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Evaluation of the effect and profitability of gene-assisted selection in pig breeding system*

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Abstract: Objective: To evaluate the effect and profitability of using the quantitative trait loci (QTL)-linked direct marker (DR marker) in gene-assisted selection (GAS). Methods: Three populations (100, 200, or 300 sows plus 10 boars within each group) with segregating QTL were simulated stochastically. Five economic traits were investigated, including number of born alive (NBA), average daily gain to 100 kg body weight (ADG), feed conversion ratio (FCR), back fat at 100 kg body weight (BF) and intramuscular fat (IMF). Selection was based on the estimated breeding value (EBV) of each trait. The starting frequencies of the QTL's favorable allele were 0.1, 0.3 and 0.5, respectively. The economic return was calculated by gene flow method. Results: The selection efficiency was higher than 100% when DR markers were used in GAS for 5 traits. The selection efficiency for NBA was the highest, and the lowest was for ADG whose QTL had the lowest variance. The mixed model applied DR markers and obtained higher extra genetic gain and extra economic returns. We also found that the lower the frequency of the favorable allele of the QTL, the higher the extra return obtained. Conclusion: GAS is an effective selection scheme to increase the genetic gain and the economic returns in pig breeding.

Key words: Swine, Gene-assisted selection (GAS), Selection efficiency, Extra returns
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INTRODUCTION

In recent years, more and more quantitative trait loci (QTL) and their closely linked markers have been identified (Georges *et al*., 1995; Blattman *et al*., 1996; Heyen *et al*., 1999; Schrooten *et al*., 2000). The direct marker (DR marker), the functional polymorphism that can be genotyped directly (Dekkers, 2004), is used in breeding programs. Many simulation studies have shown that marker-assisted selection (MAS) can improve the genetic merit of livestock (Lande and Thompson, 1990; Meuwissen and van Arendonk, 1992; Meuwissen and Goddard, 1996; Ruane and Colleau, 1996; Gomez-Raya and Klemetsdal, 1999). Although there are a few studies investing the profitability that the MAS is used in breeding programs in livestock enterprise (Brascamp *et al*., 1993; Spelman and Garrick, 1998; Gomez-Raya and Klemetsdal, 1999; Hayes and Goddard, 2003), no study on the profitability using gene-assisted selection (GAS) in breeding programs has been reported. While Hayes and Goddard (2003) assessed the profitability of implementing MAS in pig breeding programs, the population and the construction of the breeding system in their study did not fit reality. Moreover, the effective way to improve the genetic gain is to use the DR markers in GAS (Villanueva *et al*., 2004). There has been no paper on the economic profit of applications of GAS schemes in a pig enterprise, either. Cao (2003) concluded that 5 traits, including number of born alive (NBA), days to 100 kg body weight (Day),

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feed conversion ratio (FCR), back fat at 100 kg body weight (BF), and intramuscular fat (IMF), should be selected in pig breeding programs. The purpose of the present study was to investigate the difference of the selection efficiency among these 5 traits using DR markers in GAS and profits of GAS used in a pig breeding system.

MATERIALS AND METHODS

Population model

Three discretely closed pig base populations were simulated using stochastic simulation, including 100, 200, and 300 sows plus 10 boars in each group, respectively. The pigs in the base populations (t=0) had no inbreeding.

The 5 traits under selection were genetically controlled by an infinite number of additive loci, each with an infinitesimal effect (polygenes), plus a single bialleles (alleles B and b) QTL. The total genetic value of the ith individual was $G_i=q_i+u_i$, where q_i is the genotypic value due to the QTL and u_i is the polygenic effect. The QTL had an additive effect (a), defined as half the difference between the two homozygotes, and a dominance effect (d) defined as the difference between the heterozygote and the average of the two homozygotes. Thus, genotypic values due to the QTL were a, d, and $-a$ for individuals with genotypes BB, Bb, and bb, respectively (Falconer and Mackay, 1996). The additive genetic variance explained by the QTL in the base population was $\sigma_q^2 = 2p(1-p)\alpha^2$, where p is the initial frequency of the QTL's favorable allele (B) and α is the effect of gene substitution, $\alpha=a-(1-2p)d$ (Falconer and Mackay, 1996). So the QTL effect v_i is $\sqrt{\sigma_q^2/2p(1-p)}$, 0, $-\sqrt{\sigma_q^2/2p(1-p)}$ for QTL of individual i with genotypes BB, Bb, and bb, respectively.

