An exact definition of meat quality, covering all aspects of production, cannot be given today. The importance of a single quality trait may not be the same in fresh and processed products. However, some measures of meat quality are important in all aspects of production. This is true for traits associated with the pale, soft exudative (P. S. E.) condition of the muscle.

P. S. E. muscle is the major meat quality problem in pigs. It results in less desirable products and in large economic losses for the pork industry (Weniger et al., 1970; Hall, 1972). Unfortunately, no objective method exists today by which P. S. E. can be measured directly. One is therefore forced to use traits more or less closely related to this problem. Meat colour, water binding capacity and muscle pH are the traits most often used.

While the inheritance of meat colour has been extensively studied, genetic studies of water binding capacity and pH are limited, and most investigations are based on relatively small samples. In the following, the main emphasis will therefore be placed on meat colour.

Inheritance of Meat Quality Characteristics

Meat colour

The relative importance of additive gene effects and environment, i.e. the combined effect of environmental and non-additive gene effects, on meat colour of the longissimus dorsi muscle has been investigated by several authors (Table 1).

These investigations have shown that meat colour to some extent is determined by additive gene effects, since the heritability found for this trait range from 0.05 (Allen et al., 1966) to 0.55 (Pease & Smith, 1965) with an overall average of approximately 0.3. However, meat colour is a complex trait. The colour impression is a function of both pigment concentration and structural condition of the muscle. Recent investigations on muscles from Danish Landrace pigs (unpublished) showed that the heritability of colour of processed muscles was considerably higher (0.5 to 0.7) than the heritability of colour of fresh muscles (0.3). This would seem to indicate that the heritability of pigment concentration is high, since structural differences to a large extent is eliminated from processed muscles. Hence, the heritability of colour of fresh muscles may be lower because the heritability of the structural condition, i.e. the P.S.E. condition is low.

TABLE 1
HERITABILITY ESTIMATES FOR MEAT COLOUR

<table>
<thead>
<tr>
<th>Reference</th>
<th>Heritability</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jonsson (1963)</td>
<td>0.23</td>
<td>1,685 males</td>
</tr>
<tr>
<td></td>
<td>0.43</td>
<td>1,687 females</td>
</tr>
<tr>
<td></td>
<td>0.30</td>
<td>2,696 males</td>
</tr>
<tr>
<td></td>
<td>0.45</td>
<td>2,700 females</td>
</tr>
<tr>
<td></td>
<td>0.34</td>
<td>1,192 males</td>
</tr>
<tr>
<td></td>
<td>0.17</td>
<td>1,192 females</td>
</tr>
<tr>
<td></td>
<td>0.41</td>
<td>800 males</td>
</tr>
<tr>
<td></td>
<td>0.55</td>
<td>800 females</td>
</tr>
<tr>
<td></td>
<td>0.05</td>
<td>87 males</td>
</tr>
<tr>
<td></td>
<td>0.18</td>
<td>2,904</td>
</tr>
<tr>
<td></td>
<td>0.28</td>
<td>585</td>
</tr>
<tr>
<td></td>
<td>0.28</td>
<td>11,379</td>
</tr>
<tr>
<td></td>
<td>0.10</td>
<td>650</td>
</tr>
<tr>
<td></td>
<td>0.19</td>
<td>616 males</td>
</tr>
<tr>
<td></td>
<td>0.30</td>
<td>4,500 females</td>
</tr>
<tr>
<td></td>
<td>0.35</td>
<td>1,437</td>
</tr>
<tr>
<td></td>
<td>0.21</td>
<td>1,695</td>
</tr>
</tbody>
</table>

During a period with severe P.S.E. problems (approximately 40 per cent) among pigs slaughtered from a progeny testing station at a particular bacon factory, it was observed that progeny from certain sires never had P.S.E. muscles. One of these sires had more than 20 litter groups slaughtered. One litter group consists of 2 females and 2 castrated males. With a heritability of no more than 0.3 for meat colour, these results were unexpected. A possible explanation could be that the P.S.E. condition is influenced by non-additive inheritance. An investigation was therefore made in order to estimate the relative influence of additive and non-additive gene effects on meat colour.

