

Effect of growth selection on morphology in Pirenaica cattle

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Abstract – Twelve variables were identified to define morphology in 109 calves sired by eight Pirenaica bulls widely used in artificial insemination. The effect of selection for weight at 210 days of age (W_{210}) was detected from the regression coefficient between the 12 variables and the selection index for W_{210} used in the breeding plan. Unbiased estimates of the genetic correlated responses on the morphology were obtained without previously estimating the genetic correlation among traits. In Pirenaica cattle, selection for W_{210} increased slaughter live weight, chest depth and corporal length. The expected changes on height (withers, back and rump), rump width and thoracic perimeter were lower but positive and statistically significant.

indirect response / morphology / growth / weight to 210 days / cattle

Résumé – Effet de la sélection pour la croissance sur la morphologie de la race Pirenaica. Sur 109 veaux, fils de 8 taureaux de race Pirenaica largement utilisés en insémination artificielle, on a obtenu 12 variables qui définissent la structure morphologique des animaux. Les effets de la sélection pour le poids à 210 jours d'âge (W_{210}) sur la morphologie ont été détectés à partir du coefficient de régression entre ces variables et l'indice de sélection pour le caractère W_{210} utilisé dans le plan d'amélioration de la race. Ainsi nous avons obtenu des estimations non biaisées des réponses génétiques corrélées à la morphologie sans avoir besoin d'estimer la corrélation génétique entre caractères. On souligne que, dans la race Pirenaica, la sélection selon W_{210} tend à produire des animaux avec un plus grand poids vif, avec une plus grande profondeur de la poitrine et longueur corporelle, tandis que les changements espérés sur les hauteurs (garrot, dos et croupe), largeur de la croupe et périmètre thoracique sont positifs et de plus petite importance, mais statistiquement significatifs.

réponse indirecte / morphologie / croissance / poids à 210 jours / bovin

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1. INTRODUCTION

The effect of selection in a population can be evaluated by considering the traits included in the selection criteria, but a more general approach requires the detection and prediction of correlated responses in the rest of the traits of interest. However, normally there is a lack of accurate information a priori about the importance or the direction of the genetic change associated with the selective process.

The most important genetic mechanisms that generate indirect responses to selection [10] are pleiotropy and linkage disequilibrium. In quantitative genetics, they are predicted from the genetic correlation among pairs of traits. However, estimation requires large amounts of information. In general it is inaccurate [11, 12, 26] and recording the data can be quite costly. Additional problems arise if the traits are complex, if special environments are needed or when the interval between generations is long.

An alternative is to base the detection of potential indirect responses to selection on empirical approaches. Different generations are compared by specific statistical designs to detect differences attributed to genetic change [18]. Comparisons are usually carried out between a previous control group and one or several selected groups. The approach is especially useful in populations with a short generation interval, such as rabbits or even pigs.

Most of the selection programs in extensive beef cattle populations are focused on a few traits [7], given the difficulty of measuring several traits in a large group of controlled animals. In general, weights at weaning or at seven months of age [6] are included. In this context, changes in the appearance of the breed or carcass and meat quality are difficult to detect in the short and medium terms. However, they can be important and may decrease the morphological and productive identity of the breed, apart from reducing their adaptability and acceptability for the producer.

In this study we evaluated the potential correlated response after growth selection on the morphology of Pirenaica cattle. The simple method described by Altarriba et al. [2] was used since it does not require previous estimates of genetic correlation or specific experimental designs.

2. MATERIALS AND METHODS

The study animals included 109 Pyrenean calves born in different farms in the province of Navarre (Spain), sired by one of eight different bulls (Tab. I). At five months of age they were moved to the Centre for Selection and Animal Reproduction (CEN-SYRA at Movera, Spain) in six groups between 1998 and 2000 (two groups per year). Feeding was ad libitum with a high energy concentrate to promote maximum growth. The animals were divided into 12 groups and the study ended at 398 ± 23 days of age. Twelve zoometric measurements were recorded under the standard conditions described by Aparicio [3] and following EAAP nomenclature [9], detailed in Table II. The measurements were carried out by means of a measuring stick, except for thoracic perimeter (with metric tape) and live weight. Preventive treatments were given against internal and external parasites and a vaccination against infectious rinotraqueitis.

