SELECTION AGAINST HALOTHANE REACTION IN A COMMERCIAL LANDRACE
NUCLEUS HERD

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SUMMARY

Data are presented showing the incidence of halothane reaction in 10657 British Landrace tested in a commercial nucleus herd, in which positive reactors (HP) animals were not allowed to breed. Incidence of halothane reaction declined from 0.42 to 0.16 over a period of 4 years, but the calculated gene frequency only changed from 0.58 in non-selected pigs to 0.43 in halothane negative (HN) pigs over two generations of selection. Estimated penetrance for the recessive homozygotes was 0.8 to 0.9, and 0.0 to 0.018 for the heterozygotes. There was some evidence to suggest that heterozygotes had a selective advantage, and that this was leading to stabilising selection. The study demonstrates that halothane screening can successfully lower the incidence of halothane reaction under field conditions, although the rates at which this is achieved may be slow.

INTRODUCTION

The importance of the halothane gene (HAL) in pigs was first recognised over ten years ago (Eikelenboom and Minkema, 1974). The effects of the gene on carcass traits have been reviewed by Webb et al (1982) who conclude that over a wide range of breeds it may be economically beneficial to produce heterozygous slaughter generation animals, but that a net loss would occur in homozygous recessives. The advantage in heterozygotes, which comes largely from an increased lean yield, does not appear to be as great in British Landrace (BLR) as in other, meatier breeds such as the Dutch or Belgian Landrace (Simpson et al 1985). It has been demonstrated that the frequency of the halothane gene can be readily modified by selection (Webb, 1981). However, Smith (1982) has suggested that simultaneous selection for other traits could lead to stable equilibria, and losses in selection differential at the equilibria. Furthermore, in BLR it has been suggested that the mode of inheritance does not conform to a single, completely-recessive gene hypothesis. An average of 22% of the heterozygotes may react to a halothane test, and the penetrance of the homozygous recessive is incomplete (Carden, 1982, Carden et al, 1983). These factors are likely to affect the rate at which the gene frequency is reduced by selection against halothane reactors.

This paper examines the effect of selection against the halothane gene in a commercial population of BLR.

MATERIAL AND METHODS

The population studied over a period of 4 years was a commercial nucleus herd of BLR, consisting of approximately 170 sows and 17 boars at any one time. All progeny were halothane tested at 7 to 8 weeks (Webb and Jordan, 1978). Pigs were subsequently performance tested from approximately 40 to 90Kg, on a restricted feed regime, and selected on an index designed to improve efficiency of lean tissue feed conversion. Halothane positive (HP) animals were not retained for breeding.
Data were divided into three sections according to the sire generation, because of overlapping generations (Table 1). Gen.0 sires were not halothane tested, and were effectively present throughout the study because of the use of AI boars (accounting for less than 5% of the litters). Gen. 1 sires were halothane tested themselves and were largely offspring of Gen. 0 sires. Gen. 2 sires were also halothane tested, and all were offspring from Gen. 1. Some dams were present in more than one generation, tested and non-tested females being mated to sires of each generation. Maximum likelihood (ML) gene frequency and penetrance were estimated in each partition of the data using the model of Cannings et al (1978). The likelihood was calculated conditional on halothane negative (HN) selected parents to account for selection against homozygous recessives, and assumed Hardy-Weinburg gene frequencies in the herd. These estimated gene frequencies and penetrances were used to estimate gene frequency in selected HN parents, expected incidences from HN x HN matings, and the most probable genotype of sires.

Performance test data from HP and HN pigs were compared using Student's t-test. The traits considered were daily gain in Kg (DG), food conversion ratio (FCR), four ultrasonic backfat measurements in mm: maximum shoulder (SH), minimum loin (L), and two points 6 cm and 8 cm from the midback at the last rib (C and K), plus total index score. The data were divided into year categories which did not quite relate to the generation division because of the overlapping generations.

RESULTS

The incidence of halothane reaction decreased significantly (P<0.001) from 0.42 to 0.16 over the study period (Fig. 1), indicating an overall reduction of gene frequency in the herd. Estimated gene frequencies and penetrances for each generation are presented in Table 2. These show that selection against HP animals has reduced the gene frequency from 0.70 in Gen. 1 to 0.58 in Gen. 2. It is likely that the gene frequency in Gen. 0 was underestimated, as shown by the difference between the observed incidence and that expected from HW, suggesting a deviation from HW in the herd prior to Gen. 0. Estimated penetrance of these homozygous recessives ranged from 0.91 to 0.80, while that for the heterozygotes was slight (0.0 to 0.018). The degree of penetrance in the heterozygote was not in agreement with estimates of 0.22 obtained from an experimental BLR line (Carden, 1982), but was similar to that estimated from a survey of commercial BLR herds (Southwood et al, 1986).