The data used for the investigation were collected during the test years 1967/68 through 1969/70 from the four Danish pig progeny testing stations. Records from 7,216 pigs from 1,877 litter groups and 825 sires were included. The sires
were from 410 breeding centres. The pigs entered the test stations at 20 Kg and were fed individually on a standard ration until slaughtered at 90 Kg live weight (Clausen et al., 1970). Meat colour of the longissimus dorsi muscle was scored subjectively using a scale ranging from 0.5 (light) to 5.0 (dark) (e.g. Clausen et al., 1970).

The data were analysed on a within station year and sex basis using a conventional hierarchal type variance component analysis as described by King & Henderson (1965). The heritability estimate was based on the sire variance component, and dominance variance was estimated on the basis of the difference between sire and litter variance components as described by Giedrem & Ronningen (1970).

The average meat colour score was 2.20 with a standard deviation of 0.50. The coefficient of variation was 22.9 per cent. The results of the analysis of variance shown in Tables 2 and 3.

**TABLE 2**

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Mean square</th>
<th>Variance component</th>
</tr>
</thead>
<tbody>
<tr>
<td>Station-year-sex (SYS) groups</td>
<td>22</td>
<td>1.76</td>
<td></td>
</tr>
<tr>
<td>Breeding centres/(SYS) groups</td>
<td>796</td>
<td>0.40</td>
<td>0.0106</td>
</tr>
<tr>
<td>Sires/breeding centres</td>
<td>830</td>
<td>0.31</td>
<td>0.0103</td>
</tr>
<tr>
<td>Litter groups/sires</td>
<td>2,102</td>
<td>0.26</td>
<td>0.0345</td>
</tr>
<tr>
<td>Within litter groups</td>
<td>3,465</td>
<td>0.19</td>
<td>0.1939</td>
</tr>
</tbody>
</table>

**TABLE 3**

<table>
<thead>
<tr>
<th>Proportion of variance due to different sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breeding centre environment</td>
</tr>
<tr>
<td>Additive gene effects</td>
</tr>
<tr>
<td>Non-additive gene effects (dominance)</td>
</tr>
<tr>
<td>Random influences</td>
</tr>
</tbody>
</table>

The heritability found in this study (0.17) is within the range of previous estimates. However, it is somewhat lower than those generally found in the Danish Landrace breed (Jonsson, 1963, 1965; Staun & Jensen, 1972). An underestimation of the heritability in this study may have resulted in an overestimation of the non-additive gene effects. The validity of the procedure used to estimate the influence of dominance on meat colour score rests on the assumption that the effects of common environment can be neglected. No information concerning this subject as found in the literature.

Since all pigs entered the test station at a live weight of 20 Kg breeding centre environment (4 per cent) must have exerted its effect at a stage prior to 20 Kg, and it is likely that most of the difference between breeding centres reflects a
difference in breeding policy from one breeding centre to another and therefore is of genetic origin. This means that approximately 60 per cent of the variation in meat colour score is determined by genetic factors (additive and non-additive) and 40 per cent by environmental factors. Results of calculation of the relative influence of additive gene effects and dominance on meat colour from earlier studies are presented in Table 4.

**TABLE 4**

<table>
<thead>
<tr>
<th></th>
<th>JENSEN <strong>et al.</strong> (1967)</th>
<th>STAUN &amp; JENSEN (1972)</th>
<th>Present study</th>
<th>Cured 1. dorsi (unpublished)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Additive gene effects</td>
<td>0.28</td>
<td>0.32</td>
<td>0.17</td>
<td>0.49</td>
</tr>
<tr>
<td>Dominance</td>
<td>0.35</td>
<td>0.29</td>
<td>0.39</td>
<td>0.10</td>
</tr>
<tr>
<td>Random influences 1)</td>
<td>0.37</td>
<td>0.39</td>
<td>0.40</td>
<td>0.41</td>
</tr>
<tr>
<td>Random influences 2)</td>
<td>0.63</td>
<td>0.59</td>
<td>0.69</td>
<td>0.48</td>
</tr>
</tbody>
</table>

1) Assuming dominance.
2) Assuming no dominance.