In the statistical analysis, we evaluated the influence of sire effects on the variation in recorded traits. Then we analysed the consequences of selection by weight at 210 days of age (W_{210}) on the analysed traits.

The sire effects on morphology were tested using the linear model:

$$y_{ijk} = \mu + b_a A_{ijk} + L_i + S_j + e_{ijk} \quad (1)$$

where y_{ijk} is the phenotypic value of the corresponding morphological variable of the k th individual son of the j th bull of lot i , b_a is the regression coefficient with the age at

Table I. Selection indexes (\hat{u}_{210}) and accuracy for the weight at 210 days trait of the eight sampled bulls and the average values in the progeny.

Sire	Born	\hat{u}_{210}	Accuracy	Progeny				
				n	\hat{u}_{210}	S.D.	Accuracy	S.D.
Kinto	1995	-28.42	0.975	21	-14.63	3.42	0.537	0.051
Andia	1989	-26.87	0.989	5	-19.01	11.16	0.568	0.071
Golbai	1991	-12.14	0.951	8	-8.38	6.34	0.492	0.026
Ekia	1991	-9.10	0.989	21	-6.92	5.33	0.542	0.055
Izaga	1989	-5.03	0.966	8	-1.45	3.59	0.563	0.055
Sarvil	1992	-6.98	0.792	9	-3.63	4.67	0.388	0.048
Jaberri	1994	3.76	0.975	19	2.19	3.49	0.536	0.061
Kaiku	1995	21.14	0.979	18	9.72	5.42	0.551	0.060
Total				109	-4.06	9.89	0.528	0.070

the moment of the measurement (A_{ijk}), L_i is the lot effect, S_j is the sire effect of the j th bull and e_{ijk} the residual.

The potential genetic response was detected using an independent linear model for each studied trait (l):

$$y_{ijl} = \mu + b_a A_{ijl} + L_i + b(y_{ijl}, \hat{u}_{210}) \hat{u}_{ijl} + e_{ijl} \quad (2)$$

where y_{ijl} is the phenotype of the j th individual belonging to lot i (L), b_a is the regression coefficient with age (A_{ijl}), $b(y_{ijl}, \hat{u}_{210})$ is the slope of the covariance that relates individual phenotype for the morphological trait with breeding value for W_{210} (\hat{u}_{210}) and e_{ijl} is the residual.

The selection index or estimated breeding value (EBV) for W_{210} (\hat{u}_{210}) was calculated by the method described in Varona et al. [24] from 18 788 weight data obtained between 110 and 310 days of age, corresponding to 14 378 animals that allowed to evaluate 24 212 animals of the population. Live weight (W_{210}) was not recorded in the 109 calves at the farm of origin (Tab. I). In turn, the data of 156 maternal sibs of the 109 animals were removed, as justified below.

The $b(y_l, \hat{u}_{210})$ effect of equation (2) helps to evaluate the potential correlated response between the selection criterion

Table II. Parameters* of the 12 studied traits in the sampled progeny.

Trait	N	Average	S.D.	C.V.
Withers height (cm)	109	124.8	4.13	3.3
Back height ¹ (cm)	109	123.8	4.06	3.3
Rump height (cm)	109	130.0	4.48	3.4
Buttocks width ² (cm)	107	51.9	2.81	5.4
Width of shoulder points (cm)	107	43.9	3.59	8.2
Shoulder width ³ (cm)	107	53.1	3.88	7.3
Rump width ⁴ (cm)	107	41.6	2.78	6.7
Corporal length ⁵ (cm)	108	142.2	7.26	5.1
Rump length ⁶ (cm)	108	43.9	3.14	7.1
Thoracic perimeter ⁷ (cm)	107	188.1	7.30	3.9
Chest depth ⁸ (cm)	107	58.2	3.55	6.1
Live weight (kg)	125	582.3	65.42	11.2

*: S.D., standard deviation; C.V., coefficient of variation (%); ¹ in the half of the back; ² among thurls; ³ among elbows; ⁴ inter-iliums; ⁵ scapula-ischium length; ⁶ from ilium to ischium; ⁷ vertically to withers; ⁸ from withers to sternum.