Table 3. shows the predicted frequency of the halothane gene in the animals used as parents in Gen. 1 and Gen. 2, given the estimated herd gene frequencies and penetrance values in each generation. The incidence of halothane reactors expected from matings between HN parents was close to that observed, which supports the model used. The most likely genotype was found for each of the 70 sires involved in the study, 77.1% of which could be genotyped with a probability > 0.9 that the right assignment had been made (Table 4). In each generation there was an apparent excess of heterozygotes, suggesting a possible selective advantage.

Differences in performance over the study period of animals included in the halothane test data are presented in Table 5. The overall trends in both males and females were that HP animals had poorer daily gains, and slightly reduced fat depths relative to HN pigs, but that there were no differences in FCR, or overall index scores. There was no evidence to suggest that the relative performance of HP pigs to HN was changing over time. As there was no difference in total index score between the two groups, neither could be said to have an advantage, but it is likely that this reflects the predominance of
DISCUSSION

It would appear from the data that selection has reduced the frequency of the halothane gene in the herd, and also the incidence of positive reactors. However, progress has not been very rapid, given the estimated herd gene frequencies. This may be partly explained if the initial herd frequency had been underestimated, the gene no longer segregating according to HW because of a selective advantage in the heterozygote.

If heterozygotes did have a selective advantage then it is likely that stabilising select on would occur, leading to a situation where the gene frequency was no longer reduced, but would increase slightly to an equilibrium state with continued discrimination against reactors (Webb et al, 1985). Relaxation of selection against reactors would lead to an increase in gene frequency. The high proportion of heterozygotic sires in each generation and the low rate of response to selection appear to confirm the advantage, but the incidence of reactors in HN x HN matings continues to decline, suggesting that an equilibrium has not yet been reached. Herd trends are obscured to some extent by the population structure. It appears that the gene frequency in dams is lower than in sires in Gen 2, as the observed incidence of reactors in HN x HN matings is less than the 0.20 predicted if all the dams were also heterozygotic. This may indicate that the greater selection differential in boars leads to the selection of a higher proportion of heterozygotes than in gilts. Implicit in this is the presence of a measurable advantage in performance for the heterozygotes relative to the homozygotes.

There is no direct evidence from performance test data that one genotype has any selective advantage over the other, however the HN group consisted largely of heterozygotes, which would in fact be favoured over the homozygous negative animals. The index most closely reflects FCR, which was no different in the two groups. If heterozygotes are assumed to be intermediate in performance, then relative to homozygous negative pigs they would have less fat and presumably more lean which would give them a selective advantage. No direct assessment of relative lean content can be made but previous studies indicate that the lean content of the heterozygote is intermediate (e.g. Webb et al 1982). The lack of difference in FCR between the groups would suggest that any differences in lean content between genotypes are small.

There is no indication from this study of what the effects of selection against the halothane gene have been on rates of genetic progress in other desirable performance traits. However, it seems likely that in the current population an increase in the frequency of the halothane gene has been at least partly responsible for the high lean content and genetic merit of the stock relative to other Landrace populations as seen from MLC sib-test results (e.g. MLC, 1979) and indeed CPE results (MLC, 1982).

Selection for improved lean tissue food conversion and against halothane reaction appears to some extent to be antagonistic. This leads to the possibility that an on-going cost will have to be suffered in order to maintain an equilibrium gene frequency. The situation would have to be continued until such a time as a reliable test for distinguishing between the heterozygote and homozygous negative is developed. The minimum effect of continued selection against HP pigs on desirable performance traits is a loss of selection differential. Should the gene be eliminated it seems likely that there is still plenty of variation present for continued improvement of the lean content of...
the carcass. The rate at which reduction of the gene frequency occurs is de-
dependent on the degree to which stabilising selection is occurring and also the
degree of penetrance. Ultimately the value of any selection response must be
weighed commercially against the cost of achieving it, and may be beneficial
even if an equilibrium state is reached. There remains little doubt that the
frequency of the halothane gene can be manipulated under field conditions.

ACKNOWLEDGMENTS

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this paper.

