction and disease resistance. Existing quantitative methods of improvement are very cost effective. The greatest challenge for molecular technologies may be the genetics of the immune system.

Key words: swine, selection, lean growth, reproduction

Abbreviation key: LTGR = lean tissue growth rate, VFI = voluntary feed intake.

INTRODUCTION

Over the past 30 yr, no one has done more than Charles Smith to direct pig improvement programs along the path of simple and effective selection for clearly defined economic objectives. With this clear vision, straightforward performance testing has been highly successful in reducing backfat and increasing feed efficiency. More recently, the advent of BLUP technology and a leaner carcass have allowed a shift of emphasis toward litter productivity and, through the halothane gene, meat quality.

In the future, in addition to the efficient production of lean pigs, pressure will increase to improve the quality and uniformity of pork and to provide breeding stock that are easy to manage in larger herds that perhaps will have a more complex pattern of disease challenges. At the same time, the current revolution in molecular biology, together with rapid advances in the application of electronics to animal measurement, promises faster genetic change across a wider range of traits. These developments will be watched by a public that is ever more critical with regard to ethics, animal welfare, and the environment. From the perspective of an international breeding company, this review examines the impact of these changes on pig improvement strategies over the next 10 yr.

GENETIC OBJECTIVES

For the pig producer, the clear requirement is to produce quality lean pork at minimum cost and in a manner that is acceptable to the public. The genetic objectives fall into two distinct categories: those that raise the potential for higher performance levels and those that increase the probability of actually realizing the existing potential on the farm. Traits involved in raising potential include lean percentage, lean tissue growth rate (LTGR), feed efficiency, carcass value and conformation, pigs per sow per year, and uniformity. Traits involved in realizing potential include manageability, disease resistance, adaptability, and stress resistance.

In practice, maximizing the probability of actually delivering the current genetic potential is likely to be more important over the next 5 yr and should stabilize the financial performance of larger enterprises. Despite progress with vaccines, there could well be an increase in the prevalence of diseases that are caused by several different organisms, with the added complication of changing levels of genetic resistance. Examples are porcine respiratory syndrome and porcine
TABLE 1. Components of sow productivity with typical heritability and heterosis values.1

<table>
<thead>
<tr>
<th>Component</th>
<th>Heritability</th>
<th>Heterosis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age at puberty</td>
<td>30</td>
<td>5</td>
</tr>
<tr>
<td>Conception rate</td>
<td>20</td>
<td>5</td>
</tr>
<tr>
<td>Litter size</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. born alive</td>
<td>10</td>
<td>15</td>
</tr>
<tr>
<td>No. weaned</td>
<td>5</td>
<td>20</td>
</tr>
<tr>
<td>Ovulation rate</td>
<td>40</td>
<td>?</td>
</tr>
<tr>
<td>Embryo survival</td>
<td>20</td>
<td>?</td>
</tr>
<tr>
<td>Uterine capacity</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Weaning to service interval</td>
<td>20</td>
<td>10</td>
</tr>
<tr>
<td>Birth weight</td>
<td>20</td>
<td>5</td>
</tr>
<tr>
<td>Weaning weight</td>
<td>15</td>
<td>10</td>
</tr>
</tbody>
</table>

1Assumes fully crossbred sire, dam, and progeny.

locomotor syndrome, each apparently the result of several different factors. Pigs will need to adapt to new management systems, including solid versus liquid feeding and group versus individual housing.

SOW PRODUCTIVITY

Litter productivity traits typically show low heritabilities but high heterosis. Past genetic programs, therefore, relied on crossbreeding to boost litter size, and selection effort was concentrated on lean growth. With the successful reduction of backfat and new methods of selection for litter size, the emphasis in selection is now swinging back toward reproduction.

Some of the components of sow productivity as well as rough guides to heritabilities and heterosis of those components are shown in Table 1. Although the interval from weaning to insemination was successfully reduced in one study (21), the improvement obtained at the first parity was not expressed at later parities. Selection on component traits, such as ovulation rate, embryo survival, and uterine capacity, is theoretically possible using surgery but would probably be neither desirable nor cost effective. Weaned litter size involves the complication of cross-fostering. The limiting factor most accessible to genetic improvement is, therefore, litter size of pigs born alive. With its low heritability, expression only in females, and late age of measurement, selection of herd replacements from the largest litters would lead to very slow improvement.

