Heritability of a canalized trait : teat number in *Iberian* pigs

M.A. TORO, María Teresa DOBAO, J. RODRIGÁÑEZ and L. SILIO

Departamento de Genética Cuantitativa y Mejora Animal
Instituto Nacional de Investigaciones Agrarias,
Carretera de La Coruña, Km. 7. 28040 Madrid, Espagne

Summary

Teat number is a discontinuous and often canalized trait in populations of domestic swine. This is the case in the *Iberian* pig where 90 p. 100 of individuals show 10 teats.

The estimation of genetic parameters for this discrete and strongly leptokurtic trait presents difficulties similar to those encountered in dichotomous ones, and several specific methods of estimation have been suggested, generally assuming the existence of an underlying normally distributed random variable.

Heritability estimates of teat number, based on 30 271 animals of three strains of *Iberian* pig, have been obtained both using conventional correlation and regression methods and through 3 specific techniques proposed by ROBERTSON, GIANOLA and TALLIS. These methods allow one to estimate what proportion of the heritability of the assumed underlying variable (h^2) can be accounted for by the heritability estimated in the observed scale (h_o^2). The estimated proportion ranged between 0.30 and 0.75 depending on the degree of canalization of the trait in the 3 different populations considered. The use of these specific methods, despite their interest, may present serious difficulties in practical breeding conditions.

Key words : Heritability, discrete traits, teat number, canalization, Iberian pig.

Résumé

Héritabilité d'un caractère canalisé : le nombre de tétines chez le porc Ibérique

Le nombre de tétines est un caractère discret qui est souvent canalisé dans les populations de porcs domestiques. Tel est le cas chez le porc *Ibérique* où près de 90 p. 100 des individus possèdent 10 tétines.

L'estimation de paramètres génétiques pour ce caractère discret et à une forte leptokurtosis pose des problèmes similaires à ceux rencontrés dans l'étude des caractères dichotomiques, pour lesquels ont été proposées plusieurs méthodes d'estimation qui, généralement, supposent l'existence d'une variable aléatoire sous-jacente ayant une distribution normale.

Des estimations de l'héritabilité du nombre de tétines ont été obtenues sur un total de 30 271 animaux appartenant à 3 souches de porc *Ibérique* par des méthodes conventionnelles de corrélation et régression ainsi que par 3 techniques spécifiques proposées par ROBERTSON,

GIANOLA et TALLIS. Ces méthodes permettent d'estimer le rapport de l'héritabilité estimée sur l'échelle observée (h_o^2) à l'héritabilité de la variable sous-jacente (h^2).

L'estimation de ce rapport varie entre 0,30 et 0,75 selon le degré de canalisation du caractère dans les 3 populations considérées. L'utilisation de ces méthodes spécifiques, malgré leur intérêt, peut poser de sérieuses difficultés dans les conditions pratiques d'élevage.

Mots clés : Héritabilité, caractères discrets, nombre de tétines, canalisation, porc Ibérique.

I. Introduction

Teat number in pigs is a meristic trait that sometimes presents a distribution with positive kurtosis, i.e. an excess of values close to the mean. This poses methodological problems in the estimation of genetic parameters similar to those of dichotomous traits.

The main objective of the present work is to obtain heritability estimates of teat number in 3 populations of *Iberian* pig by means of conventional methods of correlation and regression between relatives and also by specific methods of estimation for discrete traits (DEMPSTER & LERNER, 1950 ; TALLIS, 1962 ; GIANOLA, 1979 ; GIANOLA & NORTON, 1981).

Conventional methods estimate the heritability of the trait in the measured scale. Other methods assume the existence of an underlying normally distributed random variable which results in a discontinuous distribution of observed phenotypes due to several threshold values. With these methods heritability estimates in the underlying scale can be obtained.

II. Material and methods

The data come from the experimental herd of *Iberian* pig of « El Dehesón del Encinar » (Oropesa, Toledo) whose origin, characteristics and management conditions have been previously described (ODRIOZOLA, 1976 ; DOBAO *et al.,* 1982 and 1983).

