

RESEARCH ARTICLE

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# Genotype by environment interaction for carcass traits and intramuscular fat content in heavy Iberian pigs fattened in two different free-range systems

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## Abstract

Genotype by environment interaction (G×E) is a potential source of reduced efficiency in genetic improvement programs in livestock. The objective of the current work consisted of checking the existence of G×E interaction in carcass traits and in intramuscular fat content (IMF) in Iberian pigs fattened in two free-range systems. Genetic component and estimated breeding values (EBV) of the percentage of hams, shoulders and loins and IMF in loin were obtained from records of 4,348 and 1,818 pigs fattened in *campo* (C) and *montanera* (M) systems, respectively. A multitrait model where the performances of each system are considered as different traits was implemented. Three selection indexes were built with different treatments about the quality trait, two of them based in the optimal trait theory. The Pearson correlation between EBV and indexes and the Spearman correlation between the rankings of progenies of 21 boars fattened in both systems were calculated. Heritability results were different in both systems ( $h^2$  range from 0.43 to 0.66 and from 0.24 to 0.33 in C and M system, respectively) and genetic correlation of same traits expressed in the two systems also pointed out to a weak G×E interaction (0.64, 0.67 and 0.66 in hams, shoulders and IMF, respectively). Pearson and Spearman correlations were always significantly different to 1. The obtained results advised to consider this G×E interaction in the analysis model of a breeding program focused on free range production system and to include IMF in the index selection assuming an optimum range for this quality trait, in order to avoid negative effects of selection for carcass performances.

**Additional key words:** premium cuts; intramuscular fat; breeding values; economic values.

## Introduction

Iberian pigs are produced in a range of low, medium and high input production systems, all of them focused on obtaining meat and dry-cured products characterized by their high sensorial quality. The traditional production system includes a finish-fattening period of four or five months (November to March) known as *montanera* (M) and based on the *ad libitum* intake of

acorns and pastures (López-Bote, 1998). However, most of the Iberian pigs are fattened with an intensive management using commercial feeds. A medium input production system has been recently developed, where the pigs also use the territory (free-range rearing) but are mainly fattened with commercial feeds besides of the seasonal availability of grass or stubble. This second free-range feeding system is named *campo* (C). The percentages of these three production systems are

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Abbreviations used: AECERIBER (Spanish Association of Iberian Pig Breeders); C (Campo); CV (coefficient of variation); EBV (estimated breeding value); EV (economic value); G×E (Genotype by Environment); IMF (intramuscular fat); IND (index); M (Montanera); PROC (procedure).

**Table 1.** Numbers of sires, dams and animals with records, according to variety and type of feeding and, between brackets, corresponding number of progenies of the 21 common boars

Variety	Sires	Dams	<i>Montanera</i>	<i>Campo</i>	Total
<i>Retinto</i>	312 (12)	558	2,962 (142)	828 (124)	3,790 (266)
<i>Entrepelado</i>	114 (6)	82	787 (57)	537 (36)	1,324 (93)
<i>Lampiño</i>	13 (—)	197	145 (—)	28 (—)	173 (—)
<i>Mixed</i>	54 (3)	1,246	454 (27)	425 (53)	879 (80)
Total	493 (21)	2,583	4,348 (226)	1,818 (213)	6,166 (439)

18.6% (M), 80% (intensive) and 1.4% (C), respectively.

The public selection scheme managed by the Spanish Association of Iberian Pig Breeders (AECERIBER) includes into its breeding goal the percentages on carcass weight of trimmed hams, shoulders and loins, and the percentage of intramuscular fat (Silió, 2000). The breeding values for these traits are estimated from data recorded on pigs fattened in one of the two quoted free-range systems. While in *montanera* long distances are covered by the pigs for a massive acorn intake, the *campo* system is based on conventional feeding and a lower fenced open-air terrain. These remarkable differences between both systems in feeding and exercise make advisable to study the possible interaction between genotype and environment (G×E). G×E interaction occurs when performances of different genotypes are not equally affected by different environments (Falconer, 1952), and it is a potential source of reduced efficiency in selection programs because of the best genotypes in one environment are not necessary the best in the other one.