To overcome this slowness, the hyperprolific approach was proposed by French scientists (14) in 1976. This approach generates a large superiority for litter size by returning the genes from a small proportion of prolific sows in multiplier herds to the nucleus. Drawbacks are that hyperprolific sows lag behind the nucleus in LTGR and that each cycle of selection, during which the breeding pyramid (nucleus, multiplier, and commercial herds) fills with hyperprolific sows, takes up to 7 yr.

The BLUP technique increases the accuracy of predicting genetic merit by combining records for all related pigs in the population over many generations and by separating environmental effects from genetic influences on performance, allowing genetic comparisons of pigs measured in different environments.

Because members of the same family resemble one another in performance, BLUP quickly eliminates poorer performing families. Although this elimination leads to faster improvement, the rate of inbreeding increases, which in turn could lower reproductive performance in the nucleus. Selection for litter size using BLUP, therefore, requires a larger nucleus population.

The group nucleus structure uses BLUP and AI to connect individual herds together to form much larger nucleus populations. Cotswold established group nucleus populations in 1986 for each of its key dam lines (3). Over 90% of matings are by AI, and, because progeny of the same AI boars are present on all farms, BLUP provides precise comparisons between and within farms. Progeny are preselected for performance testing using BLUP at each farrowing. The genetic merit of sows is recalculated using BLUP after each litter so that they can be replaced by genetically superior gilts that have completed their performance test (sequential culling). To produce rapid turnover of generations, AI boars are replaced after only 12 wk, and at least 60 boars are used annually in each line to ensure sufficient families to avoid inbreeding.

The latest multiple-trait BLUP programs harness modern computational power in order to estimate genetic merit for a range of traits simultaneously. These programs also consider the farm environment, season, parity, litter environment, all relatives, and the genetic associations among all traits. In the Cotswold group nucleus, roughly equal emphasis is given to litter size and lean growth. The BLUP estimates for genetic trend show annual improvements in litter size born alive that are close to the realistically expected levels of 0.2 piglet per year. From the outset, Cotswold has written its own in-house BLUP programs, and the next step will be to incorporate data on individual genes and quantitative traits. Very soon weekly combined BLUP and REML analysis may be possible, which will simultaneously provide estimates of heritabilities and genetic correlations on which the accuracy of BLUP depends. Eventually BLUP itself may be superseded by neural networks in which the
computer “learns” to predict genetic merit from vast quantities of data over many generations (22).

**MEISHAN BREED**

Although a few parent gilts containing Meishan traits appeared on the market in the early 1990s, the promise of a commercial boost to litter productivity has not yet been realized. The reason is that the large advantages in litter size are finely balanced with equally large disadvantages in growth and carcass value. Research consistently shows differences of 4 piglets born alive per litter between Meishan and European breeds; Meishan have advantages in both ovulation rate and embryo survival (Table 2) and reach puberty at around 3 mo of age. Crosses inherit the Meishan advantage as a uterine trait rather than a fetal trait and show very high levels of heterosis.

Selection in pure Meishan pigs is expensive and is complicated by the early sexual activity of males and the difficulty of ultrasonic measurement of backfat. The solution has been to select for LTGR while attempting to retain the litter size advantage in a composite line containing both Meishan and European pigs. At Cotswold, one such line has already undergone seven generations of selection. The resulting 25% Meishan parent gilts show around 1.6 extra live piglets per litter, and their 12.5% Meishan slaughter progeny have approximately 1.3-mm extra backfat at 92 kg of live weight. This backfat can be removed by mating the female pig to an ultralene terminal sire or by restricting nutrient intake. Even so, the following potential problems remain to be solved:

- difficulty in maintaining the Meishan advantage at later parities (which may be solved by correct feeding),
- reduced killing out percentage,
- adverse distribution of lean and consequential lower carcass value, and
- increased risk of boar taint because of earlier puberty.

