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Original article

Genetic parameters and genetic trends in the Chinese x European *Tiameslan* composite pig line. I. Genetic parameters

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Abstract – Genetic parameters of body weight at 4 (W4w), 8 (W8w) and 22 (W22w) weeks of age, days from 20 to 100 kg (DT), average backfat thickness at 100 kg (ABT), teat number (TEAT), number of good teats (GTEAT), total number of piglets born (TNB), born alive (NBA) and weaned (NW) per litter, and birth to weaning survival rate (SURV) were estimated in the Chinese × European *Tiameslan* composite line using restricted maximum likelihood methodology applied to a multiple trait animal model. Performance data from a total of 4 881 males and 4 799 females from 1 341 litters were analysed. Different models were fitted to the data in order to estimate the importance of maternal effects on production traits, as well as genetic correlations between male and female performance. The results showed the existence of significant maternal effects on W4w, W8w and ABT and of variance heterogeneity between sexes for W22w, DT, ABT and GTEAT. Genetic correlations between sexes were 0.79, 0.71 and 0.82, respectively, for W22w, DT and ABT and above 0.90 for the other traits. Heritability estimates were larger than (ABT and TEAT) or similar to (other traits) average literature values. Some genetic antagonism was evidenced between production traits, particularly W4w, W8w and ABT, and reproductive traits.

pigs / genetic parameters / performance trait / reproductive trait / Chinese breed

Résumé – Paramètres génétiques et évolutions génétiques dans la lignée composite sino-européenne *Tiameslan*. I. Paramètres génétiques. Les paramètres

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génétiques des poids corporels à 4 (P4s), 8 (P8s) et 22 (P22s) semaines d'âge, de la durée d'engraissement de 20 à 100 kg (DE), de l'épaisseur de lard dorsal à 100 kg (ELD), du nombre total de tétines (TET), du nombre de bonnes tétines (BTET), du nombre de porcelets nés totaux (NT), nés vivants (NV) et sevrés (SEV) par portée, du taux de survie naissance-sevrage (TS) ont été estimés dans la lignée composite sino-européenne Tiameslan par la méthode du maximum de vraisemblance restreinte appliquée à un modèle animal multicaractère. Les performances de 4 881 mâles et 4 799 femelles issus de 1 341 portées ont été analysées. Différents modèles ont été ajustés aux données afin d'estimer l'importance des effets maternels sur les caractères de production, ainsi que les corrélations génétiques entre les performances mâles et femelles. Les résultats ont montré l'existence d'effets maternels significatifs sur P4s, P8s et ELD, ainsi que des hétérogénéités de variances entre sexes pour P22s, DE, ELD et BTET. Les corrélations génétiques entre sexes s'élevaient à 0,79; 0,71 et 0,82, respectivement, pour P22s, DE et ABT et étaient supérieures à 0,90 pour les autres caractères. Les valeurs d'héritabilité étaient supérieures (TET et ELD) ou comparables (autres caractères) aux moyennes de la littérature. Un certain antagonisme génétique a été observé entre les caractères de production, en particulier P4s, P8s et ELD, et les caractères de reproduction.

porcin / paramètres génétiques / caractère de production / caractère de reproduction / race chinoise

1. INTRODUCTION

Sow numerical productivity is a major component of the economic efficiency of pig production [10, 40]. Its major component traits, litter size at birth and piglet survival during the nursing period, are unfortunately difficult to improve through selection because of their low heritabilities [12, 37]. Another possible way to increase sow productivity is to take advantage of the outstanding reproductive ability of some native Chinese breeds such as Meishan, Jiaxing, Erhualian, Fengjing or Min breeds. Studies performed in France [2, 4, 20], Great Britain [14, 19] and the USA [42] confirmed the high prolificacy, the good mothering ability and the strong hardiness of Meishan, Jiaxing, Fengjing and Min purebred and crossbred sows. Their poor growth and carcass performance, however, makes it very difficult to use them in crossbreeding systems, particularly in markets where heavy slaughter weights and/or high carcass lean contents are required [5]. This problem may be overcome by creating a Chinese × European composite line and selecting it for growth and carcass traits [1, 5]. In collaboration with INRA, the Pen Ar Lan breeding company has undertaken since 1983 the constitution and selection of a Chinese × European composite population, the *Tiameslan* line. The value of such lines depends on the efficiency of selection for production traits [5] and, therefore, on the available genetic variation. The purpose of this study was to estimate genetic variability of both production and reproduction traits in the *Tiameslan* line.

2. MATERIAL AND METHODS

Creation, management and selection of the *Tiameslan* line

Two similar sublines were created in 1983 and 1985 in the nucleus herd of the Pen ar Lan breeding company, by mating *Meishan* × *Jiaxing* F1 boars to multiparous sows from the *Laconie* line. The Laconie line was constructed in 1973 and has been maintained as a closed line and selected for growth and carcass traits since that time. A total of 21 Meishan × Jiaxing boars and 55 Laconie sows selected for their high reproductive performance were used as founder animals. No immigration occurred later. The two sublines were managed similarly, but independently, until 1988. During this period, sows were allowed to produce only one litter in order to minimise the generation interval, so that the generations did not overlap. The two sublines were mixed in 1988 by mating breeding pigs from the 4th and the 2nd generations of sublines 1 and 2, respectively. Since then, sows have been allowed to farrow several litters, so that generations have become overlapping. The size of the line changed from around 50 sows and 12 boars in early generations to more than 200 sows and 15 boars in recent years.

