

EFFECT OF IDENTICAL HOMOZYGOSITY ON GROWTH IN PIGS.

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SUMMARY

Four litters produced by father-daughter matings (back crosses) resulting in animals with an inbreeding coefficient of 25 percent were typed with 21 informative genetic markers with respect to identical homozygosity. On the basis of these markers the realized inbreeding was found to vary between 6 and 42 %. The linear decrease in weight at day 1, 26, 88 and 136 regressed on relative degree of identical homozygosity was estimated to -.71, -4.8, -10 and -31 kg respectively. Correspondingly a decrease in daily gain of 182 g and an increase of 2.3 percent of lean was found. Calculations show that the effect of each locus with identical homozygosity was generally small and in most cases the effect was, as expected, negative on growth.

INTRODUCTION.

The general theory behind the negative linear relationship between a production trait and the inbreeding coefficient is well described in textbooks, e.g. Falconer (1989). In a recent paper by Christensen et al. (1993) details on the decrease in production traits in pigs due to inbreeding is given. The inbreeding coefficient represents the expected proportion of the individual's genome which is identical by descent. The realized proportion of inbreeding varies between individuals with the same inbreeding coefficient. The realized inbreeding can be studied using genetic markers to identify chromosomal segments which are identical by descent. Recently, the markers of choice for genetic analysis of genomes have been the microsatellite markers (Weissenbach et al., 1992; Serikawa et al., 1992). The present investigation relies primarily on microsatellites, most of which have been described previously (Winterø et al., 1992; Fredholm et al., 1993).

A pig family was founded and maintained as a closed line with inbreeding (Fredholm et al., 1993) with the objective of establishing family material for linkage studies, where specifically genes with a dominant/recessive type of inheritance could be subjected to study. In the present paper we analyze the degree of realized inbreeding in the first inbred generation of the family, and analyze its effect on growth and percentage of lean.

MATERIAL AND METHODS

Animals. The animals were kept at the Pig Research Station for sows and piglets, Sjælland III. The founder boar and sow were of the Landrace and Yorkshire breed, respectively. The first inbred generation was produced by father-daughter matings giving an inbreeding coefficient of 0.25, see Fig. 1. All live born pigs survived to slaughter, however, two pigs (No. 27 and 32) were excluded from the statistical analyses due to abnormal low birth weights (0.6 and 0.7 kg, respectively). The pigs were weaned at four weeks of age, after which they were kept in heated pens until 10 weeks of age. They were fattened by restricted feeding with a standard commercial fodder mixture and each litter were kept in a separate pen. The males were not castrated. Weight was recorded at day 1, 26, 88 and 136. Furthermore, just before slaughter the animals were weighed and scanned for backfat thickness, and average daily gain and percentage of lean meat were calculated.

Genetic markers. Twenty one informative markers with mutual linkage relationship of >20cM (Fredholm et al., 1993) were analyzed in all animals including the parental animals. These markers constitute 3 blood group loci (EAD, EAI, EAL), 3 protein polymorphisms (HPX, Po1, SLA), 2 RFLP markers (GPI, α_{s1} -casein) and 13 microsatellite markers.

Scoring of identical homozygosity. Based on homozygosity in either of the two alleles from the founder boar 21 marker systems were informative with respect to identical homozygosity in at least two of the litters. For each animal the number of loci with identical homozygosity relative to the number of informative loci was calculated for the 21 systems (realized inbreeding).

Statistical methods. The influence of realized inbreeding on the measured growth traits was investigated within

litter and sex. Let Y_{ijk} be a growth trait measured on animal k of sex j ($j =$ male or female) in litter i ($i = 1, \dots, 4$). The variable X_{ijkl} attains the value 1 if there is identical homozygosity on the locus l ($l = 1, \dots, 21$) of animal (ijk) , and X_{ijkl} attains the value 0 if there is not identical homozygosity. If the locus is uninformative about identical homozygosity then X_{ijkl} is missing. A realized inbreeding coefficient was calculated for each animal as 100 times the average of the non missing X_{ijkl} . The influence of each locus on the trait was analyzed according to the model

$$Y_{ijk} = \mu + \text{litter}_i + \text{sex}_j + \text{litter} * \text{sex}_{ij} + \beta X_{ijkl} + \epsilon_{ijk}$$

The effect of realized inbreeding was analyzed in a similar model with X_{ijkl} replaced by X_{ijk} .