(\hat{u}_{210}) and the corresponding phenotype of any studied trait (l). As deduced analytically by Altarriba et al. [2], the expected value depends on the genetic correlation

between l and $W_{210}(r_u)$ and on the genetic standard deviations of both traits:

$$b(y_l, \hat{u}_{210}) = r_u \sigma(u_l) / \sigma(u_{210}) = b(u_l, u_{210}). \quad (3)$$

Furthermore, the correlation coefficient among y and \hat{u} , has the following causal components:

$$r(y_l, \hat{u}_{210}) = r(u_{210}, \hat{u}_{210}) r_u h_l = r(u_l, u_{210}) \quad (4)$$

where $r(u_{210}, \hat{u}_{210})$ is the accuracy of the selection index (\hat{u}_{210}) and h_l^2 is the heritability coefficient of the l th trait.

Hence, following Falconer and Mackay [10], the correlated response (CR_l) is the following:

$$CR_l = R_{210} b(u_l, u_{210}) = R_{210} b(y_l, \hat{u}_{210}) \quad (5)$$

where R_{210} is the direct response for the W_{210} trait and $b(y_l, \hat{u}_{210})$ is the expected genetic response in the morphological trait l for each unit of direct genetic response in W_{210} (kg). Therefore, we obtain an unbiased estimate of the correlated response of the morphological traits from a sample of the population.

An interesting aspect of this approach is the relationship among the following observable parameters and the causal components:

$$\frac{\sigma(y_l) r(y_l, \hat{u}_{210}) / b(y_l, \hat{u}_{210})}{r(u_{210}, \hat{u}_{210}) \sigma(u_{210})} = \quad (6)$$

which is constant and independent of morphological trait l , since in each case they estimate $\sigma(\hat{u}_{210})$.

Equations (3) and (4) are not affected by components of environmental or residual correlation, unless the \hat{u}_{210} of the studied animals are built with their own phenotype for W_{210} and/or with the phenotypes of individuals that share a common environment. Since the genetic evaluation model [24] did not include maternal effects, the data of the mother's siblings were excluded. The statistical analyses were carried out

with the ANOVA – Linear Models procedure [20].

The models applied were not balanced and the indexes of the individuals selected for W_{210} were not independent (109 sons of eight bulls). Therefore, the levels of significance and power of the statistical analyses could not be calculated directly [17], but had to be simulated. They were obtained by replicating an experimental design that mimicked the original design. For each possible value of heritability, the threshold significance of $b(y, \hat{u})$ was calculated for $P = 0.05$ (a) as the 5th percentile of 30 000 repetitions under the null hypothesis ($r(u) = 0$). Then, the percentage of replicates over this threshold were used as an estimate of the power of the test ($1 - b$) [21] for each (r_u and h_l^2) combination.

3. RESULTS AND DISCUSSION

The zoometric values of the study animals (Tab. II) correspond to improved Pirenaica animals, according to Mendizabal et al. [15]. The values were lower than for mature cows but higher than the functional genetic evaluations of 439 young bulls of the same breed carried out in the CEN-SYRA at Movera (24 test series) between 1975 and 1990 at 12 months of age [14]. Live weight was a 38% higher and thoracic perimeter and withers height were 8% and 5%, respectively. Corporal length, rump width and chest depth were similar to previous reports. However, it was difficult to evaluate the differences since the average ages between both groups of animals differed by more than one month, and the sampling strategy and diet were different. Among the other effects, there may be a direct effect of selection for W_{210} , because the selection index used by the National Confederation of Associations of Pirenaica Breeders (CONASPI) is defined for this trait [1].

The variation coefficient of the studied traits (Tab. II) was below 10%, except for live weight (11.2%). The coefficient for the

Table III. Statistical significances obtained from the models (1) and (2), and regression coefficients and correlation obtained from model (2).