The Maxent Nucleus herd includes a total of about 500 sows belonging to three different lines (*Laconie*, *Penshire*, *Tiameslan*), distributed in 21 farrowing batches. Breeding animals were selected at the end of the performance test at 22 weeks of age. Gilts were bred after a synchronisation treatment with a progestagen that began at 27 weeks of age. Matings were mainly performed using artificial insemination (AI). Females were inseminated twice at a 12-h interval before 1992 and three times at a 12-h interval between successive AI since then. Parturition was induced by injecting prostaglandin analogues at day 112 or 113 of gestation. Litters were born in individual crates. Piglets were identified at birth and the numbers of piglets born alive, stillborn, crossfostered and weaned were recorded. Crossfostering was practised in order to adapt litter size to the sow nursing abilities. Piglets were weaned at 4 weeks of age, weighed and transferred to a postweaning unit. They were weighed again at the age of 8 weeks and transferred to the fattening unit where, with the exception of animals born in small litters and of a limited number of runt piglets, they were performance tested in crates of 15–16 animals belonging to the same line and sex. Each farrowing batch corresponded to a performance test batch. During the test, animals were given ad libitum access to two successive diets containing 17.5% crude protein and 3 230 kcal DE/kg until 4 months of age and then 17% crude protein and 3 250 kcal DE/kg. Animals were weighed and measured for backfat thickness (BT) at the end of the test period at 22 weeks of age. The total number and the number of good teats (evaluated by a visual examination) were also recorded. BT was measured on each side of the spine at the levels of the shoulder, the last rib and the hip joint.

Breeding animals were selected on an index comprising the average of the six BT measurements (ABT), adjusted to a 100 kg basis, and days on test (DT). DT was computed as the difference between the age at the end (A100) and at the beginning (A20) of the test period, adjusted to 100 and 20 kg, respectively, using the following equations:

$$A100 = 118.5378 - 1.0953W_{22W} + 0.9081A_{22W}$$

$$A20 = 39.5137 - 1.6436W_{8W} + 0.9517A_{8W}$$

where W_{8W}, W_{22W} were, respectively, weights at 8 and 22 weeks of age and A_{8W}, A_{22W} the exact ages (in days) of pigs when the two weight measurements occurred. Some selection was made on teat number (truncation selection of young candidates), litter size (animals from small litters where not performance tested) and, since 1990, on coat colour (coloured breeding animals were culled) and on the genotype at the RN locus [21]. (eradication of the RN-allele).

3. STATISTICAL ANALYSES

Because genetic (co)variances and parent-offspring covariances can vary in early generations of crossbreeding [24, 25], data and pedigrees from F1 and F2 pigs were discarded from the analysis and the F3 generation was considered as the base population. The performances of a total of 9 680 pigs (4 881 males and 4 799 females) from 1 341 litters were considered. The structure of the data set analysed is shown in Table I. A total of 11 traits were analysed in this study: ABT and DT as defined above, weight at 4 weeks (W4w), 8 weeks (W8w) and 22 weeks (W22w) of age, total teat number (TEAT), number of good teats (GTEAT), total number of piglets born (TNB), born alive (NBA) and weaned (NW) per litter and survival rate from birth to weaning (SURV), defined as the ratio 100 × NW/TNB. Means and standard deviations for the 11 traits studied are shown in Table II.

Table I. Structure of the data set analysed.

Number of pigs tested	
Males	4 881
Females	4 799
Total number of animals in the pedigree	9 768
Number of sires	148
Number of dams	578
Number of litters	1 341
Number of test batches	208
Number of farrowing batches	37

(Co)variance components were estimated using restricted maximum likelihood (REML) methodology [34] applied to both univariate and multivariate animal models. Four different models were fitted to the 5 performance traits, TEAT and GTEAT. The first two models included both direct and maternal genetic effects and considered the same measurement in males and females either as two different traits (model 1) or the same trait (model 2). Models 3 and 4 were similar to models 1 and 2, respectively, but without maternal effects. Models 1 and 3 included the test batch as a fixed effect, the direct (and maternal for model 1) additive genetic effect(s) of each animal, the common environment of birth litter as random effects and age, weight, number of litter mates or inbreeding coefficient as covariates. Hence, inbreeding was considered when building the relationship matrix to account for its effects on genetic (co)variances and as a covariate to account for inbreeding depression. Models 2 and 4 were similar to models 1 and 3, respectively, with the exception of

Table II. Overall means and standard deviations for the 11 traits studied.

Trait[(1)]	Mean			Standard deviation		
	Male	Female	Overall	Male	Female	Overall
ABT (mm)	10.3	11.8	11.1	2.0	2.8	2.6
DT (d)	113.9	114.0	114.0	9.6	8.7	9.1
W4w (kg)	7.33	7.24	7.29	1.49	1.47	1.48
W8w (kg)	20.2	20.2	20.2	2.9	3.0	3.0
W22w (kg)	87.4	86.2	86.8	9.4	8.6	9.0
TEAT	15.4	15.4	15.4	1.2	1.2	1.2
GTEAT	15.2	14.8	15.0	1.7	2.2	2.0
TNB	–	12.9	–	-	3.4	–
NBA	–	12.0	–	–	3.2	–
NW	–	10.0	–	–	3.0	–
SURV (%)	–	79.0	–	–	17.3	–

(1) ABT = Average backfat thickness; DT = days on test (20 to 100 kg); W4w, W8w, W22w = weights at 4, 8 and 22 weeks of age, respectively; TEAT = total number of teats; GTEAT = number of good teats; TNB, NBA, NW = total number of piglets born, born alive and weaned, respectively; SURV = piglet survival rate from birth to weaning.

the batch effect, which was replaced by a sex × batch combination. The four models can be written in matrix notation:

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Za} + \mathbf{Wp} + \mathbf{e}$$

$$\text{with } E\begin{bmatrix}\mathbf{a}\\ \mathbf{p}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{0}\\ \mathbf{0}\\ \mathbf{0}\end{bmatrix} \text{ and Var}\begin{bmatrix}\mathbf{a}\\ \mathbf{p}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{G_a} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{G_p} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{R}\end{bmatrix}$$

where $\mathbf{y}$, β, $\mathbf{a}$, $\mathbf{p}$ and $\mathbf{e}$ are vectors of observations, fixed effects, additive genetic effects, birth litter effects and residuals, respectively. $\mathbf{X}$, $\mathbf{Z}$ and $\mathbf{W}$ are incidence matrices relating observations to the above mentioned vectors. $\mathbf{G_a}$, $\mathbf{G_p}$ and $\mathbf{R}$ are variance-covariance matrices of additive genetic, birth litter and residual effects, respectively. The structure of both vectors and matrices depends on the model considered. The structures of vectors and incidence matrices are straightforward and will not be detailed. The structures of $\mathbf{R}$ and $\mathbf{G_p}$ matrices are as follows:

$$\mathbf{R} = \begin{bmatrix}\mathbf{I_m}\sigma^2_{\mathbf{e_m}} & \mathbf{0}\\ \mathbf{0} & \mathbf{I_f}\sigma^2_{\mathbf{e_f}}\end{bmatrix} \quad \text{and} \quad \mathbf{G_p} = \begin{bmatrix}\mathbf{I_m}\sigma^2_{\mathbf{p_m}} & \mathbf{B}\sigma_{\mathbf{p_{mf}}}\\ \mathbf{B}\sigma_{\mathbf{p_{mf}}} & \mathbf{I_f}\sigma^2_{\mathbf{p_f}}\end{bmatrix}$$

in models 1 and 3 and $\mathbf{R} = \mathbf{I}\sigma^2_{\mathbf{e}}$ and $\mathbf{G_p} = \mathbf{I}\sigma^2_{\mathbf{p}}$ in models 2 and 4,

where $\mathbf{I}$, $\mathbf{I_m}$ and $\mathbf{I_f}$ are identity matrices, $\mathbf{B}$ is a rectangular matrix linking male and female progeny of a litter, $\sigma^2_{\mathbf{p_m}}$, $\sigma^2_{\mathbf{e_m}}$, $\sigma^2_{\mathbf{p_f}}$, $\sigma^2_{\mathbf{e_f}}$, $\sigma^2_{\mathbf{p}}$ and $\sigma^2_{\mathbf{e}}$ are the common birth litter and the residual variances for males, females and both sexes respectively ; $\sigma_{\mathbf{p_{mf}}}$ is the common birth litter covariance between male and female traits. The structure of the $\mathbf{G_a}$ matrix is as follows:

$$\mathbf{G_a} = \begin{bmatrix} \mathbf{A}\sigma^{\mathbf{2}}_{\mathbf{a^d_m}} & \mathbf{A}\sigma_{\mathbf{a^d_{mf}}} & \mathbf{A}\sigma_{\mathbf{a^{dm}_{mm}}} & \mathbf{A}\sigma_{\mathbf{a^{dm}_{mf}}} \\ \mathbf{A}\sigma_{\mathbf{a^d_{mf}}} & \mathbf{A}\sigma^{\mathbf{2}}_{\mathbf{a^d_f}} & \mathbf{A}\sigma_{\mathbf{a^{dm}_{mf}}} & \mathbf{A}\sigma_{\mathbf{a^{dm}_{ff}}} \\ \mathbf{A}\sigma_{\mathbf{a^{dm}_{mm}}} & \mathbf{A}\sigma_{\mathbf{a^{dm}_{mf}}} & \mathbf{A}\sigma^{\mathbf{2}}_{\mathbf{a^m_m}} & \mathbf{A}\sigma_{\mathbf{a^m_{mf}}} \\ \mathbf{A}\sigma_{\mathbf{a^{dm}_{mf}}} & \mathbf{A}\sigma_{\mathbf{a^{dm}_{ff}}} & \mathbf{A}\sigma_{\mathbf{a^m_{mf}}} & \mathbf{A}\sigma^{\mathbf{2}}_{\mathbf{a^m_f}} \end{bmatrix} \quad \text{in model 1,}$$

$$\mathbf{G_a} = \begin{bmatrix} \mathbf{A}\sigma^{\mathbf{2}}_{\mathbf{a^d}} & \mathbf{A}\sigma_{\mathbf{a^{dm}}} \\ \mathbf{A}\sigma_{\mathbf{a^{dm}}} & \mathbf{A}\sigma^{\mathbf{2}}_{\mathbf{a^m}} \end{bmatrix} \quad \text{in model 2,}$$

$$\mathbf{G_a} = \begin{bmatrix} \mathbf{A}\sigma^{\mathbf{2}}_{\mathbf{a^d_m}} & \mathbf{A}\sigma_{\mathbf{a^d_{mf}}} \\ \mathbf{A}\sigma_{\mathbf{a^d_{mf}}} & \mathbf{A}\sigma^{2}_{\mathbf{a^d_f}} \end{bmatrix} \quad \text{in model 3,}$$

$$\mathbf{G_a} = \mathbf{A}\sigma^{\mathbf{2}}_{\mathbf{a^d}} \quad \text{in model 4,}$$

where $\mathbf{A}$ is the relationship matrix, $\sigma^{\mathbf{2}}_{\mathbf{a^j_i}}$ is the additive genetic variance for direct ($j = d$) or maternal ($j = m$) effects for sex i ($i = m$ for males, $i = f$ for females and is removed when the same trait is considered for both sexes); $\sigma_{\mathbf{a^{dm}_{mm}}}$, $\sigma_{\mathbf{a^{dm}_{ff}}}$, $\sigma_{\mathbf{a^{dm}_{mf}}}$, $\sigma_{\mathbf{a^{dm}}}$ are covariances between direct and maternal additive genetic effects for males, females, between males and females and averaged over sexes, respectively; $\sigma_{\mathbf{a^d_{mf}}}$ and $\sigma_{\mathbf{a^m_{mf}}}$ are covariances between male and female traits for direct and maternal additive genetic effects, respectively. A group of unknown parents was considered for each subpopulation in early analyses. No difference appeared between subpopulations, so that a single base population was considered in final analyses.