At Cotswold, the carcass value of 12.5% Meishan pigs was about 3% lower than current commercial slaughter generation. Females containing Meishan genetics appear to be very docile, and, for markets with a low investment in buildings and less concern over lean yield, Meishan crosses may well find acceptance within 5 yr.

Other related Taihu strains from the same Shanghai region (Fengjing, Jiaxing, and Erhualien) show similar characteristics. The Min from North China also appears to have high litter size but possibly via another physiological route. Research in the US shows useful heterosis taking litter size even higher in crosses of Min and Taihu types (25). Strangely disappointing is the lack of success in identification of the mechanism for the superiority of Taihu. Apparently, no single physiological switch is involved. A recent report shows a smaller placenta per unit of uterine space in the Meishan breed, together with reduced embryonic estrogen production, allowing greater embryo survival (24).

### EFFICIENT LTGR

Heritabilities and heterosis of growth and quality components are shown in Table 3. Unlike sow productivity, LTGR traits have high heritabilities and low heterosis and are easy to measure. Growth rate of pigs fed for ad libitum intake is favorably correlated (0.5) with feed conversion, but unfavorably correlated (0.2) with lean percentage. The quality traits have lower heritabilities, partly because of poor accuracy of measurement; heterosis levels are not well estimated, but are assumed to be low. Heritabilities may well have been overestimated in the past because of the presence of the halothane gene, which caused increased genetic variation among sire families.

Past selection using a simple performance test of growth rate and ultrasonic backfat from roughly 30 to 100 kg has been highly effective. For example, in Canada, the annual genetic trends over the past 20 yr have been 1.4% for backfat and 0.4% for growth rate (9). It is well recognized that this selection can take one of two routes: increased daily LTGR, with little change in daily fat deposition, or decreased daily fat deposition through a reduction in daily feed intake, with little change in daily LTGR (6).

**TABLE 2. Performance of Meishan pigs in United Kingdom studies.**

<table>
<thead>
<tr>
<th>Trait</th>
<th>Large White</th>
<th>Meishan</th>
<th>F1 Cross</th>
</tr>
</thead>
<tbody>
<tr>
<td>Born alive, no.</td>
<td>9.8</td>
<td>13.2</td>
<td>13.8</td>
</tr>
<tr>
<td>Ovulation rate</td>
<td>14.9</td>
<td>18.9</td>
<td>17.7</td>
</tr>
<tr>
<td>Prenatal survival, %</td>
<td>66</td>
<td>71</td>
<td>78</td>
</tr>
<tr>
<td>Piglet birth weight, kg</td>
<td>1.28</td>
<td>0.93</td>
<td>1.20</td>
</tr>
<tr>
<td>Teats, no.</td>
<td>14.2</td>
<td>17.3</td>
<td>16.3</td>
</tr>
<tr>
<td>Growth rates, g/d</td>
<td>801</td>
<td>500</td>
<td>711</td>
</tr>
<tr>
<td>Feed conversion ratio</td>
<td>2.49</td>
<td>3.37</td>
<td>2.76</td>
</tr>
<tr>
<td>P2 fat, mm</td>
<td>8.5</td>
<td>22.5</td>
<td>15.3</td>
</tr>
<tr>
<td>Slaughter weight, %</td>
<td>75.7</td>
<td>75.9</td>
<td>75.0</td>
</tr>
<tr>
<td>Carcass length</td>
<td>732</td>
<td>701</td>
<td>721</td>
</tr>
<tr>
<td>Eye muscle area, cm²</td>
<td>35.6</td>
<td>20.2</td>
<td>28.0</td>
</tr>
</tbody>
</table>

1From work of E. D'Agaro and M. Ellis, cited by Webb (23).
2P2 = Ultrasonic fat depth 6.5 cm off the midline at the last rib.
of growth rate, as it would occur with ad libitum feeding, have taken the second route of a decline in feed intake. In a selection study at the Biotechnology and Biological Sciences Research Council, Roslin Institute (Edinburgh, United Kingdom) and Wye College (London University), halothane-free Large White and Landrace lines were selected over eight generations for four objectives: LTGR of pigs fed for ad libitum intake, LTGR at 70% of ad libitum intake (scale feeding), lean tissue feed conversion at ad libitum intake, and voluntary feed intake (VFI) at ad libitum intake.