Trait (y)	P-sire ¹	P- $b(y, \hat{u}_{210})$ ²	$b(y, \hat{u}_{210})$ ³ (S.E.)	$r(y, \hat{u}_{210})$ ⁴
Withers height (cm)	0.020	0.001	0.140 (0.040)	0.335
Back height (cm)	0.030	0.002	0.128 (0.040)	0.311
Rump height (cm)	0.006	0.001	0.155 (0.044)	0.338
Buttocks width (cm)	0.018	0.156	0.037 (0.026)	0.147
Width of shoulder points (cm)	0.113	0.167	0.047 (0.034)	0.143
Shoulder width (cm)	0.092	0.401	0.031 (0.036)	0.087
Rump width (cm)	0.029	0.030	0.054 (0.024)	0.223
Corporal length (cm)	0.015	0.001	0.209 (0.061)	0.334
Rump length (cm)	0.463	0.335	0.031 (0.032)	0.099
Thoracic perimeter (cm)	0.075	0.042	0.144 (0.070)	0.209
Chest depth (cm)	0.019	0.001	0.112 (0.031)	0.353
Live weight (kg)	0.001	0.001	1.919 (0.583)	0.299

¹ Sire effect signification in model (1).

² Signification of $b(y, \hat{u}_{210})$ in model (2).

³ Regression coefficient among y and \hat{u}_{210} estimated in model (2).

⁴ Correlation coefficient among y and \hat{u}_{210} estimated as $r^2(y, \hat{u}_{210}) = b(y, \hat{u}_{210}) b(\hat{u}_{210}, y)$ by means the model (2) and their reciprocal (exchanging independent and dependent variables).

three heights and the thoracic perimeter were much lower (< 4%).

The results of the sire model (1) are shown in Table III. There was a significant variance between sires for most of the variables ($P < 0.05$), except for the width of the shoulder points ($P < 0.113$) and rump length ($P < 0.463$). Shoulder width and thoracic perimeter were intermediate ($P < 0.10$). These results suggest non zero heritability for the three heights, the buttocks and rump widths, corporal length, depth of the chest and live weight, with the limitation of the sire model at small population sizes.

Our findings agreed with the estimated heritabilities determined for these traits in previous studies. Height traits have high heritabilities, such as 0.58 for back height in Brahman [13], 0.68 for withers height in Guzera cows [25] and 0.54 to 0.87 for rump height in different populations, with an average value of 0.68 [4, 5, 8, 13, 23, 25]. With respect to the corporal length, the estimated heritabilities are smaller in Brahman and Hereford [13, 22, 25] and the same as hip width [13].

In principle, there may be correlated responses for these variables since the genetic variability is a causal component, as shown in equation (3).

As expected, $b(y, \hat{u}_{210})$ was significant ($P < 0.05$) in these cases, except for buttocks width (Tab. III). So, we can assume a genetic correlation between these morphological traits and weight at 210 days (W_{210}). For width of shoulder points, shoulder width and rump length, where genetic variability was not detected by model (1), the estimated regression coefficients were not significant ($P > 0.05$). On the contrary, the genetic variability of thoracic perimeter estimated with the sire effect was almost significant ($P = 0.075$). In order to interpret the significant indirect response ($P = 0.042$) for this trait, the hypothesis of genetic variability and genetic correlation among traits should be in agreement with model (3). Magnabosco et al. [13] and Winkler et al. [25] also obtained an intermediate heritability for thoracic perimeter and a high and positive correlation of this trait with mature weight.

According to our results, effective selection for W_{210} changes animal appearance (Eq. (5)), as Mercadante et al. [16] found with Nelore (consistently high responses in height to selection for body weight). In our case, the unbiased quantification of expected indirect responses to selection according to W_{210} is given by $b(y, \hat{u}_{210})$ (Tab. III). These values constitute the expected average change (in cm or kg) in morphological traits per kg of genetic change in W_{210} . Obviously, for a more precise prediction of potential indirect response, the expected values and confidence intervals defined by the standard errors (SE) of the corresponding regression coefficients should be considered. In any case, the detected changes were positive and in the same direction as the selection criterion (\hat{u}_{210}).

