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Genetic (co)variance and plasticity of behavioural traits in Lidia bovine breed

Alberto Menéndez-Buxadera, Oscar Cortés and Javier Cañón

Departamento de Producción Animal, University Complutense of Madrid, Madrid, Spain

ABSTRACT

Scores for four behavioural traits – aggressiveness, ferocity, face hiding and nobility – recorded between 1984 and 2010 in Lidia bovine breed (the property of a single breeder in Spain), were analysed using the multi-trait and reaction norm models. The multi-trait analysis results revealed heritability values of between 0.23 for nobility and 0.33 for ferocity. Principal components analysis of the genetic correlation matrix identified two factors that explained 91.6% of the total variance. Reaction norm analysis revealed genetic correlation values across sexes and time to be $<|1|$; this indicates the existence of an interaction *genotype x environment*. Plasticity, defined as the difference between breeding values over time periods and across the sexes, can be a useful tool for taking into account the influence of the environment on the breeding goal. This allows this interaction to be managed within the framework of a selection programme. With the exception of aggressiveness, which showed significant plasticity, the behaviour of the traits was robust over time and across the sexes. This methodology therefore allows the detection of groups of animals with more robust or plastic responses, particularly with respect to aggressiveness. The use of plasticity as a selection criterion might be beneficial in Lidia bovine breed breeding programmes.

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Aggressiveness; multi-trait and reaction norm models; robustness

Introduction

Shows involving cattle evolved since thirteenth century into social events called tauromachies, a term that makes reference of a cultural and subjective representation of all types of games involving cattle bullfighting, which has been included in the inventory of intangible cultural heritage in several countries such as Spain or Perú. The Lidia breed refers to a racial grouping of bovines linked to the Mediterranean ecosystem and characterise by a low genetic and ecological exchangeability (Crandall et al. 2000; Cañón et al. 2008).

Very little is known about the genetics underpinning aggressive behaviour in animals. In dogs it has recently been proposed that at least some types of behaviour, including aggressive behaviour, are controlled by small numbers of readily mappable genes (Spady & Ostrander 2008). Little is known, however, about the genes governing aggressiveness in cattle. Most interest has focussed on reducing aggressiveness (Phocas et al. 2006; Beckman et al. 2007; Turner &

Lawrence 2007) in order to improve the management, productivity and well-being of domestic cattle (Phillips & Rind 2002; Boissy et al. 2005). However, some breeds are selected for their aggressiveness, such as the Valdostana and Hérens breeds in Italy (Sartori & Mantovani 2010, 2012) and Switzerland (Plusquellec & Bouissou 2001), respectively, and the Lidia (or fighting bull) breed in Spain (Silva et al. 2002). In the latter country, this breed is fragmented into lineages known as *encastes* which reflect different levels of aggressiveness in the ring (Boletín Oficial del Estado 2001); the breed therefore shows a strongly subdivided structure (Cañón et al. 2007; Cortes et al. 2011). Lidia bovine breed are also raised in France and Portugal, and in around fourteen Central and South American countries (<http://www.toroslidia.com/>).

The genealogical and behavioural traits of Lidia bovine breed have been recorded over many generations (for at least a century) with most breeders focussing on a very similar set of characteristics (Almenara-Barrios & Garcia 2011) referring to

CONTACT Dr. Javier Cañón  jcanon@vet.ucm.es  Department of Animal Production, Veterinary Faculty, Universidad Complutense de Madrid, 28040 Madrid, Spain

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aggressiveness and fighting capacity. Experienced technicians are charged with assessing these traits on categorical scales.

Significant additive genetic variability is suggested to underlie the behavioural traits recorded in Lidia bovine breed in Spain (Silva et al. 2006; Pelayo et al. 2015) and Mexico (Domínguez-Viveros 2007; Domínguez-Viveros et al. 2014). However, in these publications it was assumed that the results recorded in the *tienta* and the *plaza* are expressions of the same underlying genetics. Whether this is the case can be determined by examining the genetic correlations between traits recorded under both sets of conditions. Alternatively, the genetic capacity of individual animals to produce different phenotypes in response to different environmental conditions can be investigated (Via et al. 1995). This biological property, known as plasticity, an important concept in ecology and evolutionary biology, has only recently begun to appear in the animal breeding literature (de Jong & Bijma 2002). Determining phenotypic plasticity offers the opportunity to take into account the effects of the environment on the eventual breeding goal (de Jong & Bijma 2002).

The aims of the present work were to estimate the genetic parameters for four behavioural traits (aggressiveness, ferocity, face hiding and nobility) recorded in the *tienta* (cows) and *plaza* (bulls) over nearly three decades, and to determine the plasticity associated with these traits.

Materials and methods

A total of 15,580 records covering the cattle herds of a unique breeder were available for analysis. Behavioural data were collected by the breeder using legal public shows or general managements in the farm, the authors never were present when the data were recorded, so they had no intervention in the production of any stress, bad fare or disturbance over the animal. Male behaviour was scored at four years of age during an actual commercial bullfight held in a *plaza* (bull ring); cows were scored at 2 years of age in a *tienta*, i.e. a small ring on the breeding estate that simulates the environment and conditions of the *plaza*. All animals were scored only once since they learn from their experience of facing a man in the ring, making any subsequent testing too dangerous. Records were registered between 1956 and 2010. Not all traits were monitored over this entire period; the study was therefore restricted to results obtained between 1984 and 2010 (involving 14,223 animals) (Table 1). All the available pedigree information for all

Table 1. Number of animals with records, number of bulls and cows and score for each trait.