The figures in the first three columns of Table 4 are based on subjectively scored colour of *longissimus dorsi* muscles, and the figures of column four are based on objective colour measurements of cured *longissimus dorsi* muscles. Random influences have in all cases accounted for approximately 40 per cent of the variation in meat colour. Assuming no dominance, the random influences would account for 63, 59, 69 and 48 per cent, respectively, as shown in Table 4. The stabilisation of the error component by removing the presumed dominance variation would tend to support the conclusion that the differences in sire and litter variance components arise from dominance rather than from common environment. It may be concluded, therefore, that 20-30 per cent of the variation in meat colour is due to additive gene effects, 30-40 per cent to dominance and approximately 40 per cent to random influence.

**Ludvigsen** (1954) observed a close connection between P.S.E. and sudden deaths in pigs. The description of the signs he observed fits closely with the procine stress syndrome (P.S.S.) described by **Topel et al.** (1969). Furthermore, the symptoms of malignant hyperthermia susceptible (M.H.S.) pigs (**Jones et al.,** 1972; **Nelson et al.,** 1972) resemble those of P.S.S. pigs, and **Christian** (1972) concluded that M.H.S. and P.S.S. are synonymous. Thus, M.H.S., P.S.S. and at least a part of the P.S.E. problem may have a common cause.

**Hall et al.** (1966) suggested that the M.H.S. condition is inherited. **Britt et al.** (1969) and **Britt & Kalow** (1970a, b) using human data, concluded that the M.H.S. condition is inherited as an autosomal dominant of variable penetrance and expressivity. **Christian** (1972) suggested that the P.S.S. condition is due to recessive inheritance with variation in penetrance. In view of the relationship between M.H.S., P.S.S. and P.S.E., these results supports the finding that meat colour is influenced by non-additive gene effects.
A heritability of 0.2 to 0.3 indicates that selection for improved meat colour would be effective. However, if further investigations confirm that meat colour is influenced by dominance more progress may be obtained by selecting for reduced incidence of P.S.E. rather than average meat colour.

**Water binding capacity and pH**

Allen *et al.* (1966) reported heritability estimates of expressible juice of 0.46 and 0.77 in the Duroc and Yorkshire breeds respectively. These estimates were based on only 55 Duroc and 87 Yorkshire barrows. Jensen *et al.* (1967) found a heritability of 0.63 and Weniger *et al.* (1970) reported estimates of 0.37 and 0.56. These investigations were based on approximately 600 observations. Staun & Jensen (1972), in an investigation comprising 1437 Danish Landrace pigs, found heritability estimates of 0.29 and 0.14 for gilts and castrates, respectively.

As might be expected from the relatively small samples, heritability estimates of water binding capacity are quite variable. However, they indicate that water binding capacity is determined to some extent by additive gene effects.

Jonsson (1965) found heritability estimates of 45 minute pH of 0.19 and 0.45 for castrates and gilts, respectively. Weniger *et al.* (1970) reported an estimate of 0.19.

Heritability estimates of ultimate pH range from zero (Jensen *et al.*, 1967) to 0.52 (Allen *et al.*, 1966).

**Genetic correlations**

In Table 5 phenotypic and genetic correlations between meat colour score and various carcass traits are shown. These estimates are based on 7,216 Danish Landrace pigs.

<table>
<thead>
<tr>
<th>Meat colour correlated with</th>
<th>$r_p$</th>
<th>$r_g$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area of musc. longissimus dorsi</td>
<td>-0.06</td>
<td>-0.25</td>
</tr>
<tr>
<td>Sidefat thickness</td>
<td>0.10</td>
<td>-0.03</td>
</tr>
<tr>
<td>Carcass length</td>
<td>0.18</td>
<td>0.57</td>
</tr>
<tr>
<td>Per cent lean in one side</td>
<td>-0.18</td>
<td>-0.14</td>
</tr>
<tr>
<td>Daily gain</td>
<td>-0.02</td>
<td>-0.28</td>
</tr>
<tr>
<td>Freed efficiency</td>
<td>0.04</td>
<td>0.28</td>
</tr>
</tbody>
</table>

Although the genetic correlations in Table 5 are moderate in magnitude, they indicate an unfavourable association with meat colour score. In an earlier investigation of the Danish Landrace breed Jonsson (1965) reported favourable estimates of the genetic correlation between meat colour and longissimus dorsi area of 0.18 and 0.11 for castrates and gilts, respectively. Jonsson *et al.* (1972) found
a correlation of $-0.29$ and Flock (1968) estimated a genetic correlation of $-0.56$ between these two traits. Weniger et al. (1970) reported estimates ranging from $-0.26$ to $-0.62$. Jensen et al. (1967) and Arganosa et al. (1969) reported estimates of $-0.08$ and $-0.73$, respectively. Also, sidefat thickness and per cent lean in one side are unfavourably associated with meat colour. As will be seen in Table 5, there exists a positive relationship between meat colour and carcass length. Also, Arganosa et al. (1969) reported a positive correlation between these two traits. However, Weniger et al. (1970) found small negative correlations between meat colour and carcass length.