As shown in Table 4, selection for lean tissue feed conversion with ad libitum feeding regimens led to a strong reduction in daily feed intake and a smaller increase in LTGR than did selection for LTGR, which actually increased intake. Selection for high VFI produced the expected increase in backfat, but with little change in LTGR. With the particular selection index weightings used, the study suggested that

<table>
<thead>
<tr>
<th>Trait</th>
<th>Heritability</th>
<th>Heterosis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lean growth</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth rate</td>
<td>30</td>
<td>7</td>
</tr>
<tr>
<td>Feed conversion ratio</td>
<td>30</td>
<td>3</td>
</tr>
<tr>
<td>Daily feed intake</td>
<td>25</td>
<td>7</td>
</tr>
<tr>
<td>Backfat</td>
<td>40</td>
<td>-2</td>
</tr>
<tr>
<td>Lean, %</td>
<td>40</td>
<td>0</td>
</tr>
<tr>
<td>Slaughter weight, %</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>Pork quality</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meat color</td>
<td>15</td>
<td>...</td>
</tr>
<tr>
<td>pH&lt;sub&gt;45&lt;/sub&gt;</td>
<td>15</td>
<td>...</td>
</tr>
<tr>
<td>Tenderness</td>
<td>20</td>
<td>...</td>
</tr>
<tr>
<td>Juiciness</td>
<td>20</td>
<td>...</td>
</tr>
<tr>
<td>Taste</td>
<td>20</td>
<td>...</td>
</tr>
</tbody>
</table>

1Muscle pH at 4.5 min post-mortem.

LTGR selection on scale feeding might be more successful in improving efficiency for pigs fed for ad libitum consumption. In practice, selection on ad libitum intake is preferred because such selection allows expression of VFI, but the index weightings on component traits must be chosen to ensure that emphasis falls on the efficient and rapid deposition of lean tissue.

Most of the past improvement in feed conversion has arisen from the exchange of lean for fat; fat deposition requires approximately 3.5 times more energy than does lean. As fat declines, the scope for further genetic improvement of feed conversion from changes in body composition rapidly diminish. Once no further fat remains to be removed, the main route to improved efficiency is to grow the lean pig faster and to use less of the total feed for maintenance. Hence, the main selection objective for the future will be LTGR, and the challenge will be to identify pigs that can eat more but convert the extra feed to lean rather than fat.

### THE ROLE OF FEED INTAKE

Theoretically, a measurement of individual feed intake on ad libitum performance test can add 15 to 20% to the rate of genetic improvement in efficient LTGR. For some years, the only way to measure this effect was by individual penning, but such penning incurred the risk that the isolated social environment could lead to behavioral changes that, under commercial conditions, might negate any derived benefits. This difficulty has been overcome by electronic feeding stations with transponder ear tags, which record individual intake for pigs fed for ad libitum intake and penned in groups.

One such recording system (Hunday FIRE, Hunday Electronics Ltd., Newcastle-upon-Tyne, United Kingdom) has been used in nucleus populations of Cotswold sires for 6 yr. As each meal is individually
TABLE 5. Estimated feeding pattern parameters from Hunday FIRE feeders in a Cotswold United Kingdom sire line.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Mean</th>
<th>Heritability</th>
<th>Genetic correlation with</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Average backfat</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Feed conversion</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Growth rate</td>
</tr>
<tr>
<td>Daily feed intake, kg</td>
<td>2.06</td>
<td>0.21</td>
<td>0.78</td>
</tr>
<tr>
<td>Feed intake per visit, kg</td>
<td>0.20</td>
<td>0.27</td>
<td>0.35</td>
</tr>
<tr>
<td>Visits, d</td>
<td>10.1</td>
<td>0.34</td>
<td>-0.15</td>
</tr>
<tr>
<td>Time per visit, min</td>
<td>6.0</td>
<td>0.11</td>
<td>0.17</td>
</tr>
<tr>
<td>Feed rate, kg/min</td>
<td>0.14</td>
<td>0.00</td>
<td>-0.08</td>
</tr>
</tbody>
</table>

1From Hall et al. (8).

recorded, the system provides detailed measurements of feeding pattern and behavior. In cosponsored research (18) at the Scottish Agricultural College (Edinburgh, United Kingdom), there was no indication that feed intakes differed from normal commercial levels, or, more important, that selection in the stations would increase aggressive feeding behavior. However, feeding patterns varied widely in the number of meals per day and rate of eating; at higher stocking rates, pigs readily adapted by eating fewer larger and faster meals with little impact on LTGR.