REFERENCES

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Report.
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Southwood O.I; Curran M.K; Simpson S.P; Webb A.J. (1986) BSAP Winter Meeting,
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Webb A.J; Southwood O.I; Simpson S.P. (1985) EEC Seminar "Evaluation and Control
of Meat Quality in Pigs" Dublin.
Fig. 1. Trend in herd frequency of halothane reaction over time (4 week periods)

Time scale in weeks

Proportion of HP

0.50

0.40

0.30

0.20

0.10

20 40 60 80 100 120 140 160

b = -0.722 ± 0.069
### T1. Frequency Of Holothone Reactors Within Sire Generation

<table>
<thead>
<tr>
<th>Gen.</th>
<th>Sire's No.</th>
<th>Litters</th>
<th>Total Progeny</th>
<th>Proportion HP</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>41</td>
<td>603</td>
<td>5121</td>
<td>0.396</td>
</tr>
<tr>
<td>1</td>
<td>21</td>
<td>520</td>
<td>4747</td>
<td>0.737</td>
</tr>
<tr>
<td>2</td>
<td>8</td>
<td>94</td>
<td>789</td>
<td>0.170</td>
</tr>
<tr>
<td>Total</td>
<td>70</td>
<td>1217</td>
<td>10657</td>
<td>0.309</td>
</tr>
</tbody>
</table>

### T2. Estimated Parental Frequency Of The Holothone Gene In The Herd

<table>
<thead>
<tr>
<th>Gen.</th>
<th>Gene Frequency</th>
<th>Penetrance</th>
<th>Expected Incidence HP</th>
<th>Observed Incidence HP</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.58±0.02</td>
<td>0.01±0.007</td>
<td>0.91±0.01</td>
<td>0.316</td>
</tr>
<tr>
<td>1</td>
<td>0.70±0.02</td>
<td>0.01±0.005</td>
<td>0.82±0.03</td>
<td>0.396</td>
</tr>
<tr>
<td>2</td>
<td>0.56±0.06</td>
<td>0.0</td>
<td>0.80±0.13</td>
<td></td>
</tr>
</tbody>
</table>

### T3. Estimated Gene Frequency In The Selected HN Parents, Assuming The Herd Gene Frequencies And Penetrances Calculated

<table>
<thead>
<tr>
<th>Gen.</th>
<th>Gene Frequency</th>
<th>Expected Incidence HP In HN &amp; HN Matings</th>
<th>Observed Incidence HP In HN x HN Matings</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.50</td>
<td>0.215</td>
<td>0.223</td>
</tr>
<tr>
<td>2</td>
<td>0.43</td>
<td>0.144</td>
<td>0.159</td>
</tr>
</tbody>
</table>

### T4. Most Probable Genotypes Of Sires In Gen 0, 1 & 2

<table>
<thead>
<tr>
<th>Genotype</th>
<th>No. of sires</th>
<th>Gen 0</th>
<th>Gen 1</th>
<th>Gen 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>NN</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Nn</td>
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<td>19</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>nn</td>
<td>13</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

### T5. Relative Performance Of Holothone Reactors And Non-Reactors (HP-HN)

<table>
<thead>
<tr>
<th>Period</th>
<th>Sex</th>
<th>No.</th>
<th>ZHP</th>
<th>DG(Kg)</th>
<th>FCR</th>
<th>SH</th>
<th>L</th>
<th>C</th>
<th>K</th>
<th>Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>A (Years1-2)</td>
<td>M</td>
<td>581</td>
<td>35.8</td>
<td>-0.03</td>
<td>0.04</td>
<td>-0.2</td>
<td>-0.3</td>
<td>-0.4</td>
<td>-0.5</td>
<td>-5W</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>1032</td>
<td>38.4</td>
<td>-0.01</td>
<td>0.4</td>
<td>-0.4</td>
<td>-0.4</td>
<td>-0.3</td>
<td>***</td>
<td>**</td>
</tr>
<tr>
<td>B (Years2-3)</td>
<td>M</td>
<td>504</td>
<td>31.5</td>
<td>-0.01</td>
<td>0.05</td>
<td>-0.2</td>
<td>-0.3</td>
<td>-0.5</td>
<td>-0.5</td>
<td>3B</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>808</td>
<td>33.0</td>
<td>-0.01</td>
<td>0.01</td>
<td>-0.1</td>
<td>-0.2</td>
<td>-0.2</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>C (Years3-4)</td>
<td>M</td>
<td>521</td>
<td>17.1</td>
<td>-0.05</td>
<td>0.05</td>
<td>-0.2</td>
<td>-0.7</td>
<td>-0.5</td>
<td>-0.5</td>
<td>-7W</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>1251</td>
<td>19.4</td>
<td>-0.03</td>
<td>0.4</td>
<td>-0.4</td>
<td>-0.5</td>
<td>-0.5</td>
<td>4B</td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>M</td>
<td>1606</td>
<td>28.4</td>
<td>-0.03</td>
<td>0.03</td>
<td>-0.1</td>
<td>-0.4</td>
<td>-0.9</td>
<td>-0.5</td>
<td>-4W</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>3108</td>
<td>29.2</td>
<td>-0.01</td>
<td>0.0</td>
<td>-0.3</td>
<td>-0.2</td>
<td>-0.2</td>
<td>0</td>
<td>N5</td>
</tr>
</tbody>
</table>

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