The model used for TNB, NBA and NW included parity and farrowing batch as fixed effects, the additive genetic value, the permanent environment and the common effect of birth litter of the sow as random effects, as well as age within parity and sow and/or litter inbreeding coefficient as covariates. The common effect of sow birth litter allowed to account for litter environmental effects, but also for dominance relationships between full-sibs.

Multivariate analyses were performed using version 4.2 of the VCE software [32]. Since VCE does not allow the testing of the significance of maternal effects, these tests were performed using univariate analyses with the DFREML program developed by Meyer [28, 29]. A likelihood ratio test such that $-\ 2$ ($\ln \vartheta_1 - \ln \vartheta_2$) has a χ^2 distribution with $n_2 - n_1$ degrees of freedom, where n_i is the number of random effects in model i and ϑ_ι is the maximum value of the likelihood function for model i, was carried out in order to select the appropriate model for a trait.

4. RESULTS

Estimates of phenotypic variances, heritabilities of direct and maternal effects, genetic correlations between direct and maternal effects, and common birth litter effects for production traits and teat number are shown in Table III. Phenotypic variances were similar in both sexes for W4w, W8w and TEAT, but differed for the 4 other traits. Growth traits (i.e. W22w and DT) had larger variances in males, whereas ABT and GTEAT were more variable in females. Heritability estimates for maternal effects were significant for W4w, W8w and ABT, but not for the other traits. The heritability of direct effects was low and non-significant for W4w and progressively increased with increasing weights. Large heritability values were obtained for ABT and GTEAT. Ignoring maternal effects had a limited effect on the heritabilities of direct effects and common birth litter variances for W22w, DT and TEAT, but led to notable rises in the heritabilities of W4w and W8w and an important decrease of the heritability of ABT and GTEAT.

Four genetic correlations between direct and maternal effects were estimated for each trait: between male and female direct and maternal genetic effects, between male direct effects and female maternal effects and between female direct effects and male maternal effects. With the exception of TEAT, where maternal variance was very low and genetic correlations poorly estimated, these genetic correlations were all negative (Tab. IV), with low to medium values for postweaning growth traits (W8w, W22w, DT) and larger ones for W4w, ABT and above all GTEAT. Genetic correlations between performance traits in males and females for both direct and maternal genetic effects are shown in Table IV. Estimates were close to unity for W4w, W8w, TEAT and GTEAT. Estimates were lower, particularly for maternal effects, for W22w, DT, ABT and TEAT.

Estimated variance components for litter traits are shown in Table V. Estimates of heritability and permanent environmental variance were rather low and tended to decrease from birth to weaning, but were significantly positive for all traits. Conversely, common birth litter variances did not differ significantly from zero and were removed from subsequent analyses.

Estimates of genetic correlations between growth traits, backfat thickness and teat number are shown in Table VI. These estimates were obtained using the most pertinent model for each measurement, i.e. considering a single trait for both sexes for W4w, W8w, TEAT and GTEAT, and one trait per sex for W22w, DT and ABT. Maternal effects were considered for W4w, W8w and ABT but removed from the final model for W22w, DT, TEAT and GTEAT. Direct genetic correlations between weight measurements were moderately positive, whereas genetic correlations between direct and maternal effects were negative. DT was weakly to moderately correlated with W4w and W8w, but had strong genetic correlations with W22w in both sexes. Direct genetic relationships between ABT and growth traits were low for early growth traits (W4w and W8w) and tended to be favourable for W22w and DT, with slightly larger values in females than in males. Correlations involving maternal effects tended to be weakly negative. Genetic correlations between TEAT and the other traits were low. GTEAT was favourably correlated with W4w and

Table III. REML estimates of variance components(1) for performance traits and teat number using different individual animal models.

Trait(2)	Sex	Model	TS(3)	σ_p^2	$\mathbf{h_d^2}$	h_m^2	$\mathbf{r_{dm}}$	c^2
W4w	Male	1	8.3	1.85	0.01	0.11	– 0.35	0.28
		3	–		0.11	–	–	0.33
	Female	1	8.0	1.78	0.05	0.11	– 0.52	0.30
		3	–		0.10	–	–	0.35
	Both sexes	2	8.4	1.82	0.03	0.11	– 0.31	0.27
		4	–		0.09	–	–	0.33
W8w	Male	1	11.5	7.39	0.17	0.14	– 0.33	0.15
		3	–		0.26	–	–	0.19
	Female	1	6.7	8.06	0.21	0.08	– 0.11	0.19
		3	–		0.27	–	–	0.22
	Both sexes	2	8.2	7.75	0.17	0.11	– 0.22	0.15
		4	–		0.25	–	–	0.20
W22w	Male	1	4.6	87.7	0.32	0.06	– 0.12	0.13
		3	–		0.39	–	–	0.14
	Female	1	1.5	70.3	0.35	0.02	– 0.06	0.14
		3	–		0.35	–	–	0.15
	Both sexes	2	2.0	79.6	0.32	0.04	– 0.01	0.11
		4	–		0.35	–	–	0.12
DT	Male	1	2.9	83.1	0.48	0.04	– 0.30	0.12
		3	–		0.44	–	–	0.12
	Female	1	3.6	61.3	0.41	0.04	– 0.36	0.14
		3	–		0.39	–	–	0.14
	Both sexes	2	1.7	71.0	0.38	0.02	– 0.12	0.10
		4	–		0.34	–	–	0.11
ABT	Male	1	19.9	3.68	0.89	0.23	– 0.68	0.05
		3	–		0.71	–	–	0.07
	Female	1	9.2	6.08	0.90	0.11	– 0.47	0.04
		3	–		0.79	–	–	0.06
	Both sexes	2	8.5	4.82	0.73	0.07	– 0.64	0.03
		4	–		0.72	–	–	0.03
TEAT	Male	1	0.4	1.57	0.43	0.01	0.13	0.05
		3	–		0.47	–	–	0.05
	Female	1	0.7	1.60	0.53	0.01	– 0.57	0.02
		3	–		0.48	–	–	0.02
	Both sexes	2	0.5	1.59	0.48	0.01	– 0.22	0.03
		4	–		0.47	–	–	0.03
GTEAT	Male	1	2.4	3.19	0.59	0.02	– 0.54	0.03
		3	–		0.49	–	–	0.03
	Female	1	3.4	5.06	0.46	0.04	– 0.51	0.03
		3	–		0.39	–	–	0.03
	Both sexes	2	3.8	4.08	0.55	0.07	– 0.71	0.02
		4	–		0.40	–	–	0.02