Recent genetic analysis has shown that many of the feeding pattern traits are quite highly inherited (Table 5) and, through their correlations with LTGR, might actually be used to speed genetic improvement. In the Cotswold nucleus, feed intake records from 45 to 95 kg increased improvement by around 18%. Further addition of feeding pattern traits raised this value to 24% (A. D. Hall, 1997, personal communication).

Taking a simple view, the pig is overfat because its feed intake is not in balance with its genetic potential for LTGR. Fat is then a consequence of a genetic mismatch between the two traits. The ideal pig of the future would eat to realize its potential LTGR and a predetermined level of fat. In practice, the modern pig may eat too little to realize the full potential LTGR prior to 40 kg and eat too much after 70 kg (Figure 1).

The electronic feeding stations provide data that permit an individual feed intake curve to be determined for each pig. The opportunity, therefore, already exists to select pigs that eat more in early life and less later, changing the shape of the feed intake curve (Figure 2). However, this opportunity requires a knowledge of genetic potential for lean growth throughout the finishing period. To determine this potential, Cotswold has recently completed a serial dissection study with Bristol University, slaughtering pigs from Hunday FIRE feeders at 20, 40, 60, 80, 100, and 120 kg of live weight. The resulting LTGR patterns brought two surprises. First, muscle growth rates of over 400 g/d were reached before 40 kg, suggesting that selection to increase early intake may indeed be worthwhile. Second, the relationship between muscle weight and live weight was almost linear, making prediction of LTGR very easy (F. A. Smith, 1996, personal communication).

Population structures, such as the use of the group nucleus to improve litter size, make use of very cheap measurements (litter size, growth rate, and backfat) in a large population. Electronic measures of individual feed intake are much more expensive and could not be applied economically to all progeny from 1000 sows. The solution adopted for Cotswold sire lines is an open nucleus (Figure 3) in which expen-

Figure 1. Representation of muscle and liveweight. LTGR = Lean tissue growth rate.
CARCASS VALUE

The financial value of the carcass to the processor depends on the quantity, quality, and distribution of lean in the carcass and may very probably differ from the fat or lean measurements on which payment is based. Existing mechanical and optic probes used for carcass assessment estimate only lean percentages, and the accuracy of the prediction equations employed varies notoriously across lines differing in muscle depth. Genetic improvement programs require more accurate predictions of financial value from ultrasonic measurements in the live pig. In one Cotswold trial, the accuracy ($R^2$) of ultrasonic fat and muscle depths in predicting value was as low as 0.58 and 0.25, respectively, but the best equation using all measurements gave an accuracy of 0.81. The means to select for and, indeed, pay producers on financial value, therefore, already exist.

Two-dimensional (real-time) scanners are now in routine use for the Cotswold population of sire lines. Software is now available to provide an automatic computer analysis of the ultrasonic image of either a transverse or longitudinal section of the longissimus dorsi (16). This equipment could eventually provide ratios of muscle to fat in the bacon rashers as well as intramuscular fat content, although recent preliminary trials in Canada gave poor success (20). More expensive techniques, such as X-ray computed tomography scanning, offer more detailed measurement of muscle properties, such as water-holding capacity, but require anesthesia and are prohibitively expensive for all but research applications. The TOBEC (total body electrical conductivity) methods being developed in the US measure total lean content (1), but with little extra accuracy and at far greater cost than ultrasonics.
For the improvement of meat quality, most of the genetic effort has been directed at the halothane gene. Since 1991, the HAL-1843 DNA test, available on license from the Toronto Innovations Foundation (Toronto, ON, Canada), has offered a means of eliminating this gene. The effects of this gene in increasing lean yield along with risk of stress deaths and porcine stress syndrome have been very well documented. The debate centers on the case for continuing to produce heterozygous (Nn) terminal boars for mating to homozygous negative females (NN) to produce a slaughter generation containing 50%Nn and 50%NN. Within litters, Nn pigs clearly have a 1 to 3% advantage in lean yield. However, evidence continues to accumulate that the gene (n) is also additive rather than recessive for meat quality and that Nn is inferior to NN (13).