Changes in genotype re-ranking due to G×E interaction are well documented in the genetic evaluation of farm animals. Montaldo (2001) reviewed different types of G×E interaction in livestock conditional to environmental differences as feeding level or test location (station or farm). G×E interaction due to fluctuations in feed quality has also been reported by Mulder (2007), and more recently Wallenbeck *et al.* (2009) examined G×E interaction in organic pig production using animals selected for high performance in a conventional production system.

The conventional theory of economic values (Smith *et al.*, 1986) is not applicable for traits related to quality without a linear relationship to the profit function. There are several approaches for weighting the

intramuscular fat (IMF) content as a quality trait of optimum range in the selection index. Desired gains or restricted indices (Brascamp, 1984) are methods that prevent against undesirable changes in the quality trait but result in a substantial reduction in the response for other traits in the aggregate genotype (García Casco, 1993). An alternative is to apply the method proposed by Hovenier *et al.* (1993) for calculating economic weights of optimum traits.

The objectives of the present study were to investigate the presence of G×E interaction in Iberian pigs when genetic evaluations are based on records collected from the two described free-range systems. This interaction and its effects on the selection scheme were analyzed both for productive traits of high economic importance (premium cuts percentages) as for a quality trait (IMF) of optimum range.

## Material and methods

Two datasets from the AECERIBER breeding scheme were used in this study. The first one contained data recorded from 4,348 pigs born in 32 herds and fattened in the M free-range system, and the second one with records of 1,818 pigs tested on the C system and born in 22 herds. Most of animals were assigned to the different Iberian pig varieties (named *Retinto*, *Entrepelado* and *Lampiño*) following the criteria of the breed Herdbook, although the *Lampiño* variety is scarcely represented because it is nowadays in danger of extinction. The remaining ones lack of a clear adscription to any variety standard, because they proceed from ancient admixture of some varieties (*Mixed* group). Table 1 shows the distribution by variety and feeding system of the sires, dams and progenies with records. Only 21 out of the 493 boars sired progenies fattened in both production systems, and their distribution by variety and feeding system is

**Table 2.** Number of observations (N), means and coefficients of variation (CV) of the recorded traits in both systems

Traits	Montanera (acorn feeding)			Campo (no-acorn feeding)		
	N	Mean	CV	N	Mean	CV
Slaughter weight, kg	4,348	160.9	10.1	1,818	165.1	8.7
Age at slaughter, months	4,348	16.3	7.0	1,818	17.0	19.5
Carcass weight, kg	4,348	128.5	11.2	1,818	130.5	9.9
Hams, %	4,336	16.12	7.9	1,736	17.28	8.1
Shoulders, %	4,228	10.92	8.1	1,737	11.20	8.8
Loins, %	3,951	2.33	15.8	1,757	2.96	12.4
Intramuscular fat, %	3,213	9.57	33.3	1,518	9.44	32.1

also summarized in Table 1. But most of the slaughtered pigs (3,879) proceeded from 14 herds which supplied animals to both feeding systems. According to each variety, seven herds provided 2,097 *Retinto* pigs (512 to C and 1,585 to M system), four herds 775 *Entrepelado* pigs (365 C and 410 M) and three herds 415 *Mixed* pigs (227 C and 188 M).

The following traits were recorded at diverse slaughter plants: carcass weight and the percentages on the carcass of trimmed hams, shoulders and loins. Samples of *longissimus dorsi* were obtained from the caudal end of this muscle and stored at  $-20^{\circ}\text{C}$ . The percentage of IMF was measured in these samples by near infrared spectroscopy (De Pedro *et al.*, 1992). Table 2 summarizes the number of observations, means and coefficients of variations (CV) of all the traits in each system. The slaughter age showed a wide extent in the *campo* system (from 11.8 to 26.3 months, CV = 19.5) because some animals had problems to reach the commercial weight. Likewise the CVs of loin percentages were twice than those of hams and shoulders percentages.