(1) σ_p^2 = phenotypic variance; $\mathbf{h_d^2}$, h_m^2 = heritability estimates for direct and maternal effects, respectively; $\mathbf{r_{dm}}$ = genetic correlation between direct and maternal effects; c^2 = common birth litter effect; (2) see Table II for the definition of the traits; standard errors of heritability estimates in models without maternal effects ranged from 0.01 to 0.02. (3) Maximum likelihood ratio test statistic comparing model m with model $m - 2$.

Table IV. REML estimates of genetic correlations between male and female performance and between direct and maternal genetic effects⁽¹⁾.

Trait⁽²⁾	Direct	Maternal	Direct-maternal			
	$\mathbf{r^{d}_{mf}}$	$\mathbf{r^{m}_{mf}}$	$\mathbf{r^{dm}_{ff}}$	$\mathbf{r^{dm}_{mm}}$	$\mathbf{r^{dm}_{fm}}$	$\mathbf{r^{dm}_{mf}}$
W4w	0.95	0.96	– 0.52	– 0.35	– 0.34	– 0.47
W8w	0.92	0.99	– 0.11	– 0.33	– 0.16	– 0.17
W22w	0.79	0.62	– 0.06	– 0.12	0.24	– 0.25
DT	0.71	0.31	– 0.36	– 0.30	0.11	– 0.20
ABT	0.82	0.65	– 0.47	– 0.68	– 0.23	– 0.75
TEAT	0.96	– 0.24	– 0.57	0.13	0.28	– 0.46
GTEAT	0.90	0.93	– 0.51	– 0.54	– 0.44	– 0.43

(1) $\mathbf{r^{d}_{mf}}$, $\mathbf{r^{m}_{mf}}$ = genetic correlations between male and female performance for direct and maternal effects, respectively; $\mathbf{r^{dm}_{ff}}$, $\mathbf{r^{dm}_{mm}}$ = Genetic correlations between direct and maternal effects for female (ff), male (mm) performance; $\mathbf{r^{dm}_{fm}}$, $\mathbf{r^{dm}_{mf}}$ = Genetic correlations between female direct and male maternal effects and between male direct and female maternal effects, respectively; (2) see Table II for the definition of the traits.

Table V. REML estimates of genetic parameters for litter traits.

	Trait⁽¹⁾			
Parameter⁽²⁾	TNB	NBA	NW	SURV (%)
σ^2_p	10.6	9.7	8.7	297
h^2	0.19	0.14	0.08	0.19
c^2	0.02	0.01	0.01	0.01
p^2	0.07	0.05	0.05	0.03
TNB	–	0.98	0.60	– 0.66
NBA		–	0.64	– 0.67
NW			–	0.17
SURV				–

(1) TNB, NBA, NW = Total number of piglets born, born alive and weaned per litter, respectively; SURV = preweaning survival rate (SURV = 100 × NW/TNB); (2) σ^2_p = phenotypic variance; h^2 = heritability; c^2 = common birth litter effect; p^2 = permanent environmental effect. Standard errors of h^2, c^2 and p^2 ranged from 0.01 to 0.02, standard errors of genetic correlation estimates ranged from 0.02 to 0.04.

W8w for direct effects, but unfavourably for maternal effects and tended to have slightly antagonistic genetic correlations with DT and ABT.

Due to the limited number of reproductive performance, maternal effects were ignored when estimating the genetic correlations between production and reproduction traits. Estimates are shown in Table VII. Weight traits had

Table VI. REML estimates of genetic correlations between performance traits.

Trait$^{(1)}$		W4w		W8w		W22wf	W22wm	DTf	DTm	ABTf		ABTm		TEAT	GTEAT
	Effect$^{(2)}$	d	m	d	m	d	d	d	d	d	m	d	m	d	d
W4w	d	–	– 0.31	0.32	– 0.36	0.26	0.48	– 0.05	– 0.49	– 0.27	– 0.21	0.02	– 0.29	0.12	0.37
	m		–	– 0.21	0.85	0.03	0.05	– 0.12	0.00	0.17	0.01	0.14	– 0.13	– 0.08	– 0.39
W8w	d			–	– 0.22	0.48	0.49	– 0.04	– 0.29	0.08	– 0.33	0.12	– 0.18	0.07	0.11
	m				–	– 0.06	– 0.17	– 0.06	0.22	0.08	– 0.08	0.03	– 0.01	0.00	– 0.05
W22wf	d					–	0.79	– 0.90	– 0.81	– 0.38	0.20	– 0.23	– 0.16	– 0.02	– 0.15
W22wm	d						–	– 0.75	– 0.94	– 0.12	– 0.02	0.10	– 0.28	– 0.00	– 0.11
DTf	d							–	0.71	0.50	– 0.46	0.28	0.05	0.06	0.10
DTm	d								–	0.29	– 0.24	– 0.04	0.12	0.07	0.18
ABTf	d									–	– 0.47	0.82	– 0.23	0.02	0.17
	m										–	– 0.75	0.65	– 0.29	– 0.14
ABTm	d											–	– 0.68	0.15	0.19
	m												–	– 0.06	0.11
TEAT	d													–	0.92
GTEAT	d														–