In relation to the present work it must be pointed out that teat number, examined at 21 days of age, is one of the traits routinely recorded from piglets born in the herd. In general, the individuals with a teat number less than 10 have been excluded from breeding. The mating system in the 3 closed strains of the herd has not been designed to optimize the estimation of genetic parameters. As a consequence, the data reflect overlapping of generations, mating between individuals with minimum coancestry coefficient, unequal family sizes and mating structure not totally hierarchical since females have usually been mated with different males during their reproductive life.

Data from 30 271 individuals were classified into 6 files (D1, D2, E1, E2, F1 and F2) according to strain *Guadyerbas* (D), *Torbiscal* (E) and *Gamito* (F) and period

of birth : (1) animals born from 1963 to 1973 and (2) animals born from 1974 to 1979. These 2 periods correspond to changes in the management conditions of the herd (DOBAO *et al.,* 1983) and the approximate number of generations per period, about 5 generations in E2 and 4 in the others, is not excessive in order to obtain estimates of heritability from each one of the files.

Estimates of heritability in the multinomial observable scale were obtained through the following conventional methods :

1) Full-sibs (Htd) and Half-sibs (Hts) intraclass correlation.

2) Regression of offspring on parents : Sire (Hbs), dam (Hbd), mid-parent (Hbm) and sire plus mean of the dams mated with it (Hba).

In addition, among the published specific methods of heritability estimation for discrete traits, those proposed by the following authors were used :

3) ROBERTSON, who derived in an Appendix to a DEMPSTER & LERNER (1950) paper, a simple relationship by which heritabilities of a dichotomous or binary trait can be transformed from the observable to the underlying scale. More recently, GIA-NOLA (1979) has generalized the method for those discrete traits with more than 2 classes of phenotypes. This generalized formula is the one used in the present work.

4) GIANOLA & NORTON (1981), who have optimized the above method using a scale adjustment.

5) TALLIS (1962), who has applied maximum likelihood methods to the estimation of correlation between relatives from p × q contingency tables, where one of the dimensions corresponds to all the possible phenotypic classes of one parent (sire or dam) and the other to the phenotypic classes of the progeny. Contrasting with the other methods, TALLIS' method permits testing of the assumption of a normally distributed underlying variable, this being its main advantage. In the present work, its use has posed the following difficulties : a) the assumption that the data included in each cell of the contingency table come from independent observations is not fulfilled ; b) in the presence of selection and different family sizes, sampling of parents, mainly males, cannot be considered random ; c) the available computing program constrains the user to group some of the observed classes to operate on 3 × 3 contingency tables. The 3 classes considered in each table consist of the following phenotypes : $\leqslant$ 10, 11 or $\geqslant$ 12 teats, except in the file D2 where the grouped classes are : $\leqslant$ 9, 10 or $\geqslant$ 11 teats.

Recently, non-linear methods regarding the analysis of discrete traits and adopting a Bayes-like approach have been developed by several authors (GIANOLA & FOULLEY, 1983 ; FOULLEY *et al.,* 1983 ; HARVILLE & MEE, 1984). Nevertheless, as some of these authors admit, in animal breeding practice, solving the proposed equations poses a formidable numerical problem (FOULLEY *et al.,* 1983) and, for this reason, these new methods have not been tried on data.

A rough estimate of the realized heritability was obtained using a formula proposed by TURNER & YOUNG (1969) for overlapping generations, that assigns a generation number to each individual using pedigrees and therefore permits one to consider it as belonging to discrete generations. The examination of data showed that the number of teats has been subjected to a weak selection pressure in the herd. Cumu-

lative selection differentials in *Guadyerbas, Torbiscal* and *Gamito* were 0.13, 0.24 and 0.49 teats during the first period and 0.0005, — 0.25 and 0.31 during the second one. The realized heritability was estimated by regression of generation means on cumulative selection differentials (FALCONER, 1960).

III. Results and discussion

A. *Distribution of teat numbers*

Differences in teat number between males and females have not been observed. Therefore, sexes are pooled in table 1 showing teat number distribution according to the strains and periods considered, as well as the estimated values of the means, standard deviations, kurtosis and skewness coefficients. Though there are some differences between groups, all of them share the following characteristics :

1) A modal value of 10 teats, similar to that of the *Duroc-Jersey* breed related to the *Iberian* pig, and lower than those of other European and American breeds, like *Poland China* with 12 teats or *Large White, Landrace* and *Minnesota* n° 1 with 14 teats (HANSET & CAMERLYNCK, 1974 ; CLAYTON *et al.*, 1981), and, of course, much lower than the 16-18 teats of some Chinese breeds (ZHANG *et al.*, 1983 ; LEGAULT & CARITEZ, 1983).