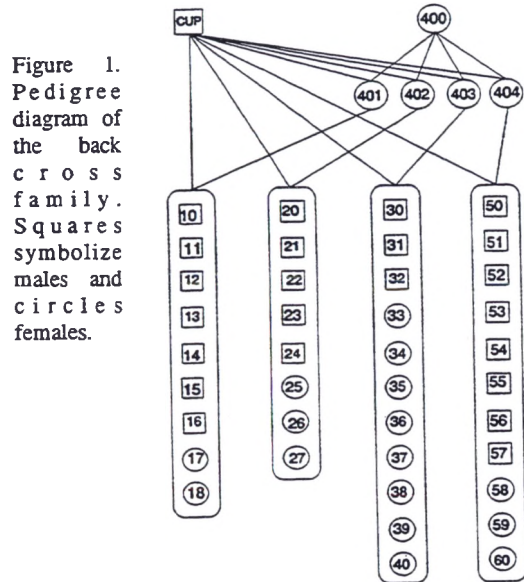
RESULTS.

The number of loci with identical homozygosity in the 37 animals studied varied between 1 and 9 out of the 21 loci analyzed, equivalent to $1/15=6\%$ and $9/19=47\%$. Of 646 possible identical homozygotic loci 164 were actually found to be identical, resulting in an average of $164/646=25.4\%$. This result is in accordance with expectations based on a Mendelian segregation ratio of 3.1 (expected value 161.5).

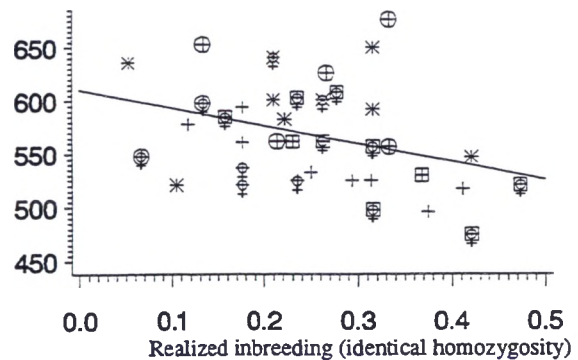
In Fig. 2 the distribution of relative identical homozygosity together with its negative effect on average daily gain is shown. Each litter have their own symbol and females are

Figure 2. Relationship between realized inbreeding, and daily gain from birth to slaughter in gram. Each litter have their own symbol (offspring from sow. 401 star; 402 circle; 403 square; 404 plus) for the individual data, females are indicated by ♀. The line is a linear regression line estimated on uncorrected data.

indicated by the ♀ symbol. The negative linear relationship can most clearly be seen for animals within litter and sex. See for instance the + symbols which represent the 8 male offspring from sow 404. In Table 1 the result from the statistical analyses giving the linear relationship between relative homozygosity and 5 measures of growth performance, and percentage of lean is presented. There were statistically significant effect of litter*sex except in the weight at 26 days and in percentage of lean. The effect of homozygosity on growth was significantly negative in all cases but one. Relative to the mean value the negative linear effect was approximately 40 percent for identical homozygosity.



Daily gain, g



The effect on production traits of identical homozygosity in each locus relative to other genotypes is shown in Table 2. On average there is a small negative effect of identical homozygosity on the traits concerning growth, whereas a positive effect is seen on the percentage of lean meat. In general the effect of each locus is small, and the majority of the loci have a sign in the expected direction, i.e. negative for the growth traits and positive for percentage of lean meat. The inbreeding did not affect litter size and general vitality of the pigs.

DISCUSSION

In the present study with offspring from father daughter matings two out of three genes contributing to the development of identical homozygosity segregated from a founder male while the third gene segregated from a female. Thus, when estimating the total coverage of the markers used, the calculation will be most accurate if based on a weighted average of the size of the porcine male and female genome. Using sex-specific recombination data, Ellegren et al. (submitted) has estimated the size of the male genome to be 1,682 cM \pm 156, whereas the female genome have been estimated at 2,408 cM \pm 299. A weighted average of two male gametes and one female gamet, which is the basis for the present study, will be close to 2000 cM.