(1) See Table II for the definition of the traits; (2) d = direct effects; m = maternal effects. Standard errors of genetic correlation estimates in models without maternal effects ranged from 0.02 to 0.05.

negative, i.e. unfavourable, genetic relationships with litter size at birth and at weaning. SURV was favourably correlated with W4w and W8w, but had slightly negative relationships with W22w. DT had low genetic correlations with litter size at birth, but also showed unfavourable relationships with NW and SURV. Similarly, some genetic antagonism was evidenced between ABT and litter traits, with increasing values from birth to weaning. Finally, TEAT and GTEAT were almost independent of litter size at birth, but had positive, i.e. favourable, genetic correlations with NW and SURV.

Table VII. REML estimates of genetic correlations between production and reproduction traits.

Traits(1)	TNB	NBA	NW	SURV
W4w	– 0.53	– 0.62	– 0.39	0.31
W8w	– 0.51	– 0.62	– 0.49	0.18
W22wf	– 0.11	– 0.23	– 0.41	– 0.19
W22wm	– 0.31	– 0.38	– 0.59	– 0.10
DTf	– 0.04	0.05	0.25	0.22
DTm	0.09	0.12	0.42	0.24
ABTf	0.11	0.19	0.31	0.16
ABTm	0.27	0.34	0.38	0.06
TEAT	– 0.01	0.03	0.36	0.34
GTEAT	– 0.15	– 0.06	0.33	0.45

(1) See Tables II and V for the definition of the traits. Standard errors of genetic correlations range from 0.06 to 0.12.

5. DISCUSSION

Methodology. First of all, it should be emphasised that estimating genetic parameters and genetic trends in a composite population such as the *Tiameslan* line is not straightforward, particularly under dominance inheritance, mainly because the assumptions concerning the structure of the base population (i.e. no selection, linkage equilibrium – e.g. see [39]) are not fulfilled. The theory for modelling (co)variances in crossbred populations was recently developed by Lo et al. [24, 25]. Under additive inheritance, a supplementary term has to be considered to account for the additional genetic variance segregating in the F2 over that in the F1 [24]. Under dominance inheritance, the general expression of the genotypic covariance between relatives involves 25 dispersion parameters. Even though the number of parameters can be reduced to 12 in the absence of inbreeding, their estimation remains impossible in most practical situations. In the current case, all traits except ABT and teat number were likely to be affected by dominance. Hence, discarding data from F1 and F2 pigs and considering the F3 generation as the base population was considered as the best compromise. Ignoring early generations also allowed to get rid of the linkage disequilibrium that could be generated by crossbreeding. Conversely, when selection occurs, properly taking into account this selection process requires considering all the information on which selection is based (e.g. [15]). This could not perfectly be done in the case of the *Tiameslan* line, since the selection practised in F1 and F2 generations could not be considered.

Univariate analyses using DFREML and multivariate analyses using VCE gave rather similar results, with a limited tendency towards lower estimates of both direct and maternal components of genetic variance in univariate analyses. This would result in a slight underestimation of the real likelihood ratio test values using a full multivariate model. However, test results clearly show that only rather large maternal effects could be detected (above about 8% of phenotypic variance). This is in agreement with the results of Thompson [41] and Meyer [30], who showed that standard errors of heritability estimates can be 3 to 5 times larger with a maternal effect model as compared to a model involving only direct effects. Based on these results, the standard errors of estimated genetic correlations should range from 0.10 to 0.20, so that genetic correlation estimates have a very low accuracy. Hence, the results should be considered with some caution and only large tendencies can be reasonably interpreted.

Results. Estimated genetic parameters of W4w, with a low heritability of direct effects, a much larger maternal heritability and a moderate genetic antagonism between direct and maternal effects, are consistent with early literature results (reviewed by Robison [35]). They are also similar to the results obtained at 3 weeks of age by Rodriguez et al. [36] in Iberian pigs (with a lower antagonism between direct and maternal effects) and at 4 weeks of age by Maignel et al. ([26] and unpublished results) in Large White and Landrace breeds. These results suggest that piglet preweaning growth is to a larger extent under the control of the environment provided by the dam than of the piglets' individual genes. These maternal effects probably reflect sow genetic merit for milk production, behaviour, ..., but not litter size, which was accounted for in the model and in fact had a limited effect on estimated genetic parameters. Maternal effects conversely had a low impact on postweaning growth, so that maternal heritabilities progressively decreased with higher weights. This is in agreement with the results of Crump et al. [9] for Landrace pigs, but not with those of Bryner et al. [7] who obtained a maternal heritability value of 0.23 for average daily gain in the Yorkshire breed. Maternal effects remained significant for ABT, as also reported by Bryner et al. [7] and Maignel et al. (unpublished results) in the Landrace breed. On the contrary, Crump et al. [9] in the Landrace breed and Maignel et al. (unpublished results) in the Large White breed obtained low and non-significant maternal heritabilities (0.00 and 0.01, respectively). Differences in body composition at weaning due to prenatal or/and postnatal maternal effects, which might result in differences in the distribution of energy during postweaning growth, has been advocated as a possible explanation for this maternal effect [16].

The negative association between direct and maternal effects for all traits studied is in agreement with previous results of Bryner et al. [7] and Maignel et al. (unpublished results). It may reflect a real genetic antagonism between performance traits and traits related to sow maternal ability such as milk production and quality. It may also be explained by a potential bias due to the fact that the environmental correlations between direct and maternal effects were assumed to be null [17, 31, and 41]. Such a bias in direct – maternal genetic correlations due to ignoring the corresponding environmental correlation was evidenced in some (e.g. [31]), but not all [8, 18] studies involving maternal effects.