Trait	Animals	Bulls	Cows	Score
Aggressiveness	14.223	330	3.466	10
Ferocity	9.156	258	2.438	10
Face hiding	8.795	256	2.376	4
Nobility	8.802	256	2.387	4

For all traits except for *face hiding*, higher value are more desirable.

these animals was included in the analysis; this involved a total of 15,215 animals. The examined traits were *aggressiveness* i.e. fighting ability and wildness (the more the animal faces the bullfighter than tries to escape), *ferocity* i.e. the animal's strength and perception of danger on the part of the observer (the animal's ability to attack strongly employing the whole body), *face hiding* i.e. turning the head towards the chest during the run up to the cape, and *nobility* i.e. a noble animal shows no unexpected behaviour that might make the task of the bullfighter more dangerous or onerous. Scores were recorded on either a 1–10 or 1–4 point scale (Table 1). All observations were made by the same observer over the entire period. In this peculiar breed, there is no genetic connection between breeders, this genetic isolation between lineages and between herds within lineages has been previously described by Cañón et al. (2008), so it is not possible to use phenotypic information coming from different breeders to perform genetic analysis. On the other hand, the material used belongs to the Domecq lineage, which at present represents around 50% of the total of animals participating in the different popular events.

The multi-trait model (MTM) and reaction norm (RN) model were used to examine the data recorded, in both cases using the ASREML 3 software developed by Gilmour et al. (2009). The MTM model makes use of the following equation:

$$y_{ijkl} = Xb + Z_1 a_i + e_{ijkl}$$

where y_{ijkl} is the corresponding vector of j traits analysed at the same time; b is a vector of fixed effects including l years of recording (1984–2010, 27 levels), k sexes (male and female), and the degree of inbreeding as a covariate; a is a random vector including the additive genetic effect of an animal i ; e_{ijkl} is the random residual effect between all traits; and X and Z_1 are incidence matrices connecting the fixed and random effects with the data vector. This MTM analysis assumed no variation in the genetic (co)variance components over time and with respect to sex.

The RN model, which is a random regression model, assumes that variation exists within the (co)variance components over the period l years and for k sexes

(male and female). It makes use of the following equation:

$$y_{ijkl} = Xb + \sum_{r=0}^3 \Phi_r b_{lr} + \left[\sum_{r=0}^1 \Phi_r \lambda_{kr} a_{lr} \right]_k + e_{ijkl}$$

The effects taken into account by this model are the same as in the MTM model. Vector b includes the effects of sex and the level of inbreeding (b_{lr}) as a covariate. The effect of l years is modelled with a fixed covariable via a Legendre polynomial (Φ_r) of order $r=3$. Genetic effects (a_i) are estimated using the random regression coefficient matrix (λ_k) over l years, using a Legendre polynomial of order 1, which replaces the Z_1 in MTM model and is assumed to be correlated with sex. The random residual effect e_{ijkl} was considered heterogeneous but no correlations were assumed, and the years l were grouped in q classes ($q_1=1984-1991$; $q_2=1992-1996$; $q_3=1997-2001$; $q_4=2002-2006$ and $q_5=2007-2010$). The MTM model assumes that

$$E(y) = Xb \text{ and } \text{var}(y) = Z_1(G \otimes A)Z_1' + R$$

and the RN model that

$$E(y) = Xb \text{ and } \text{var}(y) = \Phi_1(\lambda_k \otimes A)\Phi_1' + \left(R = \begin{bmatrix} \text{eq}_1 \\ \text{eq}_2 \\ \text{eq}_3 \\ \text{eq}_4 \\ \text{eq}_5 \end{bmatrix} \times I_{q_i} \right)$$

In the MTM model, G and R are 4×4 matrices. The genetic parameters of heritabilities (h^2) and genetic correlations (r) are estimated using a linear function of the corresponding components following the procedure of Gilmour et al. (2009). The breeding value of each animal and trait (BV_{ij}) is obtained via the use of the MTM model.

The expected values of the terms in the RN analysis are the same as in the MTM model, but the estimation of the (co)variance components over time and for sex require additional procedures. The random regression coefficients matrix (λ_k) consists of four submatrices represented by:

$$\lambda_k = \begin{bmatrix} \lambda_c = \begin{pmatrix} \sigma_{ic}^2 & \sigma_{is,c} \\ \sigma_{si,c} & \sigma_{sc}^2 \end{pmatrix} & \lambda_{cb} = \begin{pmatrix} \sigma_{ic,ib} & \sigma_{ic,sb} \\ \sigma_{sc,ib} & \sigma_{sc,sb} \end{pmatrix} \\ \lambda_{bc} = \begin{pmatrix} \sigma_{ib,ic} & \sigma_{ib,sc} \\ \sigma_{bs,ic} & \sigma_{bs,sc} \end{pmatrix} & \lambda_b = \begin{pmatrix} \sigma_{ib}^2 & \sigma_{is,b} \\ \sigma_{si,b} & \sigma_{sb}^2 \end{pmatrix} \end{bmatrix}$$

In this structure the submatrices on the diagonal (λ_c and λ_b) contain the variances of the intercept ($\sigma_{i,c}^2$), the slope ($\sigma_{s,c}^2$) and their covariance ($\sigma_{is,c}^2$) for bulls (b) and cows (c), respectively. The other sub matrices ($\lambda_{cb} = \lambda_{bc}$) correspond to the covariance between sexes for the previous elements. The genetic variance

for the trait i measured in cows (c) in the year X is then estimated using the following equation (de Jong 1995):

$$\sigma_{cx}^2 = \Phi_X \lambda_c \Phi_X'$$

while for bulls (b) the following is used:

$$\sigma_{bx}^2 = \Phi_X \lambda_b \Phi_X'$$

The genetic covariance for cows (c) and bulls (b) between X and Y years is estimated by:

$$\sigma_{cxy} = \Phi_X \lambda_c \Phi_Y'$$

$$\sigma_{bxy} = \Phi_X \lambda_b \Phi_Y'$$

The covariance between cows (c) and bulls (b) for years X and Y is:

$$\sigma_{cbxy} = \Phi_X \lambda_{bc} \Phi_Y'$$

Heritabilities and genetic correlations are therefore estimated over the studied period of time for each sex, taking into account the corresponding residual variance in the q time periods. Thus, heritability for cows in the year X is provided by:

$$h_{cx}^2 = \frac{\Phi_X \lambda_c \Phi_X'}{\sigma_{px}^2 = (\Phi_X \lambda_c \Phi_X' + \Phi_X \lambda_b \Phi_X' + \text{eq}_x)}$$

