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SUMMARY

A discussion is given on new developments and views that are relevant for present pig breeding programmes. Attention is given to simultaneous selection for production and reproduction traits, specialized sire and dam lines, use of field data, statistical techniques for breeding value estimations, and new traits to select for.

The most important conclusions are:
1. Specialization of sire and dam lines and inclusion of reproduction traits in the breeding goal leads to the requirement of a large nucleus.
2. Breeding value estimation should be based on animal models, so that optimum use is made of all information that is in the data (nucleus data as well as field data).
3. Animal models make it possible (for national programmes as well as for private companies) that the breeding programme is based on a group of nucleus herds.
4. Due to inclusion of reproduction traits and meat quality in the breeding goal, and as a consequence of G x E interactions, family information becomes very important.
5. Family information will only be relevant when efficient selection between families is possible. For this reason, a large annual number of breeding boars should be used. This will keep rate of inbreeding also to an acceptable level.

INTRODUCTION

At the moment there are many new developments, techniques and views, which may influence the optimal design of pig breeding programmes. Some of the new techniques (e.g. gene transfer) may play an important role in future breeding programmes. Their role is discussed by Kennedy (1990). Other developments are already important for today’s pig breeding programmes.

The objective of this paper is to discuss new developments and views relevant for the optimization of present pig breeding programmes. Attention will be given to (i) simultaneous selection for production and reproduction traits, (ii) specialized sire and dam lines, (iii) use of field data, (iv) statistical techniques for breeding value estimations, and (v) new traits to select for.

PRODUCTION AND REPRODUCTION TRAITS

In the past, selection was mainly for production traits (growth and carcass traits). Recently, many pig breeding organizations also select (or consider selection) for reproduction traits. Especially litter size is an important selection trait (Tess et al., 1983; Ollivier, 1988; Gu et al.,
Heritability of litter size is low, but accuracy of selection can be increased by the use of family information (Avalos and Smith, 1987).

There is still no agreement on the magnitude of the extra benefits of including reproduction traits in the breeding goal next to production traits. McPhee (1988) estimates only 3% extra genetic gain in the Australian situation, whereas Avalos and Smith (1987) and De Vries et al. (1989) predict much higher benefits (10-18% and 51% extra genetic gain, respectively, for specialized dam lines). Webb and Bampton (1987) also see large benefits in selection for litter size, as they predict reduced returns from selection for production traits in the near future when optimal levels for leanness may be reached.

The balance between selection for production and reproduction traits is determined by the weights of the traits in the breeding goal, and also by the accuracies with which the traits are measured. Nationally, the breeding goal should be based on the economic values of traits at the commercial level. However, in a situation where there are several breeding organizations competing, this competition has to be taken into account. Schultz (1986) and De Vries (1989) suggested that a trait with a low performance level (compared to other breeding organizations) should get a higher weight in the breeding goal. Effects of competitive position are especially relevant for the optimal balance between selection for production and reproduction, as breeding stock of an organization needs to be acceptable for sow herds as well as for fattening herds.

Selection response for production traits depends to a great extent on the number of test places for young boars and gilts, whereas response for reproduction traits is related to the number of breeding sows in the nucleus. De Vries et al. (1989) studied the effects of nucleus population size and annual number of breeding boars on overall selection response (i.e. sum of genetic gains for production and reproduction traits) using stochastic simulation. Fitted average responses are given in Fig. 1. From these results it was concluded that simultaneous selection for production and reproduction justifies a large number of sows in the nucleus. Another conclusion from Fig. 1 was that selection response is not much affected by annual number of breeding boars.

Enlargement of the nucleus population does not necessarily have to be accompanied by additional test places for young boars, as efficient selection of boars (on pedigree index for reproduction traits) is possible before the
test. From a large proportion of the litters born in the nucleus no boars have to be performance tested. De Vries et al. (1990a) predicted a loss of only 3-4 % in overall selection response when 50 % of the young boars would be culled on pedigree index before the test.

Use of family information (i.e. records from sibs of parents in addition to dam records) increases selection response for reproduction traits, but at the same time it increases rate of inbreeding (Toro et al., 1988). Also with combined selection for production and reproduction traits, rate of inbreeding is increased. This is demonstrated in Table 1, where realized values in simulated nucleus populations are compared to expected values for random mating.