Genetic parameters and breeding values (EBV) were estimated using multivariate animal models with the general form  $\mathbf{Y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e}$  and differences in the treatment of G×E interaction:

— PROC 1: Separate analysis for each feeding system, where  $\mathbf{Y}$  is the vector of data (percentages of hams, shoulders, loins and IMF content) registered either in M or in C systems,  $\boldsymbol{\beta}$ ,  $\mathbf{u}$  and  $\mathbf{e}$  are vectors of systematic, additive genetic and residual effects respectively and  $\mathbf{X}$  and  $\mathbf{Z}$  are the incidences matrices. Systematic effects fitted in  $\boldsymbol{\beta}$  were slaughter batch (62 levels in M and 29 levels in C) and Iberian pig variety (four levels: *Retinto*, *Entrepelado*, *Lampião* and *Mixed*).

— PROC 2: Joint analysis of all the records using a model where feeding type was fitted as another systematic effect in  $\boldsymbol{\beta}$ .

— PROC 3: Joint analysis using a model where the performances at each system were treated as different traits. The multitrait model is similar to PROC 1 but now  $\mathbf{Y}$  is a vector of eight elements.

Variety was included as fixed effect in all the models because complementary analysis of within variety variance estimation did not provide evidence of heterocedasticity of additive variances.

Components of (co)variance and breeding values were respectively estimated using the VCE 6.0.2 (Kovac *et al.*, 2008) and PEST 4.1 (Groeneveld *et al.*, 1999) software.

Three selection indexes were built for each feeding system, the first one (IND1) with the EBVs for the three carcass traits weighted by their respective economic values (EVs), without including IMF. Following the classical theory to calculate EVs (Smith *et al.*, 1986), the profit function required to set prices for the three premium cuts percentages which were calculated from averaged carcass and premium cuts prices taking into account the cutting of the carcass, the prices of fresh cuts and the carcass yield.

The other two selection indexes (IND2a and IND2b) incorporate the IMF percentage in order to avoid negative consequences of selection on meat quality (Fernández *et al.*, 2003). Economic values for IMF were calculated for different situations according to the theory developed by Hovenier *et al.* (1993) for optimum traits. Its application requires the calculation of the difference between the prices of carcasses with IMF values within and outside the range defined as optimum. These differences were calculated according to the auction price of fresh premium cuts directed to

**Table 3.** Heritabilities (diagonal) and genetic correlations (above diagonal) for the percentage of premium cuts and intramuscular fat (IMF) estimated from separate analyses (PROC1) for each production system (*Campo* and *Montanera*). Standard errors between brackets

	Hams	Shoulders	Loins	IMF
<i>Campo</i>				
Hams	0.44 (0.05)	0.70 (0.05)	0.51 (0.07)	-0.27 (0.08)
Shoulders		0.47 (0.05)	0.25 (0.08)	-0.24 (0.08)
Loins			0.44 (0.06)	-0.26 (0.09)
IMF				0.69 (0.06)
<i>Montanera</i>				
Hams	0.23 (0.03)	0.63 (0.05)	0.57 (0.07)	-0.22 (0.07)
Shoulders		0.32 (0.03)	0.33 (0.08)	0.12 (0.06)
Loins			0.32 (0.04)	-0.21 (0.09)
IMF				0.30 (0.04)

**Table 4.** Heritabilities (diagonal) and genetic correlations (above diagonal) for the percentage of premium cuts and intramuscular fat (IMF) estimated by a joint analysis of the records from both production systems (PROC2). Standard errors between brackets