The genetic correlations (r) for the same sex or different sexes between years are estimated by:

$$\text{for cows in different years } r_{c,xy} = \frac{\Phi_X \lambda_c \Phi_Y'}{\sqrt{\Phi_X \lambda_c \Phi_X' \times \Phi_Y \lambda_c \Phi_Y'}}$$

$$\text{for bulls in different years } r_{b,xy} = \frac{\Phi_X \lambda_b \Phi_Y'}{\sqrt{\Phi_X \lambda_b \Phi_X' \times \Phi_Y \lambda_b \Phi_Y'}}$$

for cows and bulls in different years

$$r_{bc,xy} = \frac{\Phi_X \lambda_{bc} \Phi_Y'}{\sqrt{\Phi_X \lambda_c \Phi_X' \times \Phi_Y \lambda_b \Phi_Y'}}$$

for cows and bulls in the same year

$$r_{bc,xx} = \frac{\Phi_X \lambda_{bc} \Phi_X'}{\sqrt{\Phi_X \lambda_c \Phi_X' \times \Phi_X \lambda_b \Phi_X'}}$$

Finally, the results of the RN model are used to estimate the breeding value of the cows (BV_{ijc}) via:

$$BV_{ijc} = [L_i \quad L_s] \begin{bmatrix} a_{ic} \\ a_{sc} \end{bmatrix}$$

and of the bulls, BV_{ijb} , via:

$$BV_{ijb} = [L_i \quad L_s] \begin{bmatrix} a_{ib} \\ a_{sb} \end{bmatrix}$$

where L_i and L_s represent the terms of the Legendre coefficients for the intercept and the slope, respectively, for a polynomial of order 1. The terms a_{ic} and a_{sc} , and the a_{ib} and a_{sb} are the solutions derived from the RN model for each trait, and include the corresponding elements of the genetic function of the intercept (i) and the slope (s) for cows (c) and bulls (b) respectively for each animal. The breeding value of plasticity is estimated via the difference between the breeding values in *tienta* and in *plaza*.

$$\text{Plasticity} = [L_i \ L_s]_X \begin{bmatrix} a_{ic} \\ a_{sc} \end{bmatrix} - [L_i \ L_s]_X \begin{bmatrix} a_{ib} \\ a_{sb} \end{bmatrix}$$

For a given year X , the values of L_i and L_s will be the same, thus the plasticity value is obtained from the difference between the genetic function coefficients of each animal. Finally the breeding value of plasticity for each trait was regressed to the year of birth in order to represent the evolution of breeding values over time.

Results

Table 2 shows the genetic parameter estimates derived using the MTM model. The heritabilities of all the traits can be considered medium. In an attempt to better interpret the meaning of the genetic correlations, PCA (Principal Component Analysis) was performed using the breeding values for the four behavioural traits (Table 3). The first two axes explained 91.6% of the total variance. The eigenvector coefficients indicate the first axis to identify animals with the greatest genetic potential for aggressiveness

Table 2. Heritabilities (diagonal), genetic (above the diagonal) and phenotypic (below diagonal) correlations for the four behavioural traits studied^a.

Trait	Aggressiveness	Nobility	Ferocity	Face hiding
Aggressiveness	0.308	0.057	0.495	0.182
Nobility	0.060	0.234	-0.492	0.148
Ferocity	0.295	-0.389	0.335	0.189
Face hiding	0.200	0.119	0.147	0.300

^aHeritability standard errors ranged from 0.021 to 0.026, genetic and phenotypic correlation standard errors from 0.051 to 0.074 and 0.012 to 0.014, respectively.

Table 3. Principal component Eigenvectors and Eigenvalues for the genetic correlation matrix.

Trait	PC ₁	PC ₂	PC ₃	PC ₄
Aggressiveness	0.740	0.660	0.079	0.104
Nobility	-0.053	0.233	-0.209	-0.948
Ferocity	0.667	-0.715	0.003	-0.213
Face hiding	0.073	0.002	-0.975	0.211
Eigenvalue	1.316	0.461	0.128	0.036
Genetic variance, %	67.8	23.76	6.57	1.88
Accumulated variance, %		91.56	98.12	100

and ferocity; the second axis identifies animals with normal aggressiveness and lower ferocity (Table 3). The breeding values were weighted by the coefficients of the first two axes and represented for each sex in the PCA biplot (Figure 1); Figure 1(a,b) show a very similar distribution pattern for both sexes. Aggressiveness, face hiding and nobility fall into the upper right quadrant. The vectors for the first two of these traits correlated strongly and exert the greatest influence. In contrast, nobility and ferocity appear close together (almost in the same position on the graph). In other words, the greater the expression of aggressiveness and the lesser the expression of face hiding (lower values are more desirable) together dominate the (co)variance pattern of behaviour.

In the above analysis, two main restrictions were assumed: that the genetic parameters of performance did not vary over the quarter century for which data were analysed, and that there was no interaction *genotype* × *sex* (i.e. where sex is represented by recording in the *plaza* or *tienta*). RN analysis showed that the genetics underlying the traits recorded in the *tienta* (cows) can be significantly different to those underlying the traits recorded in the *plaza* (bulls) (Table 4). Most of the genetic correlation values for the same trait between sexes over time were <|1| and, for most traits, point estimates of heritabilities were higher when behavioural traits were recorded in the *tienta* (cows). In fact, 32 of the 52 genetic correlations returned a value of <0.80 and only those for nobility were >0.90. These results highlight the influence of the interaction *genotype* × *environment* (Table 4).