Other studies have also found positive genetic correlations (between 0.4 and 0.9) among weight and morphological traits [13, 22, 25]. The highest estimate (0.96) corresponds to the correlation between adult weight and corporal length [25]. The lowest is between weaning weight and rump height, being 0.65 in 12 experimental populations [5] and 0.75 in different crosses [23]. Recently, Phocas and Laloë [19] found positive genetic correlations (0.22–0.41) between weaning weight and muscle score in four French beef cattle breeds.

In Table IV, the expected responses are shown by unit W_{210} (kg) with regards to the average values (Tab. II) of the morphometric variables (CR/m). This makes it possible to analyse the changes in relative terms. Indeed, live weight has more relative changes than the other variables. Thus, the changes expected in live weight after selection for W_{210} are, in relative terms, the most important. The change in chest depth is also relatively important but half that of live weight. The third most important are width of the rump and corporal length. The height variables (width of rump and corporal length) and thoracic perimeter show lower but significant changes.

Table IV. Expected correlated responses in relation to the average phenotype value of each trait (CR/m) and also with respect to the thoracic perimeter trait (CRr), with the estimate of $\sigma(\hat{u}_{210})$ according to the equation (6).

Trait (y)	CR/m (10^{-5})	CRr	$\sigma(y_l)r(y_l, \hat{u}_{210})/$ $b(y_l, \hat{u}_{210})$
Withers height (cm)	112	145	9.9
Back height (cm)	103	134	9.9
Rump height (cm)	119	155	9.8
Rump width (cm)	130	169	11.5
Corporal length (cm)	147	191	11.6
Thoracic perimeter (cm)	77	100	10.6
Chest depth (cm)	192	249	11.2
Live weight (kg)	328	426	10.2
Total			10.5

For more precise comparisons, the responses of each variable can be referred to thoracic perimeter, which changed the least (column CRr, Tab. IV). The average difference in slaughter live weight (the selection objective outlined in the breeding plan for Pirenaica [1]), is above 400%. The variable chest depth also changed by 249%. The relative changes were lower for other variables, the highest being corporal length (191%). These results, surely, can be confirmed in other breeds used on both sides of the Pyrenees mountain range since they share the same latitude, production system and commercial opportunities.

Equation (6) can be used to verify the coherence of the results. The combination of components observed in each variable l ($\sigma(y_l)r(y_l, \hat{u}_{210})/b(y_l, \hat{u}_{210})$) should be constant and similar to the combination of causal parameters of the selected trait W_{210}

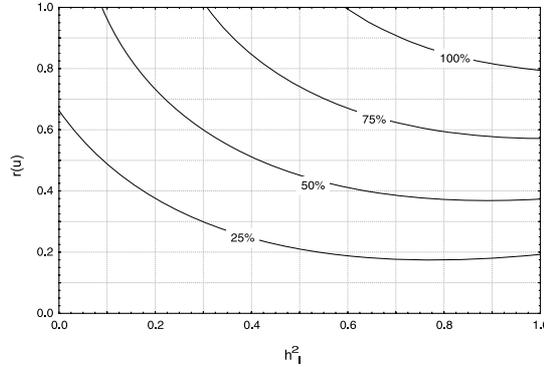


Figure 1. Contour plot for power (%) of $b(y_b, \hat{u}_{210})$ statistic, with type I error of 0.05, obtained by simulation for different values of genetic correlation ($r(u)$) and heritability (h_1^2) of recorded trait with the data set structure.

($r(u_{210}, \hat{u}_{210})\sigma(u_{210})$). Calculated values for each variable are shown in Table IV (average 10.5, range 9.8 to 11.6 kg). Nevertheless, these values are higher than the product of the causal components (9.6 kg), since the average accuracy ($r(u_{210}, \hat{u}_{210})$) of the 109 selection indexes for W_{210} is 0.528 (Tab. I) and the genetic variance ($\sigma^2(u_{210})$) used in the genetic evaluation was 324 kg², as published for this trait and population [24]. However, as mentioned in the Materials and Methods section, the combination of causal components is an estimate of the standard deviation of the selection indexes ($\sigma(\hat{u}_{210})$), being 10.1 kg in the sample of the 109 calves, which is quite close to the average value shown in Table IV (10.5). Random processes may explain variations in the different traits.