	Hams	Shoulders	Loins	IMF
Hams	0.31 (0.05)	0.65 (0.05)	0.56 (0.07)	-0.28 (0.08)
Shoulders		0.35 (0.05)	0.32 (0.08)	-0.09 (0.08)
Loins			0.38 (0.06)	-0.28 (0.09)
IMF				0.42 (0.06)

dry-curing (IMF values inside the range) and the auction price of lean meat focused to pork (IMF values outside the range). Two alternatives and their respective indices were considered: (i) IND2a where the mean of the optimum range ( $\mu_o = 9.4\%$ ) was slightly lower than the IMF population mean, and only a 10% of the animals were outside of the optimum range with a symmetric distribution: optimum ranges of  $\mu_M \pm 5.26$  and  $\mu_C \pm 4.98$  for the M and C systems, respectively; and (ii) IND2b where the mean of the optimum range ( $\mu_o = 9.4\%$ ) was slightly lower than the IMF population mean but a 25% of the population was outside the range, with an asymmetric distribution of a 15% below and a 10% above: optimum ranges of  $\mu_M - 3.135 / \mu_M + 4.256$  and  $\mu_C - 3.102 / \mu_C + 3.924$  for each system.

The Pearson correlations coefficients between EBV and between indexes were calculated for the 21 common boars with offspring fattened in both systems, likewise the values of the Spearman rank correlations as a measure of the sire similarity order according to EBV and indexes. The influence of the different alternatives about IMF on the ranking was also examined through

their Spearman correlations. All correlations were calculated using the PROC CORR of the SAS software (vers. 9.3, SAS Inst. Inc., Cary, NC, USA).

## Results

Heritability and genetic correlation estimates obtained by the three different procedures are showed in Tables 3, 4 and 5. The heritability values were clearly different in both systems (Tables 3 and 5), with values significantly larger in C than in M fattening system.

Moderate or high values of genetic correlations were estimated between all the premium cuts percentages independently of the assumption of G×E interactions. Genetic correlations between the same traits recorded in the two systems ranged from 0.64 between hams to 0.90 between loins (Table 5). All these values are significantly different from zero and from one, excepting the correlation between loin percentages ( $r_G = 0.90 \pm 0.08$ ). The estimated genetic correlations between IMF and hams and loins percentages were

**Table 5.** Heritabilities (diagonal) and genetic correlations (above diagonal) for the percentage of premium cuts and intramuscular fat (IMF) estimated by a joint analysis considering different traits the performances at each production system (PROC3). Standard errors between brackets

		Hams		Shoulders		Loins		IMF	
		<i>Campo</i>	<i>Montanera</i>	<i>Campo</i>	<i>Montanera</i>	<i>Campo</i>	<i>Montanera</i>	<i>Campo</i>	<i>Montanera</i>
Hams	C	0.43 (0.04)	0.64 (0.16)	0.70 (0.04)	0.37 (0.17)	0.50 (0.05)	0.29 (0.15)	-0.26 (0.08)	-0.19 (0.15)
	M		0.24 (0.03)	0.46 (0.14)	0.63 (0.06)	0.67 (0.12)	0.59 (0.06)	-0.52 (0.14)	-0.26 (0.09)
Shoulders	C			0.45 (0.05)	0.67 (0.13)	0.24 (0.08)	0.09 (0.12)	-0.23 (0.9)	-0.01 (0.14)
	M				0.31 (0.04)	0.22 (0.14)	0.34 (0.08)	-0.42 (0.14)	0.10 (0.09)
Loins	C					0.44 (0.05)	0.90 (0.08)	-0.27 (0.09)	-0.14 (0.14)
	M						0.33 (0.04)	-0.43 (0.14)	-0.22 (0.10)
IMF	C							0.66 (0.05)	0.76 (0.11)
	M								0.31 (0.04)

C, *Campo* system. M, *Montanera* system

**Table 6.** Economic values (EV) for percentages of premium cuts (hams, shoulders and loins) and for intramuscular fat (IMF) in *Montanera* and *Campo* systems, expressed in absolute economic value (€) and in relative value respect to hams in each system

	Hams	Shoulders	Loins	IMF	
				IND2a	IND2b
Economic (€)					
<i>Montanera</i>	5.57	2.15	6.79	-0.74	2.37
<i>Campo</i>	2.24	1.10	4.64	-0.04	0.48
Relative					
<i>Montanera</i>	1	0.39	1.22	-0.13	0.43
<i>Campo</i>	1	0.49	2.07	-0.02	0.21

IND2a, IND2b: selection index 2a and 2b, respectively.