Table 1. Realized ($\Delta F_r$) and expected1) ($\Delta F_e$) yearly relative increase in inbreeding (%) in simulated nucleus populations selected for production and reproduction traits (De Vries et al., 1989).

<table>
<thead>
<tr>
<th>Annual no. of boars</th>
<th>100</th>
<th>200</th>
<th>400</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\Delta F_r$</td>
<td>$\Delta F_e$</td>
<td>$\Delta F_r$</td>
</tr>
<tr>
<td>10</td>
<td>1.31</td>
<td>0.84</td>
<td>1.18</td>
</tr>
<tr>
<td>20</td>
<td>0.93</td>
<td>0.49</td>
<td>0.89</td>
</tr>
<tr>
<td>40</td>
<td>0.63</td>
<td>0.27</td>
<td>0.58</td>
</tr>
</tbody>
</table>

1) According to Hill (1972): $\Delta F_e = (1/N_m + 1/N_f)/8L^2$

where $N_m$ and $N_f$ are numbers of males and females used per year, and $L$ is the generation interval.

De Vries et al. (1990b) studied two methods to limit rate of inbreeding: (a) within-family selection and (b) increase of the annual number of boars. The second method appeared to be the best option as it hardly affects selection response (as was demonstrated in Fig. 1). With 40 boars per year, rate of inbreeding can be limited to about 0.5 % per year (Table 1).

SIRE AND DAM LINES

Due to the good prospects for genetic improvement of reproduction traits along with production traits, it will be profitable in most situations to make use of specialized sire and dam lines (Webb and Bampton, 1987; Knap, 1990a). Individual breeders with one breed probably do not like this concept, as they would like to sell breeding boars as well as gilts to the commercial level. However, with respect to genetic gain in the total breeding system, selection in specialized lines will be worth while.

McPhee (1988) expects in the Australian situation only 2.5 % extra genetic gain from specialization of lines. This low figure is due to the predicted low extra benefits of selection for reproduction traits. Webb and Bampton (1987) estimated 15-22 % extra genetic gain for systems with specialized sire and dam lines, compared to systems with general-purpose lines.

In the short-term, total nucleus facilities and testing capacity of a breeding organization are fixed, but the distribution over lines can be

397
varied. De Vries and Van der Steen (1990) studied optimization of this distribution over sire and dam lines. They concluded (for a four-way cross-breeding system) that the sire lines can be much smaller (about 50%) than the dam lines, while testing capacity for boars should be equally distributed over the sire and dam lines.

FIELD DATA

Data from subnucleus and commercial herds can be used for breeding value estimation of selection candidates at nucleus level. Such data are very important in the presence of large Genotype x Environment (G x E) interactions (Sehested and Vangen, 1987; Merks, 1988).

The magnitude of G x E interactions is still not clear, but Dempfle and Gründl (1988) showed for a range of conditions that could be relevant to pig production traits, that the presence of these interactions can reduce response by 5% to 15%. Bampton et al. (1977), Standal (1977) and Merks (1988) reported poor genetic relationships between identical production traits measured in different environments, whereas in the study of Van Diepen and Kennedy (1989) G x E interactions were of minor importance. It is not clear whether the different conclusions are an artifact of the method of estimation. In the study of Van Diepen and Kennedy (1989), the analysis was carried out using advanced mixed model techniques.

Another question is whether the causes of G x E interactions can be identified. If this is possible, then it is more efficient to select for a certain definable environment (feasible for commercial herds) than to select for general suitability under various environments.

For reproduction traits no studies on G x E interactions within breeds could be found in the literature. However, the Crossbred type x Environment interactions reported by Knap (1990b) give an indication that G x E interactions are also relevant for this group of traits. Further research on this subject is needed.

At subnucleus level, on-farm performance tests will provide valuable data for selection on production traits. Also reproduction records will be available at subnucleus herds. Even in the absence of G x E interactions, records from subnucleus herds can be very useful to increase selection accuracy. Avalos and Smith (1987) predict 15% higher accuracy of selection for reproduction when both nucleus and subnucleus records are included ($h^2 = 0.10$, mating ratio $= 1:10$, all males used from selected litters).