2) A large majority of individuals (57-93 p. 100) shows the modal 10 teats phenotype, resulting in the positive values of the g_2 kurtosis coefficient, highly significant in all cases. CLAYTON *et al.* (1981) have observed the same fact, although less marked, in *Large White* and *British Landrace* pigs : 55 p. 100 of animals show the modal number of 14 teats. These authors mention the surprising lack of previous comments on this peculiarity of the trait.

3) The values of the g_1 skewness coefficient are also positive and highly significant showing an excess of phenotypes lower than the mean in all populations ; a similar departure from normality has been observed in *Duroc-Jersey* breed (HANSET & CAMERLYNCK, 1974).

Teat number in pigs, according to the features of its frequency distribution, may be considered, from a genetic approach, as a trait arising from a process of canalized development, i.e., fitted to produce a definite phenotype with independence of a certain degree of genetic or environmental variation (WADDINGTON, 1957). The idea of genetic canalization, like that of dominance, refers to the existence of constraints in the phenotypic expression of different genetic combinations.

The work of RENDEL (1967), among others, on the scutellar bristles in *D. melanogaster,* shows that a system of canalization can be modified through selection or because of the effect of mutants with pleiotropic influence on several processes of development. WADDINGTON (1975) suggests that the effectivity of some colour mutants in the decanalization of developmental processes in domestic animals explains why these genes had been incorporated so frequently in the formation of great breeds of livestock during the XIXth century.

TABLE 1

Teat number distribution in 3 strains of Iberian pig : means, standard deviations and skewness (g_1) and kurtosis (g_2) statistics.

Strain	File		Teat number 8	9	10	11	12	13	14	Total	$\bar{x}$	$\hat{\sigma}$	g_1	g_2
Guadyerbas (D)	D_1	N	5	51	2181	114	19	1	0	2371	10.04	0.32	1.91	20.26
		%	0.21	2.15	91.99	4.81	0.80	0.04	0					
	D_2	N	1	24	2851	149	22	0	0	3047	10.06	0.29	3.40	22.57
		%	0.03	0.79	93.57	4.89	0.72	0	0					
Torbiscal (E)	E_1	N	7	94	6938	929	219	24	7	8218	10.17	0.50	2.56	12.64
		%	0.09	1.14	84.42	11.30	2.66	0.29	0.09					
	E_2	N	20	50	8884	2033	601	55	5	11648	10.29	0.60	1.82	6.91
		%	0.17	0.43	76.27	17.45	5.16	0.47	0.04					
Gamito (F)	F_1	N	1	7	2009	491	120	3	1	2632	10.28	0.56	1.83	6.27
		%	0.04	0.27	76.33	18.65	4.56	0.11	0.04					
	F_2	N	3	7	1605	833	339	18	0	2805	10.55	0.73	0.92	3.05
		%	0.11	0.25	57.22	29.70	12.09	0.64	0					

All the g_1 and g_2 values are statistically significant (P < 0.001) from the zero expected values for a normal distribution (SOKAL & ROHLF, 1981).

From this point of view the observed differences between strains and between periods in means and g_2 values can be interpreted satisfactorily. Strains *Guadyerbas* and *Gamito* are particularly interesting. Coming from the same population of black coated pigs, these strains only differed originally in the pair of alleles responsible for coat colour : the wild E allele, black, dominant, fixed in *Guadyerbas* and the e allele, red, recessive, fixed in *Gamito*. This pair of alleles has in the *Iberian* pig, according to ODRIOZOLA (1976), pleiotropic effects on other traits : body length, age of maturity and teat number. The higher frequency of deviant phenotypes in the strain *Gamito* has favoured a greater intensity of selection for teat number, increasing the mean value and reducing the degree of canalization of the trait. Analogous differences between periods, ascribable to selection, are also observed in *Torbiscal* but not in *Guadyerbas*, where the extreme canalization has not made possible in practice any appreciable selection for this character.