Usually, the effect of the interaction *genotype* × *environment* is accounted for by ranking animals in the different environments studied. However, in the present work plasticity was estimated, i.e. the difference between the breeding values recorded in the *tienta* and *plaza* for each trait, using the more accurate RN model. The results for each trait were represented over the animals' years of birth (Figure 2). These showed the genetic merit for the plasticity of ferocity, nobility and face hiding to have remained virtually constant for nearly 50 years, and indicate that the results recorded in the *tienta* were as useful a guide as those recorded in the *plaza*. However, for aggressiveness, the pattern across years differed.

Figure 2 shows the global trends in traits over time, but does not identify the cause of the pattern. According to Figure 3 and the results of the RN analysis, the robustness of ferocity, nobility and face hiding are the consequence of a counterbalance between the reaction capacity of the animals to environmental change (slope) and the evolution of the average

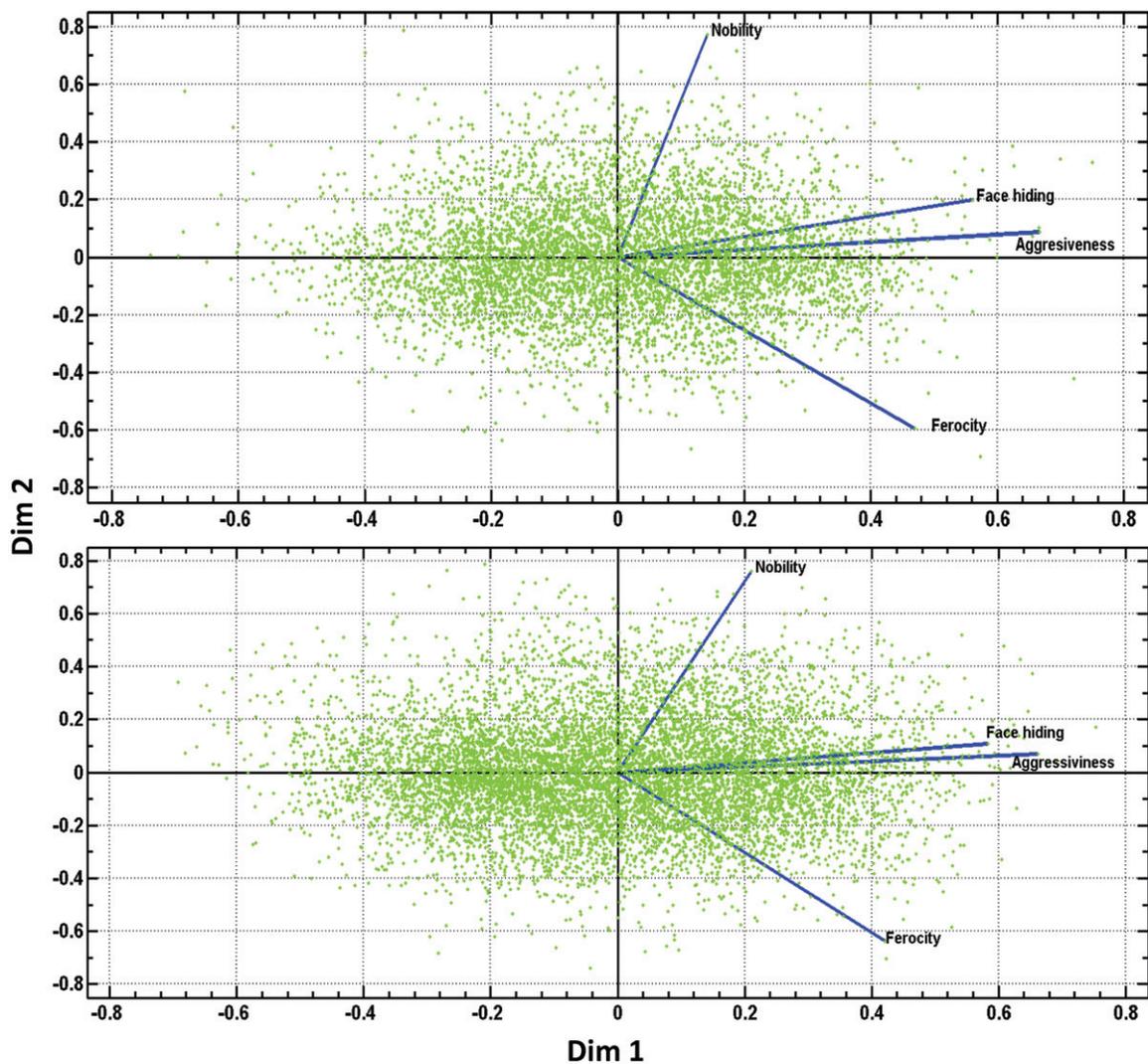


Figure 1. PCA biplot of the cows' (upper, $n = 9196$) and bulls' (lower, $n = 6019$) breeding values for the four behavioural traits.

Table 4. Heritabilities in cows (h^2_C) and bulls (h^2_B), and the genetic correlations between the sexes (r) for the behavioural traits, between 1984 and 2010.

Year	Aggressiveness			Ferocity			Nobility			Face hiding		
	h^2_C	h^2_B	r	h^2_C	h^2_B	r	h^2_C	h^2_B	r	h^2_C	h^2_B	r
1984–1986	0.25	0.12	.79	0.27	0.31	.82	0.47	0.10	.99	0.32	0.24	.46
1987–1988	0.27	0.13	.77	0.27	0.30	.81	0.45	0.09	.98	0.29	0.24	.45
1989–1990	0.27	0.13	.76	0.26	0.29	.81	0.42	0.08	.97	0.27	0.24	.45
1991–1992	0.26	0.13	.74	0.26	0.27	.81	0.38	0.08	.96	0.25	0.24	.46
1993–1994	0.27	0.15	.72	0.25	0.26	.80	0.34	0.08	.93	0.21	0.22	.49
1995–1996	0.26	0.15	.71	0.24	0.24	.80	0.29	0.08	.89	0.20	0.23	.54
1997–1998	0.26	0.16	.69	0.21	0.21	.79	0.26	0.09	.86	0.20	0.23	.58
1999–2000	0.25	0.17	.68	0.20	0.19	.79	0.23	0.11	.86	0.20	0.24	.63
2001–2002	0.25	0.18	.67	0.19	0.17	.78	0.21	0.12	.88	0.22	0.25	.66
2003–2004	0.26	0.21	.66	0.22	0.20	.77	0.18	0.12	.91	0.21	0.23	.69
2005–2006	0.25	0.22	.66	0.21	0.19	.76	0.19	0.14	.93	0.22	0.24	.71
2007–2008	0.27	0.26	.66	0.20	0.18	.76	0.22	0.15	.94	0.23	0.24	.72
2009–2010	0.26	0.28	.66	0.19	0.18	.76	0.25	0.17	.95	0.25	0.25	.73
SE	± 0.06	± 0.06	± 0.09	± 0.07	± 0.06	± 0.10	± 0.08	± 0.08	± 0.12	± 0.07	± 0.08	± 0.13