Due to the increased use of management computers, also many data at commercial herds become available. Reproduction data are recorded on individual sows, which make these data useful for breeding value estimation of their relatives in the nucleus. For production traits, usually no individual data are available, but this may change when electronic identification of growing pigs is introduced (Merks and Lambooy, 1989; Wittman and Király, 1989). When nucleus boars are used also as terminal sires, data from the commercial herds can be used as sib information for selection in the nucleus population. However, in many situations, commercial slaughter pigs do not descend directly from nucleus boars (e.g. a situation with crossbred boars as terminal sires).

STATISTICAL TECHNIQUES

There has been significant progress in recent years in techniques for breeding value prediction. This development, which is primarily based on BLUP methodology (Best Linear Unbiased Prediction) follows after the contributions of C.R. Henderson and has also relied on new theory and in-
creased computer power. The latter makes it possible to use in a unified approach, animal models in relatively large data sets, both for prediction of breeding values and for variance component estimation. Animal models have a number of desirable properties, many of which are a consequence of the fact that they make optimum use of all the information that is in the data.

In the context of prediction of breeding values, the animal model yields predictors with higher accuracy than alternative ones that use less information from the data. The efficient use of the available information can eliminate biases due to genetic trend, and fixed effects are adequately estimated. Animals from different generations or born in different years can be compared and those with the highest breeding values, regardless of age, can be selected.

Use of animal models are especially advantageous in sex limited traits of low heritability, such as reproduction traits. Both boars and sows receive an evaluation, and with for example information on two parities on 3 full-sibs and 30 half-sibs (10 groups of 3 full-sibs), on the boar side, and similar amount of information plus two records on the sow itself, on the sow side, the accuracy of the boar and sow is about 0.47 and 0.60 respectively ($h^2 = 0.10, r = 0.15$).

The relative increase in selection response obtained using an animal model over alternative predictors depends on the structure of the data, on the genetic parameters of the criterion of selection, and on the competing predictor. Simulation results of a closed pig herd by Belonsky and Kennedy (1988) showed that response to univariate phenotypic selection, relative to an animal model, was of 64 % and 91 %, for heritabilities of 0.10 and 0.60, respectively. Simulation of a national breeding programme with central testing was performed by Sorensen (1988), yielding a fairly balanced data structure. The study showed that a univariate index using information on the individual, its full and half sibs, and progeny, if available, yields responses of 89 % and 96 % relative to those obtained using an animal model, for heritabilities of 0.10 and 0.50, respectively. The extra response obtained using the animal model was due to elimination of selection bias in the estimation of fixed effects and due to the extra information, the latter having a larger influence on response at low heritabilities. The extra information leads also to higher rates of inbreeding, and this effect is again more pronounced at lower heritabilities. With 40 males and 200 females used as parents each generation, the rate of inbreeding using the animal model was 1.8 % and 1.0 % at heritabilities of 0.1 and 0.5 respectively. The comparable rates of inbreeding for the selection index were 1.2 % and 0.9 %, and with random mating and no selection, 0.4 %.

Wray (1989) studied the effects of using an animal model for closed nucleus herds. The study showed the high benefits of the animal model with respect to selection response, but on the other hand it also clearly demonstrated the increased rate of inbreeding.

The efficiency of the animal model, like any other predictor, depends partly on the accuracy with which the genetic parameters (e.g. heritability) are estimated (Harris, 1964; Sales and Hill, 1976). The extra information available in an animal model may contribute rather little, if it is not weighed in an optimum manner due to the use of wrong genetic parameters. This will be accentuated in cases of highly unbalanced data. Part of this argument is illustrated in Table 2, which shows simulation results based on the model and data structure described in Sorensen (1988). When a prior of 0.2 is used instead of the true heritability (0.4), the response is 95 % of the optimum response.

Estimated responses are much more sensitive to the choice of priors than the true response. (See Sorensen and Kennedy (1986), Kennedy et al. (1988), and Hill and Meyer (1988), for a discussion of statistical and genetic as-
sumptions of the animal model). In practice, these departures from some ideal model, caused either by ignorance or by limitations in computer power, are inevitable, and often are more widespread in computationally demanding animal models. Their consequence is that the advantage of the improved methods over others becomes smaller.