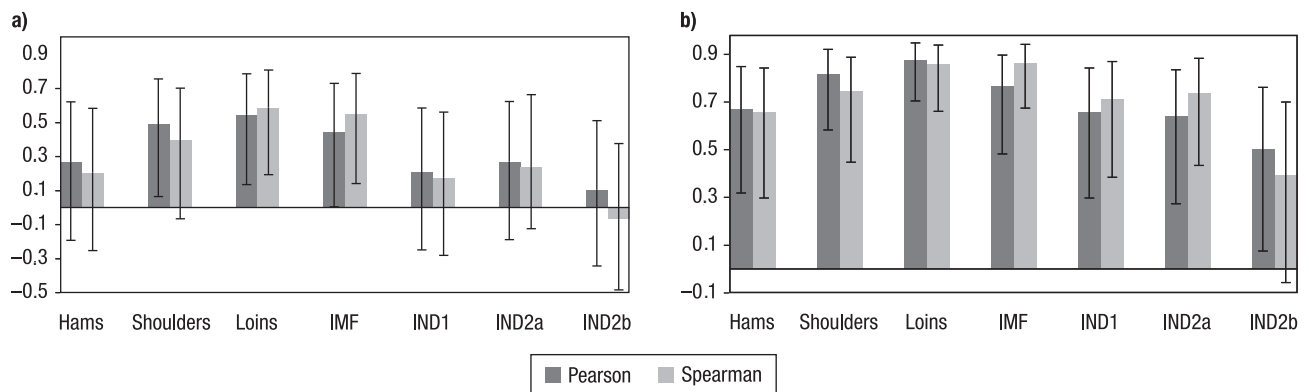
clearly negative in both systems. However, the genetic correlation between IMF and shoulder percentages is dependent on the fattening system: slightly negative in *campo* and null in *montanera*.

The EVs for premium cuts and IMF calculated for both systems under the two optimum ranges defined for IMF (IND2a and IND2b) are presented in Table 6. EVs are expressed both as absolute (€) or relative values respect to hams. According to the higher market price of *montanera* pigs and products, absolute EVs are clearly greater in this system than those of *campo*. In the second option (IND2b), positive EVs for IMF were always obtained although the population mean was slightly greater than the optimal mean due to the asymmetric distribution of the population out of the optimal range.

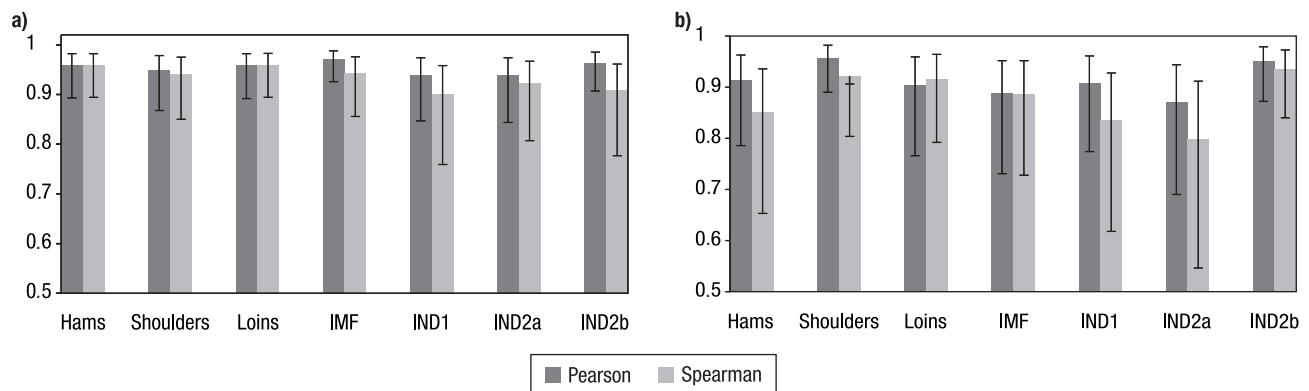
Pearson and Spearman correlation coefficients between *montanera* and *campo* EBVs and indexes of