(SE: the average standard error of the estimates).

genetic level for those traits (intercept). With respect to aggressiveness, however, the results are explained by the genetic change in the slope but no change in the intercept.

Table 5 shows results of the genetic (co)variance matrix derived from the RN model. The variance of the intercept, expressed with respect to the overall mean (Table 1), represents the coefficients of genetic

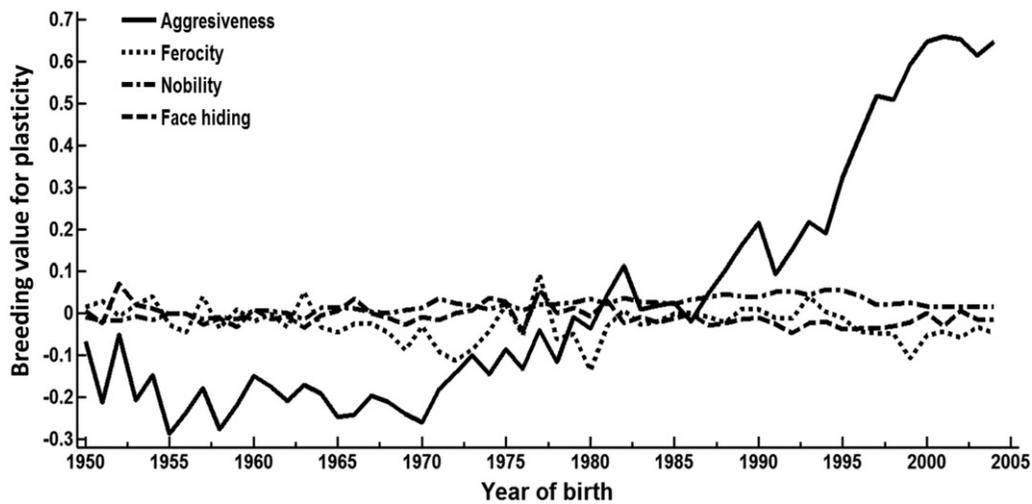


Figure 2. Genetics trends in plasticity, i.e. the difference in breeding values for the behavioural traits estimated in the *plaza* and *tienta*.

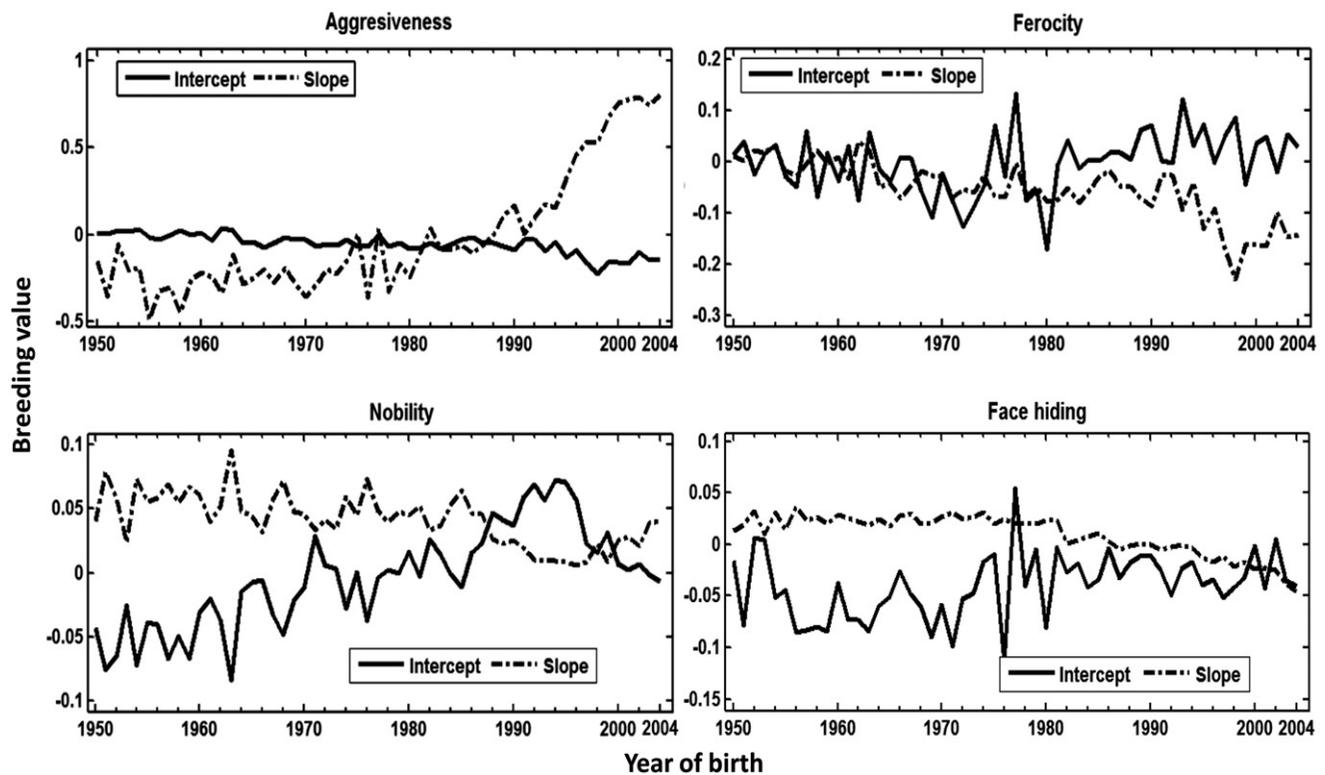


Figure 3. Trends of the intercept and slope breeding values derived by the reaction norm model for the four behavioural traits.