Table 2. Effects of choice of parameters on selection response.

<table>
<thead>
<tr>
<th>True heritability</th>
<th>0.4</th>
<th>0.0</th>
</tr>
</thead>
<tbody>
<tr>
<td>Assumed heritability</td>
<td>0.4</td>
<td>0.2</td>
</tr>
<tr>
<td>True selection response</td>
<td>5.80</td>
<td>5.52</td>
</tr>
<tr>
<td>Estimated response</td>
<td>5.81</td>
<td>3.47</td>
</tr>
</tbody>
</table>

1) Average of 10 replicate runs.
2) Computed using the whole data at the end of the selection process with an animal model using a prior of 0.4 or of 0.2.

An important consequence of the availability of animal models is the possibility they offer to use more efficient structures in the design of a breeding programme. Traditionally, pig breeding programmes have been based on within herd selection or on central test stations allowing comparison of animals across herds. With the use of artificial insemination which creates genetic links among herds, use of animal models allows the programme to be based on on-herd recording schemes, testing all animals from one or more litters. A discussion of the impact of the use of animal models on population structure can be found in Webb and Bampton (1988).

NEW SELECTION TRAITS

Lean growth rate and feed efficiency are the most relevant production traits to select for, while litter size is the most important reproduction trait. In present genetic improvement programmes, also meat quality traits, oestrus traits and sow longevity can play an important role. The importance of these traits depends to a great extent on their level as well as on their variance.

Lundström (1989) reports on the perspectives for genetic improvement of meat quality. A problem with meat quality traits is the difficulty of obtaining breeding value estimates based on the individual itself. As a result, information from relatives needs to be used as selection criterion, although in the last few years some research is aimed at studying meat quality traits in muscle biopsies (Essén-Gustavsson and Fjelkner-Modig, 1985).

Oestrus traits and longevity can be improved in the same way as litter size, i.e. by selection based on family information.

DISCUSSION

The extra benefits of including reproduction traits in the breeding goal depends on the method of breeding value estimation. Assume for a dam line that, without use of family information, \( \sigma_f \) (stand. dev. of aggregate genotype) for production traits is 1.0 monetary unit and \( \sigma_r \) for reproduction traits is 0.7 unit (with \( \sigma_f = r_{\text{IM}} \times \sigma_g \) where \( r_{\text{IM}} \) is accuracy of index and \( \sigma_g \) is stand. dev. of aggregate genotype expressed in monetary units). Use of family information would increase \( \sigma_f \) for production traits with about 10 \% and for reproduction traits with about 40 \%. Assuming no correlation between pro-
duction and reproduction traits (Brien, 1986) and infinite population size, this leads to the results given in Table 3. The table shows that the extra benefits from reproduction traits are much increased when family information is used.

Table 3. Extra benefits of including reproduction traits in the breeding goal, depending on method of breeding value estimation (INDIV: only individual performance data; FAMILY: use of family information).

<table>
<thead>
<tr>
<th>Method of estimation</th>
<th>$\sigma_I$</th>
<th>$\Delta G$</th>
<th>Extra benefits from repr.</th>
</tr>
</thead>
<tbody>
<tr>
<td>prod.      repr.</td>
<td>prod.</td>
<td>repr.</td>
<td>prod.</td>
</tr>
<tr>
<td>INDIV       INDIV</td>
<td>1.0</td>
<td>0.7</td>
<td>0.82</td>
</tr>
<tr>
<td>INDIV       FAMILY</td>
<td>1.0</td>
<td>1.0</td>
<td>0.71</td>
</tr>
<tr>
<td>FAMILY      INDIV</td>
<td>1.1</td>
<td>0.7</td>
<td>0.93</td>
</tr>
<tr>
<td>FAMILY      FAMILY</td>
<td>1.1</td>
<td>1.0</td>
<td>0.81</td>
</tr>
</tbody>
</table>

Increase of nucleus population size will lead to considerable extra genetic gains, but it will also raise the costs of the breeding programme. In dam lines, however, extra costs can be limited, since not all animals have to be performance tested for production traits. Webb and Bampton (1987) report on a breeding programme with dam lines that were enlarged to 1000 sows. In these lines 40 % of the progeny is performance tested. The enlarged nucleus in this breeding programme removed the need for purebred multiplication herds, which resulted in a reduced genetic time lag between nucleus and commercial herds.