There are four primary reasons for favoring complete elimination of the halothane gene in the short term:

1. New controlled atmosphere packaging systems to prolong the shelf-life of fresh pork require that the meat retain its natural content of water to the fullest extent.

2. As lean percentage and LTGR increase by selection, the adverse effects of the gene on quality and stress susceptibility are very likely to increase also.

3. In addition to the high cost of maintaining stress-susceptible (nn) nucleus populations, there are also welfare concerns.

4. Continued presence of the halothane gene may obscure important, longer term relationships between meat quantity and quality.

After approximately 15,000 DNA tests, Cotswold is in the final stages of elimination of the halothane gene from all lines. In one very lean composite line, the frequency of the gene has been reduced from 90% to 0 over 10 yr, first by halothane testing, then by blood typing for neighboring marker genes (PHI, PO2, and 6-PGD), and finally by DNA testing. During this time, the lean content that was lost with the halothane gene has been almost completely restored to within 0.5% lean by selection on the many other genes with smaller effects on yield. Meat color, however, has been improved in the pure line by 40%. The line is currently used to produce a crossbred terminal sire bearing the HAL-1843nm trademark, guaranteeing freedom from the gene.

Theoretically at least, there conceivably could be ways in which the advantages of the gene might be exploited without incurring the disadvantages for quality. One possibility might be the occurrence of recombinants either between closely linked genes between or within the halothane gene for separate elements influencing meat quantity and quality. If so, multiple copies of the favorable element might be created for insertion by new molecular genetic techniques. Should the halothane gene be eliminated and then required again, the one or more mutations could presumably be quickly recreated and reintroduced by molecular methods.

Once the halothane gene has been removed, there are a number of critical questions for the future:

1. How far will quality deteriorate as a consequence of continued selection for lean growth?
2. What is the scope for further improvement of quality?
3. How much of the selection effort within lines should be diverted to quality traits?

In a recent study of halothane-negative NN Dutch Yorkshires, there were no unfavorable genetic correlations of lean growth with water-holding capacity or meat color (5). However, each 1% genetic increase in lean content was predicted to reduce intramuscular fat by around 0.07%. A threshold at which low intramuscular fat becomes a limiting factor on quality could therefore be reached within 5 to 10 yr. If so, in vivo prediction of intramuscular fat becomes a priority. Dutch reports (26) of a marker gene accounting for half the genetic variation in intramuscular fat are still under investigation.

Duroc crosses certainly improve tenderness, but at the expense of lean yield and feed conversion. Less clear is the extent to which this improvement is due to higher intramuscular fat content. Trials (27) conducted by the Meat and Livestock Commission in the United Kingdom suggest that at least 50% Duroc genes may be needed for a worthwhile improvement, requiring a very high premium to compensate for the loss of lean growth. Meishan crosses appear to show less advantage in meat quality than do their Duroc counterparts, even though the Meishans probably have more intramuscular fat. The RN− gene that was discovered in France reduces curing yield but can improve eating quality (15); this gene appears to be largely confined to the Hampshire breed.

Until quality can be more easily measured in the live pig, the selection effort is probably best concentrated on lean growth. Possible approaches to in vivo measurement might involve ultrasonic, X-ray, or other scanning technologies, but the most promising approach may be the use of marker genes. Meanwhile, research is urgently needed on basic biology and quality measurements. Recent studies suggest
that a fast LTGR may improve quality through increased post-mortem activity of proteolytic enzymes. Another approach might be to select for a more favorable distribution of fiber types in the muscle by using marker genes.

RELIABILITY

Reliability is a difficult but important concept to define, but the main components appear to be ease of integration into the herd, general disease resistance, behavior in individual or group housing, feet and leg condition, and a long productive life.

