

Assessing the effects on litter size of age of inbreeding in an ancient line of Large White pigs

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ABSTRACT: Different pedigree parameters were computed from the complete genealogy of a small herd of Large White pigs, kept closed from 1931 to 1992, with 14 unrelated founders and 1,358 reproducers. The mating design was remarkably changed at 1956 to restrict the rate of inbreeding. Total inbreeding was divided into “old” and “new” components with respect to this year. Inbreeding depression on litter size was estimated on 1,638 records from 613 sows born after 1956 using both metrics and their rates per generation. Negative effects of a 10% of new inbreeding were inferred (-0.45 piglets born and -0.62 piglets born alive), while the impacts of total inbreeding were less substantial (-0.28 and -0.50 piglets) or negligible relative to those of old inbreeding. This departure of classical model suggests that, when deep pedigree exists, more accurate depression estimates may be obtained using new inbreeding metrics.

Keywords: Large White; new inbreeding; inbreeding depression

Introduction

Inbreeding depression exists to some degree in every population of small effective census and it is often observed in reproductive and fitness traits (Falconer and Mackay, 1996). An understanding of inbreeding and its possible negative effects is relevant both in conservation or selection programs of farm animals. Measuring inbreeding depression is not a difficult task on contemporary animals with a large variation of inbreeding values (Fernández et al., 2002), but this situation is unusual and most of the studies in livestock species should be performed on data recorded in progressively inbred populations.

Both simulation and empirical studies show that the level of inbreeding depression may depend upon the increase of inbreeding by generation (ΔF), with the faster rates having more negative impact (Lacy and Ballou, 1998; Wang et al., 1999; Wang, 2000). Moreover, individual ΔF has been proposed as an alternative choice to measure inbreeding depression in populations with incomplete pedigree (González-Recio et al., 2008). Even when occurring at a constant rate, the inbreeding effect may also differ between the recent (new) and the distant (old) inbreeding in the past population history (Hinrichs et al., 2007). From this viewpoint, the effects of recent inbreeding could represent the impact of new mutations, whereas the ancient deleterious recessive alleles could have been previously purged in the population (Wang et al., 1999).

The goals of this study were *a*) to perform a genealogical analysis of the trends of inbreeding, coancestry and effective population size along the generations of an ancient closed line of Large White pigs, and *b*) to compare the effects on litter size of metrics of old,

new and total inbreeding and of their rates by generation. To obtain accurate inferences about inbreeding effects, data were analyzed using a Bayesian procedure which takes into account all the available information and allows a joint analysis of systematic effects, variance components and breeding values (Rodríguez et al., 1998).

Materials and Methods

Data. A herd of Large White pigs was established since 1931 in an experimental farm of the Misión Biológica de Galicia (Salcedo, Pontevedra, Spain) from a group of reproducers imported from England representing most of the variability existing at this time within the Herd Book of the breed. The starting group was formed by four boars and four sows, three of them pregnant to other unrelated boars. The herd was kept closed, with overlapping generations and a census of 8-10 boars and 30-35 sows, since its foundation until its final removal in 1992, being available the complete and deep genealogy from the 14 unrelated founder animals to all the reproducers with 1,358 triads (individual-sire-dam). Litter size records were also systematically collected in the farm (Rodríguez et al., 1998).

Pedigree analysis. The coancestry coefficient (f_{ij}), inbreeding coefficient (F_i) and the number of discrete equivalent generations (EqG_i) were calculated for each pair of reproducers i and j and for each i individual respect to the base generation of unknown parents (Wooliams and Mäntysaari, 1995). The approximate individual coancestry and inbreeding rates by generation were computed by the expressions $\Delta f_i = 1 - \frac{EqG_i + EqG_j}{2} \sqrt{1 - f_{ij}}$ (Cervantes et al., 2011) and $\Delta F_i = 1 - \frac{EqG_i - 1}{EqG_i} \sqrt{F_i}$ (Gutiérrez et al., 2009). The realized effective population size was estimated from individual increases of inbreeding ($N_{e\Delta F}$) and of pairwise coancestry ($N_{e\Delta f}$). Other genealogical parameters as the effective number of founders (N_{ef}) and non founders (N_{enf}) and the founder genome equivalents (N_{ge}) were also calculated (Toro et al., 2000). A partition of the individual inbreeding coefficients in two components (F_{old_i} and F_{new_i}) was performed, according the equations proposed by Hinrichs et al. (2007), with respect to an intermediate base constituted in this case by the breeding animals born before 1956. Before this year, the line was divided into four sections and matings were mainly performed within these four sire quasi-families along the first eight rounded discrete equivalent generations ($1 \leq EqG \leq 8$). In the posterior period ($9 \leq EqG \leq 28$) the sections were blended and a mating system was designed avoiding matings between relatives, although some inbred mates were performed from 22 to 24 EqG with experimental purposes.

Bayesian analysis of inbreeding depression.