The genetic variability of performance traits was very similar in males and females during early growth, but showed notable differences for later growth, with both a scale phenomenon and genetic correlations between performance in each sex that significantly differed from one. This result disagrees with most earlier studies in European breeds (e.g. [9, 27, 33]). The earlier sexual maturity and the peculiar sexual dimorphism of founder Chinese breeds with impaired feeding behaviour of males after puberty, which result in lower growth rates than in females [5, 13], may be a possible explanation of this phenomenon.

Heritability values for ABT, TEAT and GTEAT were larger than average literature values [23, 38] and those previously obtained for ABT by Ducos et al. [11]. These large estimates might be partly explained by segregating major genes or quantitative trait loci (QTLs) in the *Tiameslan* population, which are likely to inflate heritability values. Indeed, a gene with a major effect on average backfat thickness was evidenced in the Laconie line by Le Roy et al. [22] using segregation analysis. QTLs for average backfat thickness and teat number were also evidenced in a Meishan × Large White crossbred population [6]. Further work remains to be done to test this hypothesis in the *Tiameslan* line.

Heritability estimates for DT, TNB and NW do not differ greatly from average literature values [10, 12, 38]. The low genetic correlations between production traits and teat number are also in agreement with most literature estimates (e.g. see [23]). Conversely, the genetic antagonism between performance traits and litter size evidenced in the *Tiameslan* line differs from most literature results, which tend to show the genetic independence of the two groups of traits [37]. This antagonism may either come from the existence of linkage disequilibrium between genes affecting production and reproductive traits or from pleiotropic effects of QTLs. Linkage disequilibrium was obviously present in F1 animals and may have been maintained in later generations due to selection for growth rate and carcass leanness.

6. CONCLUSION

This study clearly shows that the genetic variability of intensively studied traits such as growth and carcass composition traits may in some instances be more complex than usually thought. Both maternal effects and sex differences in genetic variability may be worth considering when predicting and estimating genetic trends as well as for genetic evaluation. Aspects related to the estimation of genetic trends will be considered in the second paper of this series. Further work remains to be done with respect to the other points in order to find the best operational model. As discussed by Bidanel [3], this is not a trivial issue, since the advantage of more sophisticated models may in some instances be annihilated by poor parameter estimates. The problem might be even more complex if departures from the polygenic infinitesimal model have to be considered. The existence of genes with large effects in the *Tiameslan* population might be tested using segregation analyses or a QTL detection design using genetic markers.

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REFERENCES

[1] Bidanel J.P., Étude de stratégies de valorisation en croisement de la race Meishan. 3-Evaluation comparée de différents systèmes de croisement, in: 21es Journées de la Recherche Porcine en France, 31 January – 2 February 1989, Institut technique du porc, Paris, 1989, pp. 361–366.

[2] Bidanel J.P., Estimation of crossbreeding parameters between Large White and Meishan porcine breeds. III. Dominance and epistatic components of heterosis on reproductive traits, Genet. Sel. Evol. 25 (1993) 639–657.

[3] Bidanel J.P., Benefits and limits of increasingly sophisticated models for genetic evaluation: the example of pig breeding, in: Proceedings of the 6th World Congress on Genetics Applied to Livestock Production, 11-16 January, University of New England, Armidale, Australia, 1998, Vol. 25, pp. 577–584.

[4] Bidanel J.P., Caritez J.C., Legault C., Estimation of crossbreeding parameters between Large White and Meishan porcine breeds. I. Reproductive performance, Genet. Sel. Evol. 21 (1989) 507–526.

[5] Bidanel J.P., Caritez J.C., Legault C., Ten years of experiments with Chinese pigs in France. 2. Utilisation in crossbreeding, Pig News & Information 12 (1991) 239–243.

[6] Bidanel J.P., Milan D., Chevalet C., Woloszyn N., Bourgeois F., Caritez J.C., Gruand J., Le Roy P., Bonneau M., Lefaucheur L., Mourot J., Prunier A., Désautés C., Mormède P., Renard C., Vaiman M., Robic A., Gellin J., Ollivier L., Détection de locus à effets quantitatifs dans le croisement entre les races porcines Large White et Meishan. Dispositif expérimental et premiers résultats, in: 30es Journées de la Recherche Porcine en France, 3–5 February 1998, Institut technique du porc, Paris, pp. 117–125.

[7] Bryner S.M., Mabry J.W., Bertrand J.K., Benyshek L.L., Kriese L.A., Estimation of direct and maternal heritability and genetic correlation for backfat and growth rate in swine using data from centrally tested Yorkshire boars, J. Anim. Sci. 70 (1992) 1755–1759.

[8] Cantet R.J.C., Kress D.D., Anderson D.C., Doornbos D.E., Burfening P.J., Blackwell R.L., Direct and maternal variances and covariances and maternal phenotypic effects on preweaning growth of beef cattle, J. Anim. Sci. 66 (1988) 648–660.

[9] Crump R.E., Haley C.S., Thompson R., Mercer J., Individual animal model estimates of genetic parameters for performance test traits of male and female Landrace pigs tested in a commercial nucleus herd, Anim. Sci. 65 (1997) 275–283.

[10] Ducos A., Evaluation génétique des porcs contrôlés dans les stations publiques à l'aide d'un modèle animal multicaractère, Doctoral thesis, Institut National Agronomique Paris-Grignon, France, 1994, 222 pp.

[11] Ducos A., Bidanel J.P., Naveau J., Estimation of genetic parameters and genetic trends for production traits in the Sino – European *Tiameslan* composite line of pigs, J. Anim. Breed. Genet. 109 (1992) 108–118.