One of the problems with a large nucleus could be the greater complexity of the selection system, especially with more herds involved. In this case, uniform management and selection procedures could be more difficult to organize. A larger nucleus might also lead to a higher frequency of errors in the data-sets, which will reduce accuracy of selection (Franklin, 1982; Richard and David, 1984).

For investment decisions (e.g. increase of nucleus size or testing capacity), either when the programme is national or when there are several breeding organizations, there is a need to compare additional financial returns from increased selection response to the additional costs involved. If there are several competing breeding organizations, the additional returns (extra sales or better prices for breeding stock) for an individual breeding organization will depend on its competitive position. The relation between returns and selection response is then non-linear (Hill, 1971).

National programmes based on central test stations are likely to become obsolete. The availability of statistical techniques that optimize the use of all available information allow for more efficient breeding structures. A national programme could be based on a small number of breeding herds of adequate size, where the use of artificial insemination provides the genetic links among the herds. Since national genetic improvement programmes are often financed by commercial producers, a cooperative type of organization could allow decisions to be taken centrally, and thus ensuring that the economic objective, defined at the producers level, could be satisfied.

When reproduction traits and meat quality are included in the breeding goal, selection will be much more based on family information. The same holds when field data are used to overcome $G \times E$ interactions.
Family information (e.g. sibs) increases accuracy of selection. However, it will increase rate of inbreeding, especially at low heritabilities, and it will also reduce effective selection intensity due to higher correlations between indexes of family members (Hill, 1976, 1977). The reduction in selection intensity can be substantial when few families are available for selection. This aspect is very relevant in pig breeding due to the continuous selection process, which implies that families from a single generation are not available for selection at the same time. Research on the value of family information (e.g. field data of sibs) should therefore not focus on their effects on accuracy of selection but rather on their effects on selection response. Also effects on inbreeding and random drift should get attention.

Results from optimization studies sometimes show small differences between alternative breeding programmes. For example, De Vries and Van der Steen (1990) showed that reduction in selection response at suboptimal distributions of nucleus and testing capacity over sire and dam lines could be limited if no extreme values were chosen. For breeding organizations, it is important to know the optimal design of the breeding programme, but information about the consequences of deviations from the optimum design can also be useful. This information helps to find the best alternative design when the optimum design is difficult to implement.

As soon as the breeding programme with the best design is operational, the various parts of the programme need to be evaluated regularly, because there might be possibilities for improvement (e.g. more accurate predictions of lean content, better recording of data, more efficient use of facilities). After a number of years, the entire breeding programme should be evaluated by estimating the genetic trends in the nucleus lines. This can be carried out using an animal model, where genetic variances are estimated using REML, and where average computed breeding values per year provide an estimate of genetic change. In addition to the data from the nucleus, also data from sub-nucleus and commercial level might be useful for this purpose.

CONCLUSIONS

- Specialization of sire and dam lines and inclusion of reproduction traits in the breeding goal leads to the requirement of a large nucleus.
- Not all progeny born in the nucleus have to be tested for production traits. For dam lines, an important step of selection should be before the performance test.
- An increasing amount of field data (at different levels of the breeding pyramid) is becoming available for selection purposes. These data can be applied optimally for breeding value estimations using advanced statistical techniques. Field data are very important in the presence of G x E interactions.
- Breeding value estimation should be based on animal models, so that optimum use is made of all information that is in the data.
- Animal models and artificial insemination make it possible (for national programmes as well as for private companies) that the breeding programme is based on a group of nucleus herds.
- Family information (sibs, progeny) becomes very important due to inclusion of reproduction traits and meat quality in the breeding goal. Also G x E interactions can increase the importance of family information.
- Family information will only be relevant when efficient selection between families is possible. For this reason, a large annual number of breeding boars should be used. This will keep rate of inbreeding also to an acceptable level.
REFERENCES