Figure 1 shows the results of the power analysis of the statistical tests used to detect a significant regression coefficient as a predictor of the genetic correlation. This parameter was calculated using the simulation outline from model (2) to mimic the structure of the experimental data. Specifically it included the number of bulls, descendants per bull, accuracy of the selection indexes, age of the animals, structures of the lots and components used in the genetic evaluation of W_{210} [24].

We detected the correlated genetic response with a power of 50% (the probability of identifying one effect as significant

if the effect exists) with genetic correlations above 0.50 and the heritability of the analysed trait above 0.4. When heritability is 0.2, the genetic correlation required to reach a minimum power of 50% is 0.7. In practical terms, we detected the relationships of W_{210} with the morphological traits with highest heritabilities, which produce substantial genetic correlated responses.

The power of the experimental design mainly depends on the accuracy of the selection indexes and the number of sampled animals. In this study it was difficult to obtain indices with higher accuracy because the phenotype of the animal was not used. Correlated responses are estimated in traits recorded to relatively early ages, without the possibility of assessed progeny. We opted for a nested sampling with a good accuracy for selection criterion of the sires, but sampling can be carried out with other structures or even at random. The goal was to obtain selection indexes with enough accuracy to reduce the variance of the estimate.

It may be more realistic to carry out extensive samplings. The results of the power analysis are shown in Figure 2 under the same conditions as the previous case but with twice the number of animals. The power of analysis increases from 0.50 to 0.75 in the milestone used as the reference. Therefore, the power is increased by 50% when the volume of information doubles.

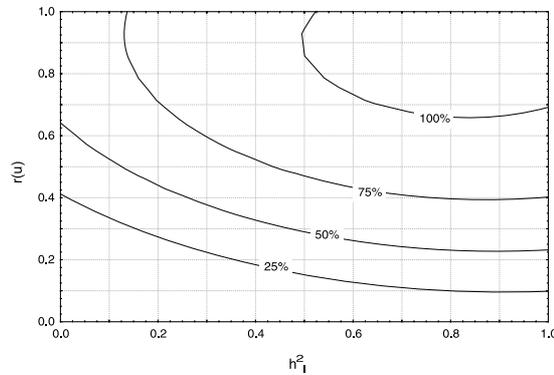


Figure 2. Contour plot for power (%) of $b(y_b, \hat{u}_{210})$ statistic, with type I error of 0.05, obtained by simulation for different values of genetic correlation ($r(u)$) and heritability (h_1^2) of recorded trait with the data set structure and double population sample size (218 males sired by 16 bulls).

The estimation of the genetic correlated response from the regression between a selection criterion and the phenotype of other traits (as done in this work), does not restrict the construction of the index of selection. Therefore, univariate as much as multivariate indexes can be used. In turn, the selection does not have to be achieved, since the observed responses are not required. It is not necessary that the potential harmful effects of the selection in the population have taken place.

Finally, with our approach the uncertainty of the estimate of the correlated response was lower than the prediction from the correlation and genetic variances [10], because multiparametric estimations imply larger sampling errors than the estimation of only one parameter.

4. CONCLUSIONS

Selection for weight at 210 days of age (W_{210}) in Pirenaica cattle affects morphological traits. The animals had higher live weight, chest depth and corporal length. The expected changes in height (withers, back and rump heights), rump width and thoracic perimeter were positive and statistically significant but small.

The procedure used was useful to predict the effect of breeding programs using a reduced data set on traits that are sensitive

to correlated responses to selection. This eliminates the requirement for estimates of genetic parameters (variances and genetic correlations) or responses to selection. In practice, it allows to detect the most important indirect consequences of selection without the necessity that these be carried out.

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