the 21 boars with offspring fattened in the two systems are represented in Figs. 1a and 1b. When the genetic evaluation was performed using PROC 1, these correlation values were non-significantly different from zero for hams and the three indexes, being intermediate for shoulder, loins and IMF. The Suppl. Fig. S1 [pdf online], representative of the boar's ranking changes according to the used index, outlines the interaction between the feeding system and the performance of boar's progeny. All the correlation values calculated with PROC 3 (Fig. 1b) were significantly different from zero and from one, except the Spearman correlation for IND2b. In this case, although the EBVs in each system of the 21 quoted boars were not so dissimilar than those obtained by PROC 1, important changes of boar ranking may be observed (Suppl. Fig. S1 [pdf online]).

Finally, the possible agreement between the genetic evaluations performed using PROC 1 and 3 was



**Figure 1.** Agreement between production systems: Pearson and Spearman correlation coefficients between estimated breeding values (EBV), selection indexes and ranking positions of the 21 boars with progeny fattened in the two feeding systems calculated for trait records obtained in *montanera* or *campo* systems using a) PROC 1 and b) PROC 3.



**Figure 2.** Agreement between evaluation procedures: Pearson and Spearman correlation coefficients between estimated breeding values (EBV), selection indexes and ranking positions of 21 boars with progeny fattened in the two feeding systems calculated using PROC 1 and PROC 3 for trait records from a) *campo* and b) *montanera* systems.

analyzed. Pearson and Spearman correlation coefficients between EBVs, indexes and rankings calculated by these procedures for each feeding system are presented in Figs. 2a (*campo*) and 2b (*montanera*). All the correlation values were close to 0.90 and significantly different from zero and from one. These high correlations do not avoid changes in ranking of best boars, more evident in the *montanera* system, as Suppl. Fig. S2 [pdf online] illustrates for the case of IND1.

## Discussion

The genetic correlation between records of the same trait obtained in different environments has been considered in animal breeding as the most useful criterion for assessing the relevance of G×E

interaction. The expected value of this correlation would be equal to one in absence of G×E interaction. If this interaction occurs, the trait is partially influenced by different genes in each environment. Genetic correlations lower than 0.80 are expected to be important for reducing the genetic changes due to selection (Robertson, 1959). These interactions may over-predict the response if they are not taken into account in the breeding program (Dominik & Kinghorn, 2008).

Different types of G×E interactions, combining small or large genotype and environmental sources of variation, have been described in farm animals (Montaldo, 2001). In absence of great environmental changes we expected a weak or moderate interaction in our study. The presence of G×E interaction has been mainly indicated by two complementary results. Different heritability values for premium cuts

percentages and IMF content were obtained for each system. Moreover, the estimated genetic correlations between records of the same trait from each system were clearly lower than one, except for the percentage of loins. The range of these values evidences weak or moderate interactions for IMF or hams and shoulders percentages (Table 5), as it was expected because of the possible source is only the distribution of sire families in two open-air environments. Hence, the analysis with models fitting the feeding system as a fixed effect (PROC 2) must be rejected because it assumes an identical expression of the traits in both systems and prevents to evaluate the G×E interaction.

G×E interactions are common in tropical areas and developing countries as results of the adaptation to diverse harsh environments or production systems (Montaldo, 2001). The pigs fattened under the *montanera* system move longer distances than those of the *campo* system. The first ones seek available acorns and pasture in a large land of variable orography, while the movement of the pigs fattened in the *campo* system is restricted to a small open air enclosure with available water and commercial feed. It may explain the observed G×E interactions and the different heritabilities estimated in each system, with lower values in *montanera* for the four analyzed traits. Similar results have been reported for other alternative production systems. Wallenbeck *et al.* (2009) found G×E interaction between organic and conventional pig production environments for growth rate and backfat thickness. Vallée (2007), analyzing growth traits in Creole beef cattle under tropical conditions, obtained lower heritabilities values in animals at pasture than those with intensive feeding regime.