Litter size data (number of piglets born and born alive, NB and NBA) recorded on 1638 litters born from 613 sows were separately analyzed using a repeatability animal model:

$$y = X\beta + Zu + Wp + e$$

where y represents the vector of data; X , Z and W are known incidence matrices relating systematic (β) and random (u and p) effects to y ; u , p and e are the vectors of random additive genetic, permanent environmental and residual effects, respectively. The systematic effects in β were parity order (five levels: 1st to 4th and ≥ 5 th), four seasons and as covariates six inbreeding metrics. Total inbreeding metrics (F and ΔF) were separately analyzed, and pairs of old and new metrics (F_{old}/F_{new} and $\Delta F_{old}/\Delta F_{new}$) were jointly fitted in different models. To obtain accurate inferences about inbreeding effects, data were analysed by a procedure of Bayesian inference using the Gibbs sampling algorithm implemented in the TM software (Legarra et al., 2008). The usual location and dispersion parameters were calculated from 1,000,000 saved samples of marginal posterior distributions of the parameters of interest with a burning of 40,000 discarded samples.

Results and Discussion

Pedigree analysis. The trends of the coancestry (f) and inbreeding (F) coefficients averaged by the 28 EqG are described in Fig. 1. The mean value of coancestry coefficients increased since $f_1 = 0.079$ in the first EqG until $f_{28} = 0.463$ in the last one, being $F_1 = 0.000$ and $F_{28} = 0.429$ the respective mean inbreeding values. The relationships between the averaged f_{EqG} and F_{EqG+1} values at two successive equivalent generations reflect the remarkable changes both in the population structure and the implemented mating tactics. From the fusion of families, the averaged F and F_{new} values increased in a similar way and a small negative trend may be observed for the F_{old} values (Fig. 1).

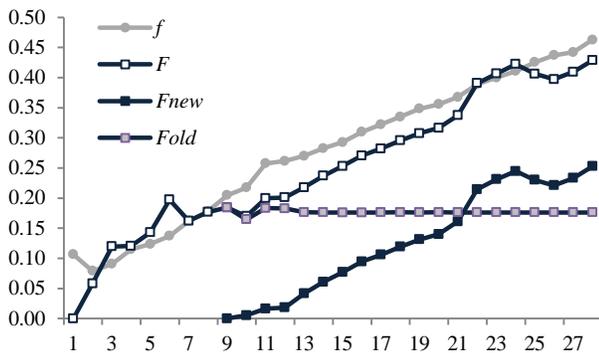


Figure 1. Changes in averaged coefficients of coancestry (f), inbreeding (F), and components of new and old inbreeding (F_{old} , F_{new}) over the rounded discrete equivalent generations (EqG).

The values of the realized effective population sizes calculated for each EqG from individual increases in

inbreeding coefficients ($N_{e\Delta F}$) or from increases in pair coancestries ($N_{e\Delta f}$) are reported in Fig. 2. In contrast with ΔF and $N_{e\Delta F}$ which are affected by population structure and preferential matings, Δf and $N_{e\Delta f}$ are more stable parameters that mainly reflect genetic drift (Cervantes et al., 2011). Both parameters may be compared to the effective number of founders (N_{ef}) which value, stabilized in 9.20 along the last 15 EqG , estimates half of the effective population size (Toro et al., 2000): the resultant value $N_e = 18.40$ is slightly lower than those calculated for the ensemble of pedigree with the other two methods: $N_{e\Delta F} = 21.45$ and $N_{e\Delta f} = 20.95$.

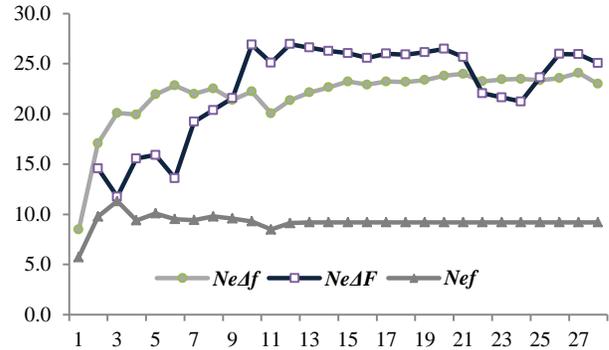


Figure 2. Effective number of founders (N_{ef}) and realized effective population sizes by discrete equivalent generations estimated from increases of inbreeding and coancestry coefficients ($N_{e\Delta F}$, $N_{e\Delta f}$)

Inbreeding depression on litter size. The analyzed data file corresponds to litters farrowed by sows born since 1956, the period after which data analysis was performed based on the decomposition into old and new inbreeding coefficients. The mean (and standard deviation) of NB and NBA records were 10.60 (SD=3.82) and 9.80 (SD=3.63) piglets, respectively. Results of the univariate analysis of these records provide Bayesian inferences about their genetic parameters and systematic effects. The means and standard deviations of the marginal posterior distributions (m.p.d.) of heritability, permanent environmental coefficient and parity order effects, expressed as differences with respect to parity one, were presented in Table 1.