In the United Kingdom, where 20% of sows are now housed outdoors, the solution has been to add a proportion of Duroc breed for robustness, increased disease resistance, very high levels of heterosis, and—in crosses with European lines—surprisingly placid behavior and good maternal performance. Typically, the parent gilt would be a static cross of Large White and Landrace types containing 25% Duroc (Figure 4).

The problem is that a pure Duroc line is expensive to maintain, making it difficult to justify nucleus populations that are large enough to allow worthwhile long-term improvement of litter size. The BLUP selection for litter size is, therefore, only applied to 75% of the genes of the parent gilt. There is also a 1-yr genetic lag in producing the three-way cross, and this lag would be increased if any proportion other than 25% Duroc were required. The solution is to incorporate a proportion of Duroc genes in one or both of the former Large White and Landrace lines (Figure 5). The two resulting composite lines can be selected as group nucleus populations of 1000 sows, allowing BLUP selection for litter size to be applied to 100% of the genes in the parent gilt.

The composite line approach has been adopted by Cotswold breeders in three steps over 8 yr. First, the red coat color of the Duroc was removed by backcrossing the dominant white coat color inhibitor gene (I) from a European white line. The resulting White Duroc line was 97% Duroc and homozygous white. Second, crosses were made to introduce the desired proportion of White Duroc into the existing European dam lines. Finally, foundation animals of the new composite lines were strongly selected for LTGR, litter size, and uniformity, followed by DNA testing to remove the halothane gene completely.

The composite line approach, in addition to removing the need for purebred Duroc, has the advantage of increasing heterosis and, therefore, litter productivity in the nucleus. This increased productivity in turn increases selection differentials, leading to faster improvement at lower cost, thus, restoring genetic variation and reducing inbreeding in breeds that have undergone 30 yr or so of scientific selection and that may be at risk from increasingly high levels of homozygosity.

Perhaps the greatest future threat to sow productivity and pig production will come from disease. Already the greater concentrations of pig herds and open borders appear to be leading to multifactorial complexes of reproductive, respiratory, and locomotor diseases. It is very difficult to gauge the potential effectiveness of new DNA-based vaccines and measures such as split-site production in controlling dis-
ease. At present, selection for resistance to any one disease would appear to be fruitless because of the faster mutation rate of the disease organism itself. The challenge is to raise general immune responsiveness by genetic means.

At least some hope of success is offered by the study at Guelph, which has completed more than six generations of selection for high and low immune responsiveness in Canadian Yorkshires (17). Pigs were selected on a BLUP index of reaction to a challenge by four foreign proteins. After four generations, the lines that were selected for the high and low response differed by over one standard deviation on BLUP index, and the heritabilities of the four component traits ranged from 13 to 32%. When challenged with Mycoplasma hyorhinis, the high line had greater antibody titers and fewer and less severe clinical symptoms. This result suggests that there may be a way of measuring general immune responsiveness that might then be used to search for marker genes as a cheaper option in practice.

MOLECULAR GENETICS

The Pig Genome Mapping Project (PiGMap), funded by the European Union, together with North American and Scandinavian gene maps (2), have already identified more than 1500 genes scattered over the 38 chromosomes of the pig. The primary objective is to understand at a fundamental level how genes work together to control development and function, and the maps are freely accessible via the Internet. However, the maps also offer the opportunity of marker genes for quantitative trait loci that might be used for marker-assisted selection.

As the first step, the search is now on for associations between markers and performance of experimental Chinese × European backcrosses and wild × domestic backcrosses that will produce the widest possible genetic variation. Approximately 80 associations have already been reported, including backfat, growth rate, litter size, intramuscular fat, coat color, and disease resistance. Much attention has been focused on the estrogen receptor gene, ESR, which appears to act as a marker for a major gene on chromosome 1 affecting litter size (19). In first parity, 50% Meishan crosses, the difference between ESR homozygotes is around 2 to 3 pigs per litter, declining to 1.0 at later parities. Also, ESR appears to be present in the Large White with an effect of 0.8 to 1.0 pigs per litter. The ESR has been patented and exclusively licensed to one breeding company, but, fortunately for others, there are several potentially alternative markers in the same region of the chromosome that are publicly available.