The pigs in generation 1 (t=1) were obtained from randomly mating pigs in base populations. The numbers of selected sows and boars were constant across generations (t=1~5). At t=0, the polygenic effect for each individual was obtained from a normal distribution with mean zero and variance σ_u^2. Alleles at the QTL were chosen at random with appropriate probabilities (i.e., those given by the initial allele frequencies). The QTL and polygenes were in linkage phase equilibrium. The phenotypic value for individual i (P_i) was obtained by adding to the total genetic value (G_i) a normally distributed environmental component with mean zero and variance σ_e^2. In base population P (phenotypic value) was assumed to equal to 1.

In subsequent generations, the offspring was obtained by random mating boars and sows without mating among full-sibs and half-sibs. The polygenic effect of the offspring was generated as the average of the polygenic effects of their parents plus a random Mendelian deviation. The latter was sampled from a normal distribution with mean zero and variance $(\sigma_u^2/2[1-(F_\mathrm{s}+F_\mathrm{d})/2])$, where F_s and F_d are the inbreeding coefficients of the sire and dam, respectively. The QTL alleles were transmitted from parents to offspring in classical Mendelian fashion. A total of 100 replicates were performed for each simulation.

Parameters used in this study were summarized in Table 1.

Table 1 The parameters used in GAS

Parameters	Value
Population scale	
Number of breeding sows (boars)	100 (10), 200 (10), 300 (10)
Average litter size	8
Traits for selection*	
NBA (Short *et al*., 1997)	0.10, 0.24
ADG (Stearns *et al*., 2005)	0.30, 0.11
BF (Sato *et al*., 2003)	0.52, 0.20
IMF (Dragos-Wendrich *et al*., 2003)	0.47, 0.39
FCR (Ovilo *et al*., 2002)	0.23, 0.23
QTL (direct marker)	
Number of QTL	1
Number of alleles	2
P_0	0.1, 0.3, 0.5
Simulated generation	5

* The data are heritability and the ratio of QTL variance to genetic variance; P_0 was the initial frequency of the favorable allele of the QTL

Genetic model and selection procedure

BLUP (best linear unbiased prediction) is a common method to estimate the animal breeding value. The pigs selected for breeding were based on the EBV (estimated breeding value) estimated by three genetic models: SBLUP (standard BLUP) model, QBLUP (QTL-BLUP) model, and FBLUP (fixed-BLUP) model.

SBLUP model was used when the QTL effect and polygenic effect were combined into the additive effect of the animal in the mixed model, as

$$\boldsymbol{Y}=\boldsymbol{Xb}+\boldsymbol{Za}+\boldsymbol{e}=\boldsymbol{Xb}+\boldsymbol{Z}(\boldsymbol{u}+\boldsymbol{v})+\boldsymbol{e}, \qquad (1)$$

where $\boldsymbol{Y}$, $\boldsymbol{b}$, $\boldsymbol{a}$, $\boldsymbol{e}$, $\boldsymbol{u}$ and $\boldsymbol{v}$ were the vectors of phenotypic value, fixed effect, additive effect, environmental effect, polygenic effect, and QTL effect, respectively. $\boldsymbol{X}$ and $\boldsymbol{Z}$ were the incidence vectors of vectors $\boldsymbol{b}$ and $\boldsymbol{a}$.

$$\boldsymbol{V}\begin{bmatrix}\boldsymbol{a}\\ \boldsymbol{e}\end{bmatrix}=\begin{bmatrix}\boldsymbol{A}_a\sigma_a^2 & \boldsymbol{0}\\ \boldsymbol{0} & \boldsymbol{I}\sigma_e^2\end{bmatrix},$$

where $\boldsymbol{V}$ is the abbreviate for variance, $\boldsymbol{A}_a$, $\boldsymbol{I}$ were the additive genetic relationship and identity matrix, respectively.

In the SBLUP model, total EBV in generation t (EBV_t) was estimated using the total initial genetic additive variance ($\sigma_q^2+\sigma_u^2$) and phenotypic values uncorrected for the QTL effect (i.e., P_i).