B. *Estimates obtained by conventional methods*

Heritability values and their standard errors estimated for the different strains and periods by 6 methods of regression and correlation between relatives are shown in table 2. The irregular structure of the mating system in the herd, mentioned above, requires that these estimates be interpreted cautiously, particularly those obtained by regression on one parent (Hbs and Hbd), based on less information.

Estimates obtained from the maternal component of variance (Htd) are equal to or greater than those obtained from the paternal one (Hts). Similar results have been consistently recorded by several authors who suggest as an explanation of them a maternal effect on teat number (HANSET & CAMERLYNCK, 1974 ; PUMFREY *et al.*, 1980 ; CLAYTON *et al.*, 1981). These authors discard the existence of non-additive genetic variation, as an alternative explanation of the observed differences between estimates, arguing that the literature does not provide clear evidence of heterosis in teat number in pigs. This reasoning is debatable, because the quoted results coming from *Landrace* X *Large White* and *Landrace* X *Poland China* crosses are not consistent, the first showing additivity and the second 4.5 p. 100 of heterosis. These breeds are very distinct both in origin and history ; they have different modal values and, presumably, diverse degrees of canalization of the character. According to FALCONER (1960), populations that are widely differentiated through adaptations to local conditions may fail to show heterosis and the failure of wide crosses to show the heterosis that might have been expected can be attributed to epistatic interaction. From a molecular approach to dominance, KACSER & BURNS (1981) have also emphasized that crosses between populations that have diverged from each other by isolation, followed by selection or drift, may show changes in dominance relations. In our opinion, this does not allow one to exclude the possible existence of non-additive genetic variation in teat number in pigs, particularly within those populations or breeds more strongly canalized such as the *Iberian* pig population.

Estimates of realized heritabilities obtained from all data of *Torbiscal* and *Gamito* strains were 0.35 ± 0.21 and 0.46 ± 0.10 respectively, these values being in agreement with those of table 2. The extremely low range of variation of cumulative selection differentials in *Guadyerbas* results in a highly inaccurate estimate (— 0.03 ± 0.27) for this strain.

TABLE 2

Heritability estimates of teat number in 3 strains of Iberian pig obtained by conventional methods.

Strain	File	H_{td}	H_{ts}	H_{bm}	H_{ba}	H_{bs}	H_{bd}
Guadyerbas	D_1	0.14 ± 0.03	0.12 ± 0.04	0.10 ± 0.04	0.05 ± 0.09	0.01 ± 0.10	0.23 ± 0.06
	D_2	0.17 ± 0.03	0.09 ± 0.03	0.11 ± 0.01	0.09 ± 0.08	0.10 ± 0.06	0.07 ± 0.06
Torbiscal	E_1	0.30 ± 0.03	0.30 ± 0.04	0.20 ± 0.02	0.19 ± 0.04	0.22 ± 0.05	0.19 ± 0.04
	E_2	0.36 ± 0.02	0.18 ± 0.03	0.32 ± 0.02	0.25 ± 0.06	0.13 ± 0.07	0.29 ± 0.04
Gamito	F_1	0.34 ± 0.04	0.26 ± 0.06	0.28 ± 0.03	0.30 ± 0.06	0.25 ± 0.09	0.20 ± 0.07
	F_2	0.48 ± 0.05	0.39 ± 0.09	0.35 ± 0.04	0.32 ± 0.09	0.34 ± 0.10	0.51 ± 0.09

Methods : H_{td} = full-sib correlation ; H_{ts} = half-sib correlation ; H_{bm} = offspring on mid-parent regression ; H_{ba} = offspring on sire plus dam average ; H_{bs} = offspring on sire ; H_{bd} = offspring on dam.

C. *Estimates obtained by specific methods*

The joint examination of tables 1 and 2 suggests that heritability values estimated by conventional methods are associated with the degree of canalization depicted by the distribution of the character in each strain and period. Generally, a greater canalization of the trait corresponds to a smaller estimated value of its heritability.

The objective of using techniques such as those of ROBERTSON & GIANOLA-NORTON is to consider the effects due to discontinuity and deviations from normality in the estimation of heritability from discrete data. In both methods, an underlying variable with normal distribution is postulated and both allows one to calculate what proportion of the heritability of this variable (h^2) is estimated in the observed scale of phenotypes (h_o^2).