[12] Haley C.S., Avalos E., Smith C., Selection for litter size in the pig, Anim. Breed. Abstr. 56 (1988) 317–332.

[13] Haley C.S., d'Agaro E., Ellis M., Genetic components of growth and ultrasonic fat depth traits in Meishan and Large White pigs and their reciprocal crosses, Anim. Prod. 54 (1992) 105–115.

[14] Haley C.S., Lee G.J., Ritchie M., Comparative reproductive performance in Meishan and Large White pigs and their crosses, Anim. Sci. 60 (1995) 259–267.

[15] Im S., Fernando R.L., Gianola D., Likelihood inferences in animal breeding under selection: a missing-data theory view point, Génét. Sél. Evol. 21 (1989) 399–414.

[16] Johnson R.K., Crossbreeding in swine: experimental results, J. Anim. Sci. 52 (1981) 906–923.

[17] Koch R.M., The role of maternal effects in animal breeding. VI. Maternal effects in beef cattle, J. Anim. Sci. 35 (1972) 1316–1323.

[18] Koerhuis A.N.M., Thompson R., Models to estimate maternal effects for juvenile body weight in broiler chickens, Genet. Sel. Evol. 29 (1997) 225–249.

[19] Lee G.J., Haley C.S., Comparative farrowing to weaning performance in Meishan and Large White pigs and their crosses, Anim. Sci. 60 (1995) 269–280.

[20] Legault C., Caritez J.C., L'expérimentation sur le porc chinois en France. I-Performances de reproduction en race pure et en croisement. Génét. Sél. Evol. 15 (1983) 225–240.

[21] Le Roy P., Naveau J., Elsen J.M., Sellier P., Evidence for a new major gene influencing meat quality in pigs, Genet. Res. 55 (1990) 33–40.

[22] Le Roy P., Elsen J.M., Naveau J., Etude de la variabilité génétique de l'adiposité dans la lignée Laconie, in: 22es Journées de la Recherche Porcine en France, 30 January-1st February 1990, Institut technique du porc, Paris, 1990, pp. 11–16.

[23] Ligonesche B., Bazin C., Bidanel J.P., Variabilité génétique du nombre de tétines chez le porc. Relations avec les caractères de production et de reproduction, in: 27es Journées de la Recherche Porcine en France, 31 January-2 February 1995, Institut technique du porc, Paris, pp. 121-126.

[24] Lo L.L., Fernando R.L., Grossman M., Covariance between relatives in multibreed populations: additive model, Theor. Appl. Genet. 87 (1993) 1215–1228.

[25] Lo L.L., Fernando R.L., Grossman M., Theory of modelling means and covariances in a two-breed population with dominance, Theor. Appl. Genet. 90 (1995) 49–62.

[26] Maignel L., Bidanel J.P., Guéblez R., Intérêt d'une pesée au sevrage dans le contrôle de performances en ferme, in: 30es Journées de la Recherche Porcine en France, 3-5 February 1998, Institut technique du porc, Paris, pp. 101–107.

[27] Merks J.W.M., Genotype × Environment interactions in pig breeding programmes. I. Central test station, Livest. Prod. Sci. 14 (1986) 365–381.

[28] Meyer K., Approximate accuracy of genetic evaluation under an animal model, Livest. Prod. Sci. 21 (1989) 87–100.

[29] Meyer K., Estimating variances and covariances for multivariate animal models by restricted maximum likelihood, Genet. Sel. Evol. 21 (1991) 317–340.

[30] Meyer K., Bias and sampling covariances of estimates of variance components due to maternal effects, Genet. Sel. Evol. 24 (1992) 487–522.

[31] Meyer K., Variance components due to direct and maternal effects for growth traits of Australian beef cattle, Livest. Prod. Sci. 31 (1992) 179–204.

[32] Neumaier A., Groeneveld E., Restricted maximum likelihood estimation of covariances in sparse linear models, Genet. Sel. Evol. 30 (1998) 3–26.

[33] Ollivier L., Dix ans d'une expérience de sélection individuelle sur des verrats utilisés en insémination artificielle. II. Paramètres génétiques estimés, Génét. Sél. Evol. 15 (1983) 99–118.

[34] Patterson H.D., Thompson R., Recovery of inter-block information when block sizes are unequal, Biometrika 58 (1971) 545–554.

[35] Robison O.W., The role of maternal effects in animal breeding. V. Maternal effects in swine, J. Anim. Sci. 35 (1972) 1303–1315.

[36] Rodriguez M.C., Rodriganez J., Silio L., Genetic analysis of maternal ability in Iberian pigs, J. Anim. Breed. Genet. 111 (1994) 220–227.

[37] Rothschild M.F., Bidanel J.P., Biology and genetics of reproduction, in: Rothschild M.F., Ruvinsky A. (Eds.), The genetics of the pig, CAB International, Wallingford, Oxon, UK, 1998, pp. 313–343.

[38] Sellier P., Genetics of meat and carcass traits, in: Rothschild M.F., Ruvinsky A. (Eds.), The genetics of the pig, CAB International, Wallingford, Oxon, UK, 1998, pp. 463-510.

[39] Sorensen D.A., Kennedy B.W., Estimation of genetic variance from unselected and selected populations, J. Anim. Sci. 59 (1984) 1213–1223.

[40] Tess M.W., Bennett G.L., Dickerson G.E., Simulation of genetic changes in life cycle efficiency of pork production. II-Effects of components on efficiency, J. Anim. Sci. 56 (1983) 354–368.

[41] Thompson R., The estimation of maternal genetic variance, Biometrics 32 (1976) 903–917.

[42] Young L.D., Reproduction of F1 Meishan, Fengjing, Minzhu, and Duroc gilts and sows, J. Anim. Sci. 73 (1995) 711–721.