QBLUP model was used when the QTL effect in the model was the random effect, as

$$\boldsymbol{Y}'=\boldsymbol{Xb}+\boldsymbol{Zu}+\boldsymbol{e}, \qquad (2)$$

where $\boldsymbol{Y}'$ was vector of the phenotypic value corrected for the QTL effect, and $y_i'=y_i-v_i$, where y_i and v_i were the phenotypic value and QTL effect of individual i, respectively. The other letters in the model denoted the same meanings as in Eq.(1).

With QBLUP selection, EBV_t=EBV_u+BV_q, where EBV_u is the estimate of the polygenic breeding value and BV_q is the breeding value due to the QTL. EBV_u for individual i is $h_u^2(P_i-q_i)$, where h_u^2 is the polygenic heritability and q_i is the genotypic value for the QTL.

FBLUP model was used when the QTL effect was fixed effect in the model, as

$$\boldsymbol{Y}=\boldsymbol{Xb}+\boldsymbol{X}_g\boldsymbol{g}+\boldsymbol{Zu}+\boldsymbol{e}, \qquad (3)$$

where $\boldsymbol{Y}$, $\boldsymbol{b}$, $\boldsymbol{g}$, $\boldsymbol{u}$, and $\boldsymbol{e}$ were the vectors of phenotypic value, fixed effect, QTL genotypic value (obtained from QTL genotype), polygenic effect, and environmental effect, respectively. $\boldsymbol{X}$, $\boldsymbol{X}_g$, and $\boldsymbol{Z}$ were the incidence vectors of vectors $\boldsymbol{b}$, $\boldsymbol{g}$, and $\boldsymbol{u}$.

$$\boldsymbol{V}\begin{bmatrix}\boldsymbol{u}\\ \boldsymbol{e}\end{bmatrix}=\begin{bmatrix}\boldsymbol{A}_u\sigma_u^2 & \boldsymbol{0}\\ \boldsymbol{0} & \boldsymbol{I}\sigma_e^2\end{bmatrix},$$

where $\boldsymbol{A}_u$ was the additive genetic relationship due to polygenic genes. With FBLUP selection, EBV_t=EBV_u+g.

Selection efficiency

Selection efficiency (SE) was a value to compare the genetic gain of different selection schemes, $SE=EBV_{\text{QBLUP or FBLUP}}/EBV_{\text{SBLUP}}$.

Economic model of pig enterprise

The pig enterprise was composed by nucleus, multiplier, and commercial populations. Gains from increase in genetic merit in the nucleus were realized from sale of slaughter pigs from a nucleus, multiplier tier and commercial tier. A gene flow method (Hill, 1974) was used to calculate the extra returns from GAS. Fig.1 gives the flow of animals between tiers and pigs sent to slaughter for a 6-month period in 100-sow nucleus (culled boars and sows have been ignored for simplification). The population construction, the replacement of breeding pigs, and pigs to slaughter in each tier per 6-month period for 100-sow, 200-sow, and 300-sow nucleus were listed in Table 2, respectively.

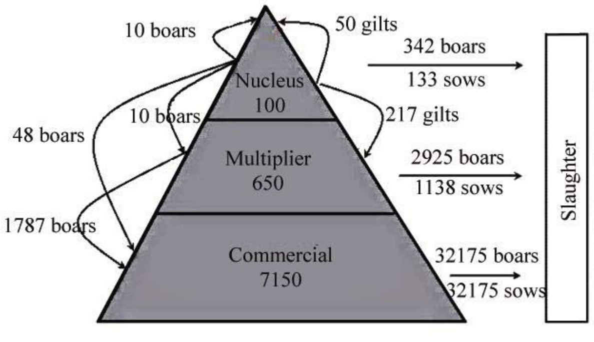

Fig.1 The flow of animals between tiers and pigs sent to slaughter for a 6-month period in 100-sow nucleus. Numbers are pigs per 6 months

The gene flow model requires a vector ($\boldsymbol{g}$) of additional gains from GAS per 6-month period in the nucleus. By considering one generation to be 18 months, $\boldsymbol{g}$ (dimensions 15×1) was derived from a 5×1