Table 5. (Co)variance components of the reaction norm intercepts and slopes for the four behavioural traits.

Components	Aggressiveness		Ferocity		Nobility		Face hiding	
	Cows	Bulls	Cows	Bulls	Cows	Bulls	Cows	Bulls
Variance intercept	2.45	1.14	1.87	1.83	0.178	0.61E-01	0.21	0.25
Variance slope	0.16	0.39	0.31	0.43	0.146	0.48E-01	0.11	0.77E-01
Covariance intercept-slope	-0.25	-0.36E-02 ^a	-0.54	-0.63	-0.763E-01	0.68E-02 ^a	0.3860E-01	0.54E-01
Correlation intercept-slope	-0.41	-0.54E-02 ^a	-0.70	-0.71	-0.47	0.12 ^a	0.26	0.39
Correlation intercept both sexes	0.77		0.79		0.86		0.58	
Correlation slope both sexes	0.91		0.84		0.96		0.70	

The ratios between variance component estimates and their standard error was associated with a high level of confidence (from Gilmour et al. 2009), exceptions are those marked with an ^a.

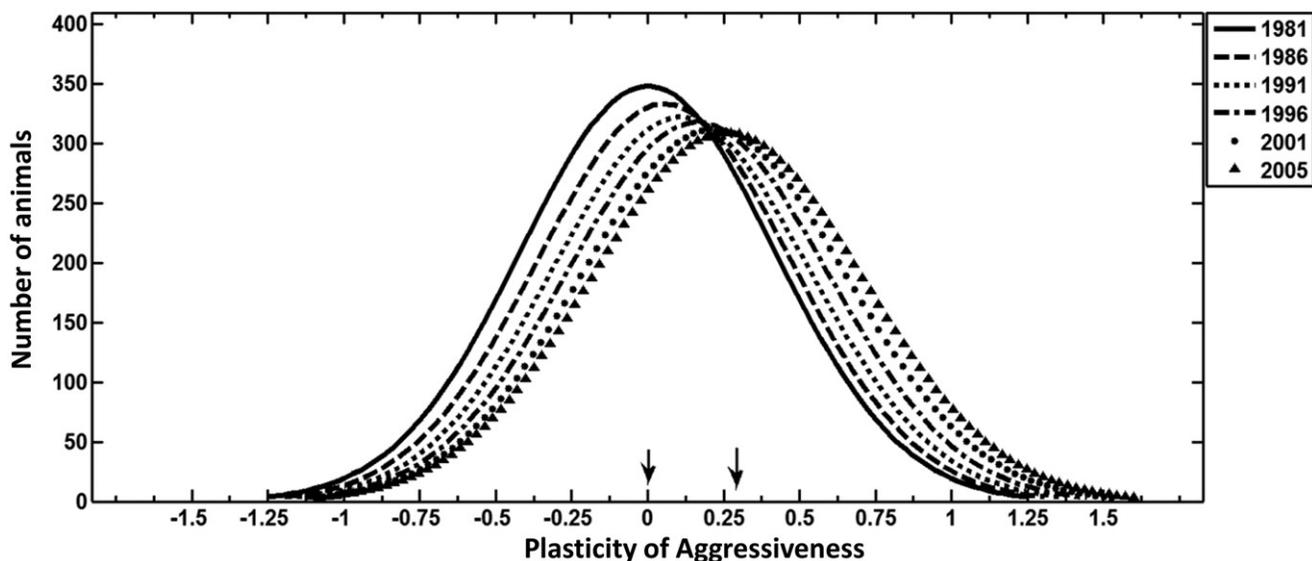


Figure 4. Evolution of the distribution in plasticity (difference between breeding values of cows and bulls) for aggressiveness by year of birth.

variation, which ranged from 12.5 to 21% for nobility and ferocity, respectively, allowing considerable margin for selection.

The results shown in Figure 3 are coherent with the overall pattern of genetic change shown in Figure 2, and identify the roles of the components estimated using the RN model. To know whether selection is possible with respect to aggressiveness, the genetic variability of plasticity should be examined. Figure 4 shows that the genetic variability for this trait was maintained over time, but the breeding value for plasticity showed a slight but steady change. This indicates that the breeding value of the bulls evolved more rapidly than that of the females. In absolute terms, the difference between the average breeding values for plasticity in the animals born in 2005 with respect to 1981 (+0.26) represented 9.8% of the total variance between the extreme breeding values (2.65). Selection is therefore possible.

Discussion

The heritability estimates of the four studied traits were found to be slightly higher than those reported by Silva et al. (2002, 2006), who used data that partially overlapped those used in the present work. Domínguez-Viveros et al. (2014) and Pelayo et al. (2015) also found an important degree of genetic influence on behavioural traits in this breed, with heritability values ranging from 0.09 to 0.47 (it should be noted that they used a slightly different scoring system). The fact that the present results are based on data from herds belonging to a single breeder may

have favoured the relatively high heritability values estimated, a consequence of the animals' similar environmental background.

PCA (Figure 1) showed a similar behavioural pattern for both the sexes. Pelayo et al. (2015) reported similar findings based on a linear scoring system procedure to assess the fighting capacity of the Lidia breed. These authors indicated the aggressiveness of the bulls to be based on two principal factors whose elements – attitude of the animals towards the horse rider, and towards the lure – are similar to the present elements examined when scoring aggressiveness.