Significant ranking changes of animal breeding values and selection indexes based on performances recorded in different environments (Suppl. Fig. S1 [pdf online]) may be caused by G×E interaction. The present study shows as the selection of the best boars at *campo* system could be wrong for the *montanera* system. The importance of the observed G×E interaction can be also examined according to its possible effect on the selection response in different scenarios. A selection program designed for the *montanera* system although only based on records from *campo* could be advisable because of its lower dependence on the variability of available pasture and acorns harvest. The expected annual response for the trait with the highest genetic correlation between systems (loin percentage,  $r_G = 0.90$ ) is similar to the

obtained from the selection based directly on *montanera* records: 0.087 vs. 0.084. However, the expected response for other trait more affected by interaction (hams percentage,  $r_G = 0.64$ ) is a 14% lower: 0.200 vs. 0.232. The alternative scenario of selection for *campo* based on *montanera* data, results in a 53% of reduction of the expected response for hams percentages and a reduction of 22% for loins percentages.

Weak G×E interactions justify the implementation of a joint evaluation considering as different traits recorded in each production system. With strong interactions, a distinct genetic evaluation for each system would be more suitable (Wallenbeck *et al.*, 2009). In our analysis, the suitability of the analysis by mean of the procedure 3 is supported by the observed weak G×E interaction and the use of the ensemble of available data.

Our study presents some suggestions about the calculation of EVs for the most relevant traits in Iberian pig production. At the present, farmers are not rewarded directly to the carcass or meat quality, and therefore the improvement of these traits does not result in an increase of their economic benefit. The joint development of farms and industries requires the implementation of procedures of carcass and meat quality classification.

The economic values for percentages of premium cuts in the different production systems may be easily corrected according to the evolution of prices of production inputs and products. The economic value for the IMF content is far-off to be solved. The assumed IMF mean value (9.5%) was determined in thousands of Iberian pigs of adequate carcass weight, and then it may be considered close to the desirable optimum. However, the Iberian pig industry lacks of well-founded arguments to set the boundaries of an optimum range for IMF. It represents an obstacle for the application of the method proposed by Hovenier *et al.* (1993). The alternatives proposed in this study, based on the proportion of dry-cured products of inadequate quality assessed by some producers, consider two possible percentages of Iberian pig population out of the hypothetical optimal interval.

Economic values for IMF are not far away zero because the population and optimum means are very close. The asymmetric assumption about the optimum interval (IND2b) brings a positive weighting of IMF until population means of 9.96% and 9.81% for *montanera* and *campo* systems, respectively. The

implementation of a selection program without the IMF content on the selection goal (IND1) must be taken with caution regarding the negative genetic correlations between quality and productive traits found in this study that corroborates previous results (Fernández *et al.*, 2003). The application of the extent of Hovenier *et al.* (1993) method to a situation in which the trait presents several quality classes (Von Rohr *et al.*, 1999) could be a future approach. The great variability of the traits included in the breeding goal in these extensive production systems, allows defining such classes and assigning different prices to each carcass class.

In spite of the notable number of analyzed animals, our study may be limited by the small number of boars with offspring on both systems which restraint the comparison of ranking orders. It could also partly explain the moderate genetic correlation obtained between traits and environments. However, note that genetic connectedness between the two productive environments was supported by other relationships because most of the slaughtered pigs proceeded from only 14 herds, of small or moderate effective size, supplying animals to both feeding systems. The genetic relatedness between the reproducers of each herd would enable the presence of related genotypes in both systems. Our results revealed G×E interaction between *campo* and *montanera* environments for all the productive and quality traits included in the objective of the public scheme of selection of Iberian pigs. A multivariate animal model should be the most appropriate to implement a new breeding program focused on free-range production systems. Changes of ranking position of breeding animals could lead to less efficient selection using other models that do not take into account the G×E interaction. Finally, the inclusion of IMF in the index selection assuming an optimum range for this quality trait could be advisable in order to avoid negative effects of selection for carcass performance. Further efforts are required to get a better understanding of the suitable level of fat infiltration on the Iberian pig premium cuts.

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