Table 2 The population construction for three groups in each tier

Sows in nucleus	Nucleus					Multiplier					Commercial				
	M:F	M	F	C (M)	C (F)	M:F	M	F	C (M)	C (F)	M:F	M	F	C (M)	C (F)
100	1:10	10	50	342	133	1:50	10	217	2925	1138	1:50	48	7150	32175	32175
200	1:20	10	100	694	266	1:87	10	434	5850	2275	1:50	96	14300	64350	64350
300	1:30	10	150	1047	400	1:130	10	650	8775	3412	1:50	143	21450	96525	96525

M:F, M, F, C (M), C (F) were the boar to sow ratio, the replacement boars, the replacement gilts, male pigs to slaughter, and female pigs to slaughter, in each 6 months in each tier, respectively

vector of additional gains per generation from GAS from the simulations, the genetic gains in each 6-month in the economic model were 1/3 of the genetic gains in each generation in the simulation nucleus (Hayes and Goddard, 2003).

In the gene flow model, boars and sows both reached puberty at 6 months old. Boars selected for breeding in the nucleus were used for 6 months, and then transferred to the multiplier herd where they were used for another 18 months. Boars not selected for breeding in the nucleus were either slaughtered or used for breeding in the commercial tier, where they were used for 18 months. In the nucleus, half of the piglets produced were from sows in their first parity, 1/3 from sows in their second parity and 1/6 from sows in their third parity. There were eight piglets weaned per mating in the nucleus. Gilts in the nucleus and not selected for use in the nucleus were slaughtered. In the multiplier tier, it was estimated that 30% of piglets were from sows in their first parity, 26% of piglets from sows in their second parity, 24% of piglets from sows in their third parity, and 20% of piglets from sows in their fourth parity. Gilts produced in the multiplier were either used for breeding in the commercial tier or slaughtered. Boars produced in the multiplier were slaughtered. In the commercial tier, it was estimated that 25%, 20%, 17%, 15%, 13% and 10% of piglets were from sows in their 1st, 2nd, 3rd, 4th, 5th, and 6th parities, respectively.

The gene flow method required the definition of tier-sex-age classes (Table 3).

Table 3 Definition of tier-sex-age classes used in the economic model

No.	Tier	Sex	Age (months)
1	Nucleus	Male	0~6
2	Nucleus	Male	6~12
3	Nucleus	Male	12~18
4	Nucleus	Female	0~6
5	Nucleus	Female	6~12
6	Nucleus	Female	12~18
7	Nucleus	Female	18~24
8	Multiplier	Male	0~6
9	Multiplier	Male	6~12
10	Multiplier	Male	12~18
11	Multiplier	Male	18~24
12	Multiplier	Female	0~6
13	Multiplier	Female	6~12
14	Multiplier	Female	12~18
15	Multiplier	Female	18~24
16	Multiplier	Female	24~30
17	Commercial	Male	0~6
18	Commercial	Male	6~12
19	Commercial	Male	12~18
20	Commercial	Male	18~24
21	Commercial	Female	0~6
22	Commercial	Female	6~12
23	Commercial	Female	12~18
24	Commercial	Female	18~24
25	Commercial	Female	24~30
26	Commercial	Female	30~36
27	Commercial	Female	36~42

Economic returns for GAS

Returns from selection in the economic mode were calculated as (Zhang, 2000):

$$E=\sum\sum \Delta G_{ij} n_{ij} W^{*}, \tag{4}$$

where ΔG_{ij} was the extra genetic gain for GAS to SBLUP selection, n_{ij} was the standardization trait discount value, and W^* was the trait's marginal profit.

The marginal profits W^* of the 5 traits, NBA, ADG (average daily gain), FCR, LMR (lean-meat rate at 100 kg body weight, indirect selection from BF), and IMF were 8.06, 0.87, 86.32, 10.78 and 23.1 (modified according to the Chinese market), respectively (Cao, 2003).

Standardization trait discount value was calculated as (Zhang, 2000):

$$\boldsymbol{n}_{ij} = \sum_{t=1}^{D} \boldsymbol{h}_i' \boldsymbol{m}_{jt} (1+\boldsymbol{r})^{-t}, \tag{5}$$

where $\boldsymbol{h}_i$ was the realization vector of the trait i, $\boldsymbol{m}_{jt}$ was the vector of gene proportion at the time t in the j selection group in every tier-sex-age group. r was the discount rate and was assumed to be 0.05 here. There were 15 selection groups, so D=15.