Exploitation of ESR might be to make existing Meishan composite or Large White lines homozygous or to backcross the gene from Meishan into European dam lines by the process of marker-assisted introgression. Depending on the initial frequency of the gene, the former might give a single improvement of 0.6 pig per litter in the parent gilt and the latter up to 1.0 pig per litter. Both would pay a price of loss of selection on other traits. It is curious that a gene with such a large, apparently beneficial effect should not have increased in frequency to 100% in populations in which it occurs. Like the halothane gene, this gene might well have some yet unknown harmful effects.

The search for marker genes in commercial populations has now begun. For the present, it seems likely that the performance advantage from making any one marker homozygous, in relation to the cost of DNA testing and loss of selection on other traits, may be small. However, the cost of DNA testing is likely to decrease, and, in Edinburgh, the Roslin Institute has established its own commercial marker genotyping company, Rosgen Ltd. Even so, the effect on performance may need to be very large to be worthwhile because BLUP is already very powerful and cost effective. Caution is also required because the effect of a single gene on performance may have been overestimated in the past by least squares (10).

Gene transfer is in its infancy, although recent success in cloning should substantially reduce the cost. Transgenic pigs containing extra growth genes have experienced well-publicized side effects on reproduction and locomotion. The transfer of sry and related genes controlling maleness on the Y chromosome might conceivably offer a means of producing a single gender to increase efficiency and uniformity. Some form of genetic manipulation might help to reduce protein turnover in order to reduce nitrogen excretion. For feed efficiency, genetic manipulation might be better targeted to fodder crops than to animals. A major goal has to be a better biological understanding of the animal and its behavior. For example, the recently discovered ob mutation in mice causes obesity through a deficiency of the satiety factor leptin. This finding could be a first step in understanding the control of feed intake at the molecular level, offering the prospect of correcting the major deficiency, overconsumption of feed. In the longer term, progress in medical research on cancer and AIDS (acquired immune deficiency syndrome) is leading to an understanding of the molecular genetics of the immune system, and there conceivably could be
a justifiable case for direct manipulation of the pig genome on the grounds that it would improve welfare.

CONCLUSIONS

As has always been advocated by Charles Smith, genetic improvement programs for pigs will continue to focus on the economic goal of reducing the cost per kilogram of lean meat. This goal requires a two-stage process: first, raising the genetic potential for litter size and LTGR, and, second, increasing the probability of success through reliability and manageability. There is no imminent sign of selection limits, so it is reasonable to speculate that BLUP selection, Meishan genes, and ESR could yield up to 4 extra pigs born alive per litter over the next 10 yr; mean growth rates of up to 2 kg/d from 30 to 100 kg seem biologically attainable.

For the foreseeable future, genetic improvement programs will likely continue to focus on quantitative rather than molecular methods and be enhanced by BLUP and other mixed model procedures. These procedures may be supplemented by marker-assisted selection, depending greatly on the balance between the costs of DNA tests and the benefits of the quantitative trait loci on performance, which may be small. Genetic manipulation may not be warranted for straightforward production efficiency, but its use in general disease resistance must be considered as a long-term option.

So, what are the key risks of genetic improvement that demand high priority in future research? With ever more accurate selection from BLUP, there is the risk of steadily increasing homozygosity for both fitness and genetic variation. Methods already being developed to balance inbreeding and selection optimally (7) may need to be extended to generate new heterozygosity through composite lines. With decreasing fat levels and faster growth, signs of declining reproductive performance (12) already exist that could result in reproduction being added to selection objectives for sire lines. In practice, interactions of genotype and diet are as prevalent as ever, and there is still a need for fundamental understanding of the control of feed intake in relation to lean growth potential. Because disease is the greatest source of economic loss in the swine industry, perhaps the most serious risk is that present selection strategies might reduce immunity. General immune responsiveness is, thus, one of the greatest genetic challenges for the future.

ACKNOWLEDGMENT

The author worked under Charles Smith and J.W.B. King at the former Agricultural Food and Research Council Animal Breeding Research Organisation, Edinburgh, from 1973 to 1986, and gives warmest thanks for all the good science, guidance, and encouragement so generously given.

REFERENCES

11 Reference deleted in proof.


REFERENCES ADDED IN PROOF