Table 1. Posterior mean (PM) and standard deviation (PSD) of heritability (h^2), permanent environmental coefficient (p^2) and effects of parity order for the number of piglets born (NB) and born alive (NBA).

	NB		NBA	
	PM	PSD	PM	PSD
h^2	0.072	0.029	0.059	0.027
p^2	0.063	0.027	0.057	0.026
Parity order				
1	0.000	-	0.000	-
2	0.675	0.235	0.510	0.220
3	0.557	0.296	0.876	0.260
4	0.697	0.370	1.431	0.312
5	0.361	0.392	0.595	0.295

In relation to inbreeding depression, the mean (and SD) of the five inbreeding metrics (F , F_{old} , F_{new} , ΔF , ΔF_{new} and ΔF_{old}) were: 0.298 (0.094), 0.175 (0.016), 0.123 (0.091), 0.020 (0.004), 0.012 (0.007) and 0.032 (0.034), respectively. The main statistics of the m.p.d. of the regression coefficients on NB and NBA of the quoted inbreeding metrics are summarized in Table 2. Empirical posterior probabilities were estimated by computing the proportion of Gibbs samples of inbreeding effects that were greater than zero [$PP(b > 0)$]. A glance at this table shows a lower inbreeding depression on born piglets than on live piglets per litter, with larger and more significant inbreeding effects on the second trait. For example, both 95% HPD intervals of the effects on NB of F and F_{new} included zero and positive values, while the two intervals of the corresponding effects on NBA only included negative b_F and $b_{F_{new}}$ values.

Table 2. Basic statistics of marginal posterior distributions of effects (b)[§] of different metrics of age and rate of inbreeding (F , F_{old} , F_{new} , ΔF and ΔF_{new}) on the number of piglets born (NB) and born alive (NBA) per litter

	Posterior mean	Posterior SD	95% HPD interval [¥]	$PP\ b > 0$
<i>NB</i>				
b_F	-0.281	0.257	-0.786/0.207	0.137
$b_{F_{new}}$	-0.448	0.277	-1.000/0.086	0.049
$b_{F_{old}}$	0.661	0.683	-0.705/1.965	0.835
$b_{\Delta F}$	-0.373	0.322	-0.989/0.287	0.125
$b_{\Delta F_{new}}$	-0.278	0.256	-0.774/0.234	0.140
$b_{\Delta F_{old}}$	0.301	0.416	-0.481/1.142	0.772
<i>NBA</i>				
b_F	-0.497	0.223	-0.955/-0.079	0.011
$b_{F_{new}}$	-0.616	0.241	-1.091/-0.145	0.005
$b_{F_{old}}$	0.205	0.608	-0.996/1.370	0.630
$b_{\Delta F}$	-0.497	0.291	-1.063/0.082	0.125
$b_{\Delta F_{new}}$	-0.388	0.227	-0.832/0.060	0.044
$b_{\Delta F_{old}}$	0.064	0.374	-0.681/0.770	0.565

[§]Effects of a 10% of inbreeding and of a 1% of inbreeding rate per generation; [¥]95% HPD = 95% of highest posterior distribution interval

The appraisal of the effect of the age of inbreeding is enabled by the comparison among the statistics of m.p.d. of $b_{F_{old}}$ and $b_{F_{new}}$ coefficients. A remarkable depression on both litter size traits may be attributed to new inbreeding, being the PP values of positive effects of F_{new} [$PP(b_{F_{new}} > 0)$] on NB and NBA 1/19 and 1/199 times lower than the respective probabilities of negative effects [$PP(b_{F_{new}} < 0)$]. However, the impact on both litter size traits of the old inbreeding ($b_{F_{old}}$) seems to be negligible, although according to their PSD and 95% HPD values these effects were inferred with a greater uncertainty. It may be attributed to the low dispersion of the old inbreeding component in the analyzed period (Fig. 1).

Slow inbreeding rates could offer more opportunities to natural selection for purging deleterious alleles (Frankham et al, 2001), but since there were a near constant N_e size in the analyzed period the results about the inbreeding rate effects were less conclusive. All the 95% HPD of these parameters included the zero value, and only

in the m.p.d. of the effect on NBA of ΔF_{new} the PP of the positive values [$PP(b_{\Delta F_{new}} > 0)$] is lower than 0.05. A more accurate inference of the inbreeding rate effect would require an appreciable variation of the individual inbreeding rates, that was only noticeable in the quoted interval from 22 to 24 EqG of the closed line history (Fig. 1).

Conclusion

These results, based on a singular dataset provide other departure of classical model suggesting that more accurate estimates of inbreeding depression may be obtained in some cases using alternative metrics such as new inbreeding. When deep pedigree exists, this measure may replace the classical inbreeding coefficient to improve the genetic management of small populations of farm animals. The usefulness of inbreeding rates as predictors of inbreeding depression is conditional on their variation and then on the population history.

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