$$\boldsymbol{m}_{jt}=\boldsymbol{R}\boldsymbol{a}_{t-1}+\boldsymbol{P}\boldsymbol{m}_{it-1}, \tag{6}$$

where $\boldsymbol{P}_{(27\times 27)}$ was the gene transmission matrix. $\boldsymbol{a}_t=\boldsymbol{Q}\boldsymbol{a}_{t-1}$ (t=1,2,…,15), where $\boldsymbol{a}_1$ was the initial vector for all selection group, and $\boldsymbol{a}_1'$=[1001000100010000 10001000000]. t was the selection generation. $\boldsymbol{Q}_{(27\times 27)}$ was the mature matrix, where the elements of the reproduction rows were 0 and the others were the same as the elements in matrix $\boldsymbol{P}$. $\boldsymbol{R}_{(27\times 27)}$ was the reproduction matrix, where the elements of the reproduction rows were the same as those in the $\boldsymbol{P}$ matrix, and the other elements were 0. According to Eq.(6), the vector $\boldsymbol{m}_{jt}$ was obtained.

Extra returns for GAS

The extra cost of the breeding program from implementing GAS was assumed to be only genotyping costs. The genotyping cost for one QTL was RMB 5 yuan. The genotyping costs for three nucleus were C_t=8×n×5×d^t, where n was the number of sows in the nucleus, d was the discounted rate, and t was the time in the selection group. So the extra returns of the breeding program from implementing GAS were calculated as:

$$R_t = E_t - \sum_{t=1}^{15} C_t. \tag{7}$$

RESULTS

Selection efficiency

The selection efficiencies (SEs) for the 5 traits using QBLUP model and FBLUP model were presented in Table 4 and Table 5, respectively. All SEs of 5 traits at generation 1 were 100%, because in this stage there was no selection for all pigs. Almost all the SEs of the 5 traits in the later generations were higher than 100%, and became lower and lower when the generations went higher. The higher initial frequency of the favorable allele of the selected QTL (P_0) was, the lower the SE. The SE was the highest for trait NBA and the lowest for trait BF.

The SE for the sex-limited trait NBA was higher while using QBLUP model in 100-sow and 200-sow nucleus, respectively, but it was higher in 300-sow nucleus when FBLUP model was used. The SE for trait FCR was higher when FBLUP model was used. Most of the SEs for trait ADG were higher when QBLUP model was used. All the SEs for trait BF were higher when FBLUP model was used. The SE for trait IMF was higher when P_0=0.1 and using QBLUP model in three populations, whereas it was higher when P_0 was 0.3 and 0.5 and FBLUP model was used in three populations, respectively.

Extra returns for GAS

The extra returns for the three populations at different initial frequencies of the QTL's favorable allele when two models were used were described in Table 6. The lower the P_0 was, the higher the extra returns were, using GAS in the breeding program. Moreover, the bigger the nucleus population was, the higher the extra returns were, while using GAS. The extra returns fell quickly with the rise of P_0.

The extra returns were higher in 100-sow population when FBLUP model was used, while higher in 200-sow population when QBLUP model was used, excluded when P_0=0.5. In 300-sow nucleus, the extra returns were higher when P_0=0.1 using QBLUP model, but lower when P_0=0.3 and 0.5, respectively.

DISCUSSION

Factors influencing the selection efficiency

The SEs for the 5 traits in the GAS scheme in pig breeding were influenced by the trait's heritability, characters (such as sex-limited), the ratio of the QTL variance to additive genetic variance, and the initial frequency of the QTL's favorable allele.

A few studies have reported that the SE in MAS or GAS was higher for lower heritability trait and sex-limited trait (Lande and Thompson, 1990; Gimelfarb and Lande, 1995; Whittaker *et al.*, 1995; Ruane and Colleau, 1995; Meuwissen and Goddard, 1996; Liu *et al.*, 2001). Ruane and Colleau (1995)

Table 4 The selection efficiency (SE) for 5 traits using QBLUP model in three different-size population