In the first 2 columns of table 3 results obtained using these methods for the 6 files of data are presented. They confirm that the value of their use is greater as the deviations from normality of the observed discrete trait become larger, and therefore when their degree of canalization is higher. The values of estimates Hts and Hbm corrected by both methods are also shown in table 3 and evidence a considerable genetic variability in all the strains.

The GIANOLA-NORTON scoring, as the authors indicate, has little advantage over the ROBERTSON method. Its utility is undoubtedly greater for some discrete traits whose scale of possible values is determined through the choice of a subjective classification, as could be conformation scores or degree of calving difficulty.

In table 4 the results of the application of TALLIS' method to the sires/progeny and dams/progeny contingency tables, constructed for different periods and strains, are shown. The χ^2 values reflecting the goodness of fit to the model are in general compatible with the assumption of a normal underlying distribution, particularly in dams/progeny contingency tables. Only in one case, the analysis of the sires/progeny table in file E1, is a highly significant value registered.

The estimates obtained confirm that the heritability of the trait is high in the underlying scale, although the values differ sometimes from those obtained by the methods of ROBERTSON & GIANOLA-NORTON, particularly in the strain *Guadyerbas*. This implies that increases in teat number can be obtained by means of artificial selection, especially when a less degree of canalization of the character permits higher selection intensities. The use of the heritability of the underlying scale for predicting the response to selection requires the subsequent transformation of the expected response to the observed phenotypic scale. DEMPSTER & LERNER (1950) showed, for an all-or-none trait, that genetic gains from mass selection will be more accurately predicted, if the assumptions of the threshold model are fulfilled, using the heritability of the underlying scale, particularly for high heritabilities and low incidence levels.

TABLE 3

Heritability estimates of teat number in 3 strains of Iberian pigs corrected by ROBERTSON *&* GIANOLA-NORTON *methods.*

Strain	File	h^2/h_o^2		H_{ts} corrected estimates		H_{bm} corrected estimates	
		ROBERTSON	GIANOLA-NORTON	ROBERTSON	GIANOLA-NORTON	ROBERTSON	GIANOLA-NORTON
Guadyerbas	D_1	0.357	0.370	0.32 ± 0.12	0.31 ± 0.11	0.28 ± 0.10	0.27 ± 0.10
	D_2	0.292	0.302	0.32 ± 0.12	0.31 ± 0.11	0.36 ± 0.11	0.35 ± 0.11
Torbiscal	E_1	0.479	0.505	0.63 ± 0.09	0.60 ± 0.09	0.42 ± 0.05	0.39 ± 0.04
	E_2	0.582	0.599	0.30 ± 0.05	0.30 ± 0.05	0.54 ± 0.04	0.53 ± 0.04
Gamito	F_1	0.571	0.583	0.45 ± 0.11	0.44 ± 0.11	0.49 ± 0.06	0.48 ± 0.06
	F_2	0.742	0.750	0.52 ± 0.12	0.52 ± 0.12	0.48 ± 0.05	0.47 ± 0.05

TABLE 4

Heritability estimates of teat number in 3 strains of Iberian *pigs obtained by the* TALLIS' *method.*

Strain	File	Sires/offspring		Dams/offspring	
		h^2	χ^2	h^2	χ^2
Guadyerbas	D_1	0.18 ± 0.17	14.82	0.62 ± 0.13	4.93
	D_2	0.48 ± 0.07	2.98	0.05 ± 0.08	2.54
Torbiscal	E_1	0.39 ± 0.05	39.82	0.34 ± 0.05	2.58
	E_2	0.24 ± 0.04	14.56	0.48 ± 0.03	15.60
Gamito	F_1	0.46 ± 0.06	15.82	0.52 ± 0.06	13.93
	F_2	0.36 ± 0.05	3.63	0.69 ± 0.05	2.97

$$\chi^2_{0.05(8)} = 15.51 \; ; \; \chi^2_{0.01(8)} = 20.09$$

In view of these results, our opinion of the applicability of these specific methods to estimate the heritability of teat number in pigs may be summarized as follows :

a) in populations where the trait is weakly canalized, the use of conventional methods is acceptable, the value of other approaches, such as that of ROBERTSON, being greater as the degree of canalization increases ;

b) in practical breeding conditions, the use of TALLIS' method is not clearly justified because of the difficulty in strictly fulfilling the assumptions and the complex computations involved.

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