Despite the similar behavioural pattern for both the sexes, and the literature that assumes that traits measured in the plaza (bulls) are the same as those recorded in the *tienta* (cows), this may not be the case. Behaviour in the *plaza* may be more affected than behaviour in the *tienta* by the interaction of a larger number of stressors e.g. animals are moved from their natural environment, transported in trucks, maintained during several days confined in cubicles, in which they have to share the area with other males coming from different herds). Reduced environmental variability in the *tienta* might explain the higher heritability values recorded for cows (Table 4).

The present results show the traits recorded in *plaza* and *tienta* (i.e. in bulls and cows) to correlate within years and over time. However, the values are clearly $<|1|$, so they cannot be considered the *same* trait (Table 4). The interaction *genotype* \times *environment* was also reported from Colombia by Calero-Quintero and Durán-Castro (2007).

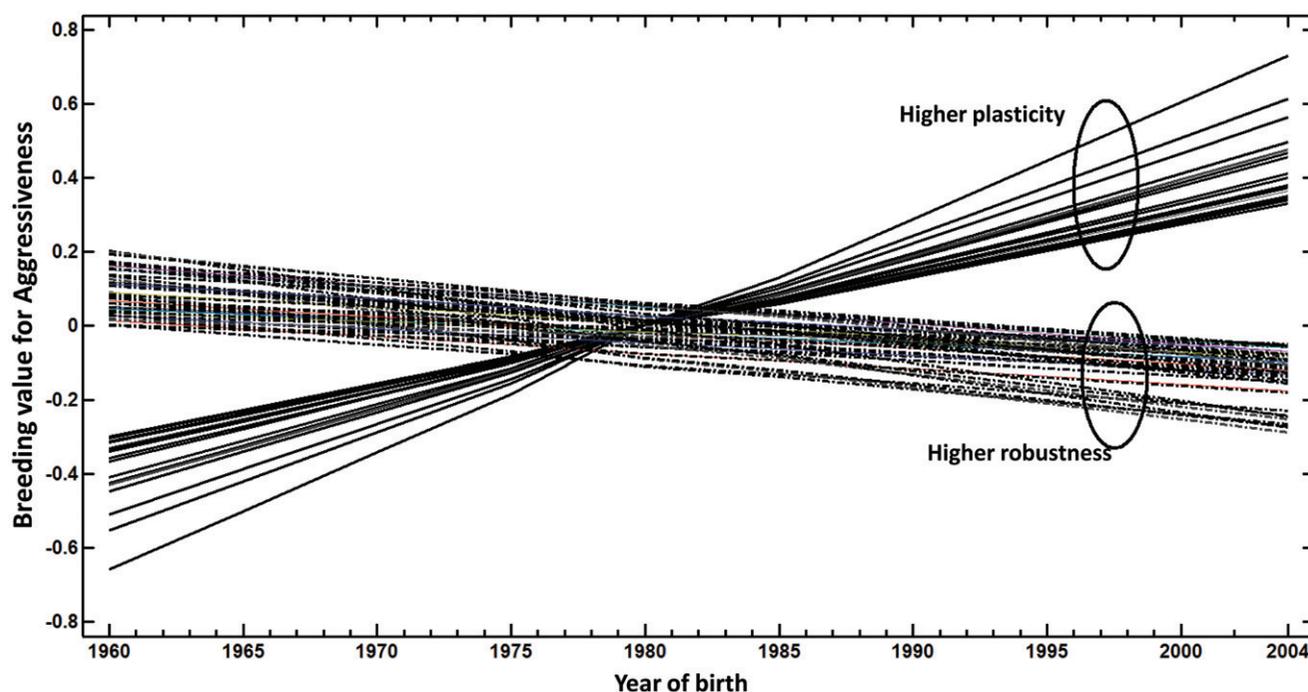


Figure 5. Evolution of breeding values for plasticity of aggressiveness.

It is therefore advisable to analyse them in an independent fashion. Random regression confirmed these types of response. It should be remembered, however, that the effect of sex is confounded by those of age and by the places (*plaza* and *tienta*) where the data were collected.

With the exception of nobility, the interaction *genotype* \times *environment* was significant for all traits (Table 4). Since the final interest is how a bull will perform in the *plaza*, this interaction might represent a problem in the genetic improvement of these traits. The RN model, however, allowed all the genetic (co)variance components (see Table 3) and the genetic function of each animal to be estimated, and thus the evolution of the breeding value for plasticity to be followed (Figure 2).

The traits analysed are function-valued traits in which the pattern of expression can be described by a function. The RN model is therefore appropriate for examining the underlying genetic variability of the causal components (Kirkpatrick et al. 1990; Meyer & Hill 1997).

The use of plasticity parameters could provide a powerful tool for improving performance in the *plaza* since it includes the effect of the environment on the breeding goal. This would allow the animals with the best plastic response (more genetic gain under *plaza* conditions) to be selected for breeding. According to the present results, no evolution of plasticity was observed for ferocity, nobility or face hiding in the

animals born since 1950 (Figure 2). In other words, the preliminary results for the breeding value of traits recorded in the *tienta* can be considered as robust as the near zero linear trends for plasticity shown by these three traits (de Jong & Bijma 2002). Thus, results recorded in the *tienta* can be used as a good guide when trying to improve performance in the *plaza*.

A completely different response was obtained, however, for aggressiveness. The bulls born over the first 20 years (1956 to 1976) had a breeding value lower than that of the cows (negative plasticity effect). From that year on, plasticity increased significantly. Thus, aggressiveness is a plastic trait and this plasticity can be used as a selection criterion to modulate their performance in the *plaza*. The procedure followed would allow animals to be selected for different patterns of plasticity with respect to aggressiveness to monitoring the level of this trait (Figure 5).