In families established by inbreeding a proportion of the genome of each individual is expected to be identical by descent. Since blocks of linked genes rather than individual genes are transmitted from parents to offspring, blocks of linked genes become identical by descent. Such blocks are called homogenic segments. The status of a marker locus thus represents the status of the homogenic segment carrying the marker. The realized inbreeding can be predicted from the status of the marker loci. The required number of marker loci depends on the lengths of the homogenic segments. Hanson (1959) and Stam & Zeven (1981) have estimated the length of the homogenic segment carrying a marker, assuming that no interference occurs and assuming that recombination takes place according to a Poisson process along chromosomes. Considering offspring from father-daughter matings and assuming a genome of infinite length the average length of the homogenic segments is 33 cM with full coverage. If only one random locus is considered it covers 66 cM. From these considerations it can be concluded that the 21 unlinked polymorphic markers used in this investigation cover approximately 50% of the genome.

The regression coefficient of growth characters on the degree of identical homozygosity compared to the mean is approximately 40 percent, lowest for weight at 88 days (28 %) and highest for weight at 26 days (68%). The average reduction can be compared to inbreeding depression calculated by ordinary phenotype data. Recently published results from the same pig family (Christensen et al. 1993) are in agreement with these findings, i.e. the linear effect of inbreeding on slaughter weight gain was found to be a 160/446= 36% decrease at 100% inbreeding.

The uniformity of the relationship between growth rate and the degree of identical homozygosity (see Fig 2) indicate that the effect of the individual genes is rather small. The fact that the effect of most of the loci are small can be seen from Table 2. Strong deviation from the linear relationship by specific animals would indicate segregation of genes with large effect. Only one animal in Fig. 2 exhibits signs of large gene effects namely the animal with the highest growth rate having a realized inbreeding of 0.35.

Families produced by father daughter mating could easily be integrated in a breeding plan and would not disturb the normal selection procedures. Such families could give information on genes with large effects on production traits using efficient DNA marker genotypings. The large phenotypic effects can either be caused by recessive genes with low frequency in the population, rearrangements by recombination or new mutations all of which will go undetected in the ordinary breeding schemes. The dominant/recessive genes with large phenotypic effects detected in these families would be of particular interest for utilization in lines used for cross breeding. The results presented here indicate that by using a well spaced set of markers to study individual inbreeding, it will be possible to analyze the basis for inbreeding and subsequently heterosis.

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Table 1. Linear regression (b) of growth traits on relative degree of identical homozygosity (b-hom). Effect of litter*sex (L*S) have been included in the model. The levels of statistical significance are given by. *, P<.05, **, P<.01. Single sided tests were used for the b-values.

Trait	Mean	L*S	b-hom
Weight day 1, kg	1.21±.11	**	-0.71±.20**
Weight day 26, kg	7.18±1.0	-	-4.8±1.9**
Weight day 88, kg	35.9±3.7	**	-10±7**
Weight day 136, kg	66.1±7.9	**	-31±14**
Av. daily gain, g	567±39	**	-182±71**
Lean %	0.5±1.0	-	2.1±2.0

Locus	Inf	Hom	ADG
GPI	30	7	-19.9
HPX	37	7	11.0
Pol	37	9	-17.5
EAD	26	7	-17.8
EAI	19	7	-8.5
SLA	37	8	-4.2
CGT40	37	13	-34.0
S00--	37	7	-29.4
S0002	37	7	-17.5
S0007	37	12	6.5
S0010	37	10	-0.7
S0062	29	7	-5.7
S0063	17	6	-35.5
S0068	37	8	-16.9
S0069	36	7	33.5
S0070	36	12	-23.2
S0071	16	3	14.2
S0075	20	2	-16.8
S0076	21	4	-4.5
S0077	30	8	-6.4
S0153	33	13	-4.7
SUM	646	164	-198.5

Table 2. Effect on average daily gain ADG of identical homozygosity in comparison to all other informative genotypes in each of the 21 loci. Inf. indicate the number of informative animals with respect to identical homozygosity and Hom the number of homozygous animals. No statistical significance is given for the individual effects, the effect can be evaluated according to its size and the number of informative individuals. Microsatellite CGT40 without locus assignment.