The genetic correlations between water binding capacity and carcass traits are also antagonistic. Thus, Weniger et al. (1970) reported estimates of $1.11$ and $0.80$ between water binding capacity and longissimus dorsi area. Jensen et al. (1967) found a correlation of $0.35$. However, Staun & Jensen (1972) reported estimates of $-0.07$ and $-0.27$.

The genetic correlations between meat quality and meatiness indicate that selection for increased meatiness will lead to a deterioration of meat quality. However, since most correlations are moderate in size, inclusion of a meat quality trait of a reasonable heritability, for instance meat colour, in a selection programme should at least prevent this deterioration and may even improve meat quality.

**SUMMARY**

The most serious meat quality problems in pigs are those connected with P.S.E. condition of the muscle.

As far as genetic analyses are concerned, meat colour is the trait that has received most attention. In most cases, the heritability of meat colour has been found to be of moderate magnitude. Thus, selection for meat colour should lead to an improvement in meat colour. Furthermore, there are indications that meat colour may be influenced by non-additive gene effects, but more research on this subject is needed.

Heritability estimates of water binding capacity and pH are based on rather small samples, but the available estimates point in the direction that these traits also are moderately heritable.

The genetic association between meat quality traits and meatiness is antagonistic. The magnitude of the correlations suggests, however, that inclusion of a trait such as meat colour in the selection programme would improve meat quality or at least prevent it from further deterioration.

**RESUMEN**

Los problemas más serios planteados con relación a la calidad de la carne son, en el caso de los cerdos, aquellos referentes a la afección del músculo blando, pálido y exudativo (PSE).

Desde el punto de vista de los análisis genéticos, el rasgo que ha recibido la máxima atención ha sido el color de la carne. En la mayoría de los casos, se ha encontrado que la heredabilidad de este rasgo es de magnitud moderada. Por tanto, la selección en el color de la carne debería conducir a una mejora del mismo. Además, existen indicaciones de que el color de la carne puede ser influenciado
mediante efectos producidos por genes no aditivos, pero es necesaria una inves-
tigación posterior sobre este punto.

Las estimaciones acerca de la heredabilidad de la capacidad de retención de
guía y del pH se basan en pruebas reducidas, pero las estimaciones de que se
disponen apuntan el hecho de que estos rasgos son también moderadamente
heredables.

La asociación genética entre los rasgos cualitativos de la carne y la carnosidad
es antagónica. Sin embargo, la magnitud de las correlaciones sugiere que la incul-
sión de un rasgo tal como el color de la carne en el programa de selección, me-
joraría la calidad de ésta o por lo menos impediría su posterior deterioro.

RESUME

Les problèmes les plus sérieux qui ont été posés quant à la qualité de la
viande sont, dans le cas des porcs, ceux qui se rapportent à la maladie éxudative
du muscle pâle (PSE).

Du point de vue des analyses génétiques, le trait qui a mérité le maximum
d'attention a été la couleur de la viande. Dans la plupart des cas, l'héréditabilité
de ce trait est de grandeur modérée. Donc, la sélection dans la couleur de la
viande, devrait conduire à une amélioration de celle-ci. En plus, il existe des indi-
cations sur l'influence des effets produits par gènes non additifs sur la couleur
de la viande, mais il faut une investigation postérieure sur ce point.

Les estimations sur l'héréditabilité de la capacité de rétention de l'eau et du pH
se basent sur des preuves réduites, mais les estimation de qu'on dispose visent
c'est fait: que ces traits peuvent être aussi modérément hérités.

L'association génétique entre les traits qualitatifs de la viande et l'excès de
viande est antagônique. Cependant, la grandeur des corrélations suggère que
l'inclusion d'un trait tel que la couleur de la viande dans le programme de sélection,
améliorerait la qualité de celle-ci ou, au moins, empêcherait sa détérioration
postérieure.

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