Conclusions

The heritability values calculated indicate that the behavioural traits studied can be improved by selection. Similar behaviour patterns were seen for both sexes; the results collected in the *tienta* can therefore be used in predicting performance in the *plaza*. In addition, the robustness of the traits nobility, face hiding and ferocity means that results collected in the females in the *tienta* confirms their value as predictors of the performance of their male relatives. However,

since aggressiveness was found to be very plastic, *teinta* behaviour cannot be said to reliably predict *plaza* behaviour with respect to this trait. The present results suggest it should be possible to increase the behavioural performance of bulls in the *plaza* (where the real spectacle takes place) by including genetic variability in plasticity in decisions taken by breeding programme managers.

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Disclosure statement

No potential conflict of interest was reported by the authors

References

- Almenara-Barríos J, García R. 2011. Assessment scale for behaviour in bullfighting cattle (EBL 10). Reliability and validity studies. *Archiv Zootec.* 60:215–224.
- Beckman DW, Enns RM, Speidel SE, Brigham BW, Garrick DJ. 2007. Maternal effects on docility in Limousin cattle. *J Anim Sci.* 85:650–657.
- Boissy A, Fisher AD, Bouix J, Hinch GN, Le Neindre P. 2005. Genetics of fear in ruminant livestock. *Livest Prod Sci.* 93:23–32.
- Boletín Oficial del Estado. 2001. Real Decreto 60/2001, de 26 de enero, sobre prototipo racial de la raza bovina de Lidia. *BOE.* 38:5255–5261.
- Calero-Quintero D, Durán-Castro CV. 2007. Genetic parameters of precise characteristics in the behavior of a bullfight herd. *Rev Colomb Cienc Pec.* 20:588.
- Cañón J, Tupac-Yupanqui I, García-Atance MA, Cortes O, García D, Fernández J, Dunner S. 2008. Genetic variation within the Lidia bovine breed. *Anim Genet.* 39:439–445.
- Cortes O, Tupac-Yupanqui I, Dunner S, Fernández J, Cañón J. 2011. Y chromosome genetic diversity in the Lidia bovine breed: a highly fragmented population. *J Anim Breed Genet.* 128:491–498.
- Crandall KA, Bininda-Emonds ORP, Mace GM, Wayne RK. 2000. Considering evolutionary processes in conservation biology. *Trends Ecol Evol.* 15:290–295.
- de Jong G. 1995. Phenotypic plasticity as a product of selection in a variable environment. *Am Nat.* 145:493–512.
- de Jong G, Bijma P. 2002. Selection and phenotypic plasticity in evolutionary biology and animal breeding. *Livest Prod Sci.* 78:195–214.
- Domínguez-Viveros J. 2007. Evaluación Genética de sementales para Lidia 2007. *Ganadería, 'Los Encinos'* 17p.
- Domínguez-Viveros J, Rodríguez-Almeida FA, Núñez-Domínguez R, Ramírez-Valverde R, Ruiz-Flores A. 2014. Genetic parameters and genetic trends for behavior traits in Mexican bullfighting herds. *Rev Mex Cienc Pecu.* 5:261–271.
- Gilmour AR, Cullis BR, Welham SJ, Thompson R. 2009. *ASREML Reference Manual.* NSW Agric. Biom. Bull. NSW Agriculture, Locked Bag, Orange, NSW 2800, Australia.
- Kirkpatrick M, Lofsvold D, Bulmer M. 1990. Analysis of the inheritance, selection and evolution of growth trajectories. *Genetics.* 124:979–993.
- Matsunaga ME, Silva JAH, de V, Toledo LM, Parahos da Costa MR, Eler JP, Ferraz JBS. 2002. Genetic analysis of temperament in Nelore cattle. 7th World Congress on Genetic Applied to Livestock Production, August 19–23 Montpellier, France Session 14 Comm N°14-16.
- Meyer K, Hill WG. 1997. Estimation of genetic and phenotypic covariances for longitudinal or repeated records by restricted maximum likelihood. *Livest Prod Sci.* 47:185–200.
- Pelayo R, Sole M, Sanchez MJ, Molina A, Valera M. 2015. Behavioral linear standardized scoring system of the Lidia cattle breed by testing in herd: estimation of genetic parameters. *J Anim Breed Genet.* 133:414–421.
- Phillips CJC, Rind ML. 2002. The effects of social dominance on the production and behavior of grazing dairy cows offered forage supplements. *J Dairy Sci.* 85:51–59.
- Phocas F, Boivin X, Sapa J, Trillat G, Boissy A, Le Neindre P. 2006. Genetic correlations between temperament and breeding traits in Limousin heifers. *Anim Sci.* 82:805–811.
- Plusquellec P, Bouissou MF. 2001. Behavioural characteristics of two dairy breeds of cows selected (Hérens) or not (Brune des Alpes) for fighting and dominance ability. *Appl Anim Behav Sci.* 72:1–21.
- Sartori C, Mantovani R. 2010. Genetics of fighting ability in cattle using data from the traditional battle contest of the Valdostana breed. *J Anim Sci.* 88:3206–3213.
- Sartori C, Mantovani R. 2012. Effects of inbreeding on fighting ability measured in Aosta Chestnut and Aosta Black Pied cattle. *J Anim Sci.* 90:2907–2915.
- Silva B, Gonzalo A, Cañón J. 2002. Genetic parameters of behavioural traits in the bovine. 7th World Congress on Genetic Applied to Livestock Production, August 19–23 Montpellier, France Session 14 Comm N°14-19.
- Silva B, Gonzalo A, Cañón J. 2006. Genetic parameters of aggressiveness, ferocity and mobility in the fighting bull breed. *Anim Res.* 55:65–70.
- Spady TC, Ostrander EA. 2008. Canine behavioral genetics: pointing out the phenotypes and herding up the genes. *Am J Hum Genet.* 82:10–18.
- Turner SP, Lawrence AB. 2007. Relationship between maternal defensive aggression, fear of handling and other maternal care traits in beef cows. *Livest Sci.* 106:182–188.
- Via S, Gomulkiewicz R, de Jong G, Scheiner SM, Schlichting CD, van Tienderen PH. 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol Evol (Amst).* 10:212–217.