G	P_0	*SE*														
		100-sow					200-sow					300-sow				
		NBA	FCR	ADG	BF	IMF	NBA	FCR	ADG	BF	IMF	NBA	FCR	ADG	BF	IMF
1	0.1	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
	0.3	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
	0.5	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
2	0.1	1309.3	145.4	114.4	113.0	144.0	26748.0	141.4	109.0	114.0	137.8	500.4	137.1	107.3	111.4	136.0
	0.3	155.4	114.2	105.9	106.7	114.7	139.8	112.5	106.3	106.3	115.0	145.8	111.7	103.8	106.7	112.9
	0.5	128.3	110.3	104.5	104.5	109.2	118.4	108.4	105.3	104.5	109.3	122.5	108.4	104.1	104.4	108.4
3	0.1	213.2	131.3	114.3	113.0	120.7	233.9	130.7	110.5	113.5	117.4	193.0	124.9	110.4	112.1	115.3
	0.3	146.7	108.0	105.5	103.5	109.3	130.1	109.8	105.7	104.7	109.7	133.1	109.9	104.6	105.1	107.5
	0.5	126.8	105.5	104.4	104.0	103.5	109.5	106.1	105.0	102.5	105.4	114.4	106.3	103.9	104.6	105.0
4	0.1	151.3	116.7	110.9	107.0	104.2	154.4	115.0	110.6	107.0	103.9	144.5	111.4	109.1	106.5	103.3
	0.3	128.4	103.7	104.8	100.9	102.4	114.0	104.3	104.3	102.1	104.1	119.4	104.2	101.9	103.8	102.3
	0.5	116.8	101.8	104.6	103.1	101.6	105.7	104.3	103.5	100.5	102.5	108.6	104.0	103.2	102.7	102.0
5	0.1	123.4	106.7	106.7	101.7	100.2	123.6	105.2	107.0	102.4	100.4	125.7	103.6	105.7	102.3	100.4
	0.3	120.9	101.0	104.3	100.8	100.5	107.2	101.6	102.4	101.2	101.9	112.9	101.3	100.2	102.5	101.6
	0.5	110.7	99.7	103.1	101.6	100.9	100.8	101.6	101.7	99.9	102.8	104.3	102.5	102.0	102.1	101.8

G: Generation; P_0: The initial frequency of the QTL's favorable allele

Table 5 The selection efficiency (SE) for 5 traits using FBLUP model in three different-size population

G	P_0	*SE*														
		100-sow					200-sow					300-sow				
		NBA	FCR	ADG	BF	IMF	NBA	FCR	ADG	BF	IMF	NBA	FCR	ADG	BF	IMF
1	0.1	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
	0.3	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
	0.5	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
2	0.1	1236.1	142.7	112.4	113.5	144.9	23991.8	137.9	106.6	114.1	136.2	465.1	135.3	105.8	111.3	133.9
	0.3	153.2	113.6	105.5	106.7	114.7	138.8	110.4	104.3	106.2	114.6	149.8	112.1	103.5	106.4	112.8
	0.5	124.9	109.5	104.5	104.7	109.1	120.0	108.5	104.9	104.6	109.4	124.3	108.4	103.7	104.8	108.3
3	0.1	210.2	133.4	113.0	114.7	120.2	230.1	132.0	111.9	114.7	116.2	199.6	124.2	111.5	111.6	114.9
	0.3	147.2	111.0	104.4	105.1	109.0	131.4	107.7	104.4	104.5	110.2	135.3	111.6	103.9	105.4	108.1
	0.5	124.6	106.2	103.7	102.9	103.4	114.6	106.0	104.2	103.3	105.8	113.9	107.0	103.1	104.6	105.0
4	0.1	157.4	120.1	110.1	107.2	104.2	157.0	116.3	110.8	108.0	102.6	151.0	111.7	109.8	106.1	103.8
	0.3	127.3	106.3	103.9	102.3	103.1	115.4	102.1	103.7	102.8	105.5	119.6	105.6	101.5	104.6	102.8
	0.5	114.6	102.9	103.4	103.1	102.0	110.0	104.3	103.2	101.5	103.4	106.3	104.1	101.9	102.4	102.6
5	0.1	131.1	108.1	105.2	101.9	99.3	125.0	105.5	107.0	102.4	99.1	128.4	103.3	106.0	101.1	100.8
	0.3	118.8	104.7	103.5	101.2	100.8	107.2	99.3	102.6	101.5	103.2	111.9	101.7	100.7	102.9	101.6
	0.5	107.6	100.6	101.8	101.9	101.7	103.9	102.1	102.1	100.8	103.8	101.5	102.7	100.7	101.3	101.7

G: Generation; P_0: The initial frequency of the QTL's favorable allele

Table 6 The extra returns for GAS in three populations

Model	Extra economic returns (RMB yuan)								
	100-sow			200-sow			300-sow		
	P_0=0.1	P_0=0.3	P_0=0.5	P_0=0.1	P_0=0.3	P_0=0.5	P_0=0.1	P_0=0.3	P_0=0.5
QBLUP	3230647.30	559532.72	86018.29	5599108.49	2243969.43	2231599.75	6726772.58	3453732.47	4955329.35
FBLUP	3768478.93	2414493.20	614107.34	5354031.78	476440.35	3306397.27	6367686.56	4132929.78	5012847.05

P_0: The initial frequency of the QTL's favorable allele found that the selected QTL's effect was a major factor to affect the selection effect of MAS, the lager the QTL effect and the higher the heritability of the trait, the more obvious the selection effect in MAS or GAS. Our result in the present study agrees with this conclusion. Among the 5 traits, NBA, a sex-limited trait, has the highest SE. IMF has the high heritability and QTL variance and its SE was next to the SE of NBA, when P_0 was lower. FCR has both the moderate heritability and QTL variance and its SE was moderate among the 5 traits. BF has the highest heritability and moderate QTL variance and at the first 3 selection generations, its SE was higher than that of trait ADG with the lowest QTL variance.

The initial frequency of the favorable allele of the selected QTL (P_0) was a major factor to influence the SE (Spelman and Garrick, 1998). The SEs for the 5 traits became lower when P_0 went up. When P_0 goes up the frequency of the QTL's favorable allele increases more slowly, so the QTL effect and the total genetic effect of QBLUP selection and FBLUP selection increase slower compared with those when P_0 was lower, but faster compared with those of SBLUP selection, which results in a low SE. Such results are consistent with the findings of Liu *et al*.(2001).

The GAS selection effect was negatively associated with the selection generation, with a reduced SE for the higher generation (Hospital *et al*., 1997; Liu *et al*., 2001). With the increase of the selection generation, the frequency of the favorable allele of the QTL increased fast and after 4 generations it almost went to purify, and the QTL variance became lower and lower, then the total genetic gain in MAS or GAS became smaller and smaller. In this study, the SEs for the 5 traits were the highest at the second generation, and decreased with the increasing selection generation. At the fifth generation, although most of the SEs were above 100%, but the effect was small, indicating that for GAS or MAS, 3 to 4 generations were optimal. This study also shows that in the selection of QTL, maximization of response in a short term can result in lower cumulative responses in a long run, which can be solved by using the optimal model (Dekkers and van Arendonk, 1998; Dekkers and Chakraborty, 2001; Chakraborty *et al*., 2002; Villanueva *et al*., 2002; 2004; 2005; Tang, 2006).

The SEs for the same trait had no big difference between two models used, but for the sex-limited trait NBA and trait ADG with the lowest QTL variance, the SEs were higher in QBLUP model. For trait FCR with moderate heritability and QTL variance and trait BF with high heritability and moderate QTL variance, the SEs for both traits were higher when FBLUP model was used. However, for trait IMF, the SEs were almost the same in these two models.

Extra economic returns for GAS

The extra economic returns for GAS schemes reduced dramatically when P_0 increased, which was consistent with the pattern that the lower the P_0 was, the higher the genetic gain of the selected trait was, using GAS scheme.

Among the 5 traits in the pig breeding plan, the trait FCR had the highest margin profit and trait IMF was next to it. According to the gene flow methods, the economic returns direct proportion to the trait's margin profit (Zhang, 2000). So the genetic gains of trait FCR and trait IMF affected the economic returns of the population markedly. So in the pig breeding program, it is important for us to identify the QTL that affect the traits with high margin profit and then clone them. Thus, the economic profit of using GAS scheme would be considerable.

Among the three populations, the 300-sow nucleus population had the highest extra profit, and the 100-sow population had the lowest one. Because with the increase of the nucleus size, the total extra genetic gain for the population increased, and the pigs sent to slaughter per 6-month period increased too. In the present study, we didn't consider that with the increase of the traits' genetic gain, the production performance increased, so the pigs to slaughter in each six-month period would increase and the extra profit would increase too. With the improvement of the technology to genotype the QTL, the cost of GAS and MAS would decrease, so the